The biosystematics of British aquatic larval orthocladiinae (diptera: chironomidae)

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THE BIOSYSTEMATICS OF BRITISH AQUATIC LARVAL ORTHOCLADIINAE (DIPTERA: CHIRONOMIDAE)

By

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" ut the flies are a small and numerous people. hen you happen on a fly that by chance draws your attention by its curious actions or appearance, it is not so easy as the uninformed person may think to ive it a ame; I have tried it and therefore know."

— . . Hudson, ture in Downland,

Longmans, 1900.

ABSTRACT

The relationships and subfamilial classification of the Chironomidae (Insecta: iptera, ematocera) are discussed and some comments made on the ecological significance of the range of larval habitats found in the family. The reasons are given for the selection of the aquatic larval Orthocladiinae for detailed morphological and ecological study.

Following a review of previous taxonomic works and an analysis of the current views on the Orthocladiinae, a method for rearing aquatic larval Chironomidae is described. his method utilises disposable petri-dishes each containing a single larva, kept in a cooled incubator. This is followed by a list of fifty-two collecting sites throughout ritain with some physical and biological data for each site.

Keys for the identification of the larvae of all known Holarctic genera are presented based on reared ritish material and incorporating published descriptions and examination of overseas specimens. Generic diagnoses to forty-one ritish genera of Orthocladiinae and descriptions and keys to ninety-one aquatic species are given. These have been p epared from examination of bout 1,200 specimens, reared, collected and sent by correspondents. For each genus the relati nships and phylogeny are discussed and for each species a full description is iven using morphological terminology outlined in a previous chapter. Over four hundred illustratiors in seventy-nine plates show the features of each species, many for the first time.

Under each species all available ecological and distributional information is given. Eleven species either cannot be associ ted with adults or else ppear to belong to undescribed species.

In a concluding chapter the relationship between the phylogeny and ecology of the subfamily is discussed incorporating additionally information about genera with terrestrial and marine larvae. The importance of species identification especially for indicator organisms in pollution biology, as well as for calculations of diversity in freshwater habitats, is stressed.

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CHAPTER 1

GENERAL INTRODUCTION

1. The Chironomidae

The Chironomidae are two winged flies (Order Diptera) known popularly as non-biting midges. The adult flies are familiar swarming at dawn and dusk particularly near water. The most familiar of the larvae are known as bloodworms on account of the haemoglobin present in the body, but those larvae without the respiratory pigment are even more frequent in most water bodies.

The antenna of the adult with many flagellomeres together with the complete larval head capsule indicates that the family belongs to the most primitive suborder, the Nematocera. This suborder contains many of the biting flies, namely the Culicidae (mosquitoes), Simuliidae (blackflies), Phlebotomidae (sandflies) and Ceratopogonidae (biting midges). These families are not closely related and it appears that the presence of functional mouthparts is a plesiomorphic (primitive) character retained in divergent lines within the Diptera. Functional mandibles have been found in the females of Sycorax (Psychodidae) (unpublished observation Cranston & Lewis), Corethrella (Chaoboridae) (Downes, 1970), Radinocerus (Tanyderidae) (Downes & Colless, 1967) and Archaeochlus (Downes & Colless, 1967; Downes 1974: 84). This confirms Downes' belief that this character state is more widely distributed in the Nematocera than previously suspected. Relationships of the families in this suborder based upon feeding habits of the adults must be treated with caution if the presence of mandibles is a plesiomorphic character.

The closest relatives of the Chironomidae are the Ceratopogonidae, the biting midges, which were included in the family Chironomidae until the 1920s. As the popular name implies an important difference between the families is the presence of functional mandibles in most Ceratopogonidae and their absence in Chironomidae (with the exception of Archaeochlus mentioned above). Also there are differences in the wing venation (although Corynoneura and Thienemanniella in the Chironomidae resemble some Ceratopogonidae) and in the antennal structure. The two families are closely related, the Chironomidae being the apomorphic sister group of the Ceratopogonidae.

Hennig (1968:20) basing his phylogenetic analysis of the Nematocera on methods he elucidated in 1950 and 1966, using characters of the base of the wings, proposes that the Simuliidae, Ceratopogonidae and Chironomidae combined (the Chironomoidea), together with the Thaumaleidae, form the sister group of the Culicidea (Culicidae, Dixidae and Chaoboridae).

In this Hennig comes close to agreement with Rohdendorf (1974: 9,44) who erected the superfamily Chironomidea for the Simuliidae, Ceratopogonidae and Chironomidae, and postulated that their closest relatives were the Culicidea. However Rohdendorf omits the Dixidae from the latter super-family, and removes the Thaumaleidae from this monophyletic unit, named the Culicomorpha by Hennig.

ii. The Ecological Significance of the Chironomidae

Adult Chironomidae are familiar as non-biting midges frequently seen swarming especially towards dusk on summer evenings near water.

The adult is short lived, but recent papers have shown that many species do feed, contrary to earlier beliefs. McAlpine (1965a,b) noted three species feeding at flower nectaries, and Downes (1974) found members of 26 genera feeding on honeydew on the leaves of bushes. These observations suggest that the adult Chironomidae may be longer lived than previously suspected. Even with several weeks of potential adult life however, the dominant stage in the life cycles of this family is the larva. Development is typically holometabolous with perhaps always four larval instars from the egg. The length of the larval stage is quite variable, from three weeks in some tropical species (Dejoux, 1978) to two years or more for some Arctic (Oliver, 1968) and Alpine (Wulker, 1961) species. British species, where the life histories are elucidated, vary from a one year life-cycle up to four generations per year. The pupal stage is normally of relatively short duration, particularly in the smaller species where it may last only two days. Oliver (1971) reviews information accumulated between 1950 and 1970 on life histories of the Chironomidae.

Although Hashimoto (in Cheng, L, 1977) lists 65 species in 12 genera from marine habitats throughout the world, and there are probably more terrestrial larvae than are currently recognised, the vast majority of larval Chironomidae are aquatic in freshwater, or brackish ecosystems. The larvae often dominate the fauna in terms of absolute numbers and sometimes even in biomass, and can tolerate extreme environments. On just one parameter - temperature, they are found not only in the Arctic and Antarctic where they resist freezing, but also in hot springs up to 45°C in New Zealand, Iceland and Java. A species examined by Hinton (1960) Polypedilum vanderplanki can survive repeated desiccation and revival, and while desiccated is able to withstand temperatures as high as 100°C and as low as immersion in liquid nitrogen (-270°C).

Although none of the 450 or so Chironomidae listed from Britain exhibit quite these extreme ecological preferences and tolerances of their overseas relatives virtually all aquatic habitats, even the most temporary, have their typical chironomid faunas.

The ubiquitousness and large numbers of species of Chironomidae with apparent tolerance of a broad spectrum of ecological conditions suggests that the family could be of ecological significance, particularly in the classification of water bodies. Much of the pioneer work with the ecology of the immature stages of Chironomidae took place in Germany under A. Thienemann (for survey of taxonomic work see Chapter 2) and all of the work of this school confirmed the ecological significance of the family. Further work by Brundin in Scandinavian lakes (1956b) added more weight, but throughout this period British freshwater biologists, with one or two exceptions, were less than fully aware of the potential significance of the family. Part of this reluctance to study the larvae stemmed from taxonomic problems (discussed in Chapter 2) but it was not strictly true that in 1959 "the larvae cannot be named at all in the present state of knowledge" (Macan & Worthington, 1959:107) since Humphries (1936) had examined the Chironomidae in Windermere and later in the Rivers Liffey and Dodder.

Perhaps there was a certain reluctance amongst British limnologists to become taxonomists, even to study a group of potentially major ecological importance. European colleagues were less reluctant and consequently studies on the family advanced outside Britain.

However by 1976 the National Environment Research Council in a "Report on the Role of Taxonomy in Ecological Research" agreed that the family was of high ecological importance, although it is noted that there are no complete keys to the larvae, the literature was scattered, collections were poor and many species had to be reared to the adult.

In the last two decades cytologists have become interested in the chromosomes of chironomid larvae, especially but not exclusively in the genus *Chironomus*, because of the presence of giant chromosomes in he salivary glands. So many people now work on the chromosomes that now up to half of the entries under Chironomidae in Entomology Abstracts refer to biochemistry or cytology. These workers also need keys to identify their material particularly if and when they work on genera other than *Chironomus*.

iii. Subfamilial Classification and Limits to Present Study

Currently eight subfamilies are recognised within the Chironomidae, although the abberant genus *Buchonomyia* may require subfamily status (Saether pers.comm.). These subfamilies are: Podonominae, Aphroteniinae, Tanypodinae, Diamesinae, Telmatogetoninae, Prodiamesinae, Orthocladiinae and Chironominae.

The British list (Cranston in Kloet & Hincks, 1975) shows 52 recorded species of Tanypodinae, 181 of Orthocladiinae and 193 of Chironominae. In the smaller subfamilies there are 2 Podonominae, 4 Prodiamesinae, 2 Telmatogetoninae and 16 Diamesinae.

In contrast to the controversy over the generic limits in the family, discussed in Chapter 2, the suprageneric rankings have been more stable, the only disagreement being over whether the taxa deserve tribal or subfamilial status. Brundin (1966:425) was the first to apply phylogenetic arguments at the subfamily level, and Saether (1976:10) using characters from all life history stages confirmed many of Brundin's conclusions on the relationships of the genera. In this paper Saether erected the new subfamily Prodiamesinae for four species in three plesiomorphic genera previously placed in the Orthocladiinae.

Saether (1977) placing more emphasis on the female genitalia reanalysed the subfamily relationships, and apart from altering the position of the Telmatogetoninae, which he argues is the sister group of all the remaining Chironomidae, confirmed his earlier findings.

There are sometimes quite distinct ecological and distributional differences between the subfamilies. In certain parts of the world, however, including the eastern Palaearctic, Australasia and central South America, the chironomid fauna is poorly known and in Asia it is virtually unknown.

The Aphroteniinae, a small subfamily not occurring in Britain, is primarily austral and rheophilic, resembling in this the larger subfamily the Podonominae. However a few of the 150 species of podonomines are found in the Northern Hemisphere including two species in Britain. A third subfamily with primarily rheophilic, cold adapted larvae is the Diamesinae, inhabiting colder regions of the world including 16 species in Britain.

These three subfamilies exhibit what Brundin (1966:434) believes to be the plesioeic requirements for the chironomid larvae:- the upper reaches of mountain streams arising from cold springs and running through temperate forests, which provide stable conditions of water level, temperature, dissolved oxygen and consequent food sources (diatoms). The more plesiomorphic Chironomidae have remained in this type of habitat while more apomorphic Chironomidae have exploited many other habitats, including the marine and terrestrial.

The Tanypodinae and Chironominae, relatively apomorphic subfamilies, diverge strongly from Brundin's plesioeic larval habitat. Both tolerate the elevated temperatures encountered in lenitic environments and both are encountered in numbers in the tropical areas of the world. The larvae of the Tanypodinae are often carnivorous on aquatic invertebrates including other chironomid larvae.

The subfamily with the greatest diversity of ecological requirements is the Orthocladiinae. Many of the more primitive genera are aquatic, frequently rheophilic, while several genera are lenitic. The strict delimitation of lotic species from lenitic species is not always possible, some species may be found in both.

Other Orthocladiinae larvae are hygropetric while several genera have become semiterrestrial or fully terrestrial. Among these genera some species have returned to freshwater, and some genera have become marine (Strenzke, 1950, 1960).

The subfamily Telmatogetoninae similarly are marine and were included with the marine Orthocladiinae in the subfamily or tribe Clunioninae until Strenzke (1960) showed that the genera centred on Clunio were unrelated to Telmatogeton and were the sister group of the Smittia group of terrestrial Orthocladiinae.

As noted previously the Orthocladiinae contain many rheophilic species, and the difficulties in identifying the larvae in this subfamily cause many problems for limnologists studying lotic ecosystems. Although Chironominae, Tanypodinae and Diamesinae also occur in running waters, and there are similar problems of identification, it was felt that with 45 genera and approximately 120 of the 180 British species living in freshwater habitats, the Orthocladiinae larvae were appropriate for a revisionary study.

Limitations of time and facilities meant that marine, terrestrial and many semiterrestrial species were outside the scope of this investigation, but were considered at the generic level for completion of the generic keys and for phylogenetic discussion.

The study involved collecting orthocladiine larvae from as varied aquatic habitats as possible and endeavouring to rear individual larvae to adults. The emergent adult was identified, and the larva described from the head capsule and exuvium.

When generic and specific keys had been prepared, based on reared material, reliably identified unreared larvae could be incorporated in the descriptions. The relationships of the genera included were discussed, and for each species as much ecological information as exists was cited, including distributional data gained in this investigation.

CHAPTER 2

HISTORICAL SURVEY

1. Survey of previous studies on larval Orthocladiinae

In the last decades of the nineteenth century several continental European authors published brief descriptions of larval Chironomidae, but it was not until 1900 that Miall and Hammond in their study on "The Harlequin Fly" gave the first English description of the immature stages. In their classic work Miall and Hammond refer mainly to an anatomical study of all stages of *Chironomus dorsalis*. There is however a description of both *Chironomus* (*Orthocladius*) near *dilatatus* Wulp and *Chironomus minutus* Zetterstedt. Both of these are recognisable orthocladiines, the former being a *Psectrocladius*, possibly *obvius*. Three years later Taylor (1903) published a short paper describing the larval and pupal habits of *Chironomus* (*Orthocladius*) *sordidellus*.

Miall and Hammond wrote that "there are many species of Chironomus, and it is remarkable that while the flies are very similar, the larvae are sometimes notably different". Despite their early recognition of the potential importance of the larvae of this family, few of their compatriots undertook the study of the immature stages, and the study of these passed to Germany. The great advances in the systematics and biology of all chironomid larvae took place in continental Europe, often in association with the flourishing study of limnology.

Foremost among the scientists to study the larvae and pupae within the framework of limnology was A. Thienemann who published over 100 papers between 1907 and 1954, on many aspects of chironomid larval biology and systematics. He also had several students whom he encouraged in the study of the family as a means of solving general limnological problems such as classification of lakes and defining biocenoses.

The earliest of the workers in what may be called the "Thienemann school" was Potthast, who in 1914 published the first major work on the metamorphosis of the Orthocladiinae (which he called the Orthocladius- group). In this he described for the first time many aquatic Orthocladiinae. The standards of the descriptions are good, as are the figures, and it is possible to recognise the current genus for most of the forms described, if not always the actual species. In the early death of Potthast the study of the Orthocladiinae was greatly set back.

Among the later students of Thienemann whose work included the Orthocladiinae were Lenz (publishing 1920-1962, see bibliography by Fittkau, 1973), Strenzke (1940-1966), Harnisch (1922-1960) and Kruger (1938-1949, see bibliography by Thienemann, 1945). All of these studied other aspects of limnology, and some, (particularly Harnisch), the physiology of the larvae.

Lenz published on the systematics of Orthocladiine larvae in his earlier papers, and later discussed the problems of lake classification. Since much of this work concerned lenitic environments he came to study the Chironominae more in his later years.

Strenzke reared many terrestrial, semiterrestrial and marine Orthocladiinae and described these in some of his 25 papers. In this study he extended the researches of Thienemann (1921, 1934, 1936c) into the non-freshwater

Orthocladiinae. Strenzke's descriptions and figures are excellent, and his resolution of the phylogeny of these genera of marine and terrestrial Orthocladiinae is unquestioned today.

Harnisch and Kruger published less on the Orthocladiinae than the two above mentioned workers, both being more involved with the Chironominae. Thienemann himself studied all Chironomidae and also Ceratopogonidae as both larvae and pupae. His orthocladiine researches culminated in his 1944 * publication, "Bestimmungstabellen fur die bis jetzt bekannten Larven und Puppen der Orthocladiinen" (a key to the yet known larvae and pupae of the Orthocladiinae). The larval key included all larvae described from everywhere in the world until 1942. For the first time all the scattered descriptions were brought together and Thienemann examined these for generic characters. Before this publication there was little agreement on generic limits at the larval level.

Some of the characters used to separate species have proved to be of limited value, particularly the use of body colour in the live larvae since this character is lost in preservation. However the key proved valuable for the identification of many Orthocladiinae.

Among non-German taxonomists looking at the orthocladiines was J. Zavrel, who published between 1906 and 1946 (see bibliography by Hrabe, 1947) and who looked particularly at lotic ecosystems, publishing several papers on glacial and high mountain streams in Czechoslovakia. He also published several taxonomic papers on orthocladiine larval genera, notably Eukiefferiella and Metriocnemus (in the broadest sense).

Thienemann's 1944 key was able to include several North American species of Orthocladiinae because O.A. Johannsen, publishing from 1903 until 1952, described the life histories of many species. His 1937 paper, part of a series desc ibing all known North American aquatic Diptera, was a major work and included many species which the author believed to be Holarctic in their distribution.

Sublette and Roback, both still publishing, having continued Johannsen's work on the American chironomid fauna, including the Orthocladiinae. Saether has produced several generic revisions of Holarctic genera including some Orthocladiinae in recent years.

Apart from these papers Saether (1978) in a valuable study of the female Chironomidae discussed the phylogeny of the genera of the Orthocladiinae based on characters of all life history stages including for the first time, characters of the female genitalia. The terminology of the head capsule and abdomen used in this thesis is based on that of Saether (1971).

The Japanese species included by Thienemann (1944) are due to Tokunaga who published from 1932-1966, and included some descriptions of species believed to be distributed across the Palaearctic r gion from ritain to Japan.

Shilova (1971) reviewing the study of the systematics of the chironomid fauna of the oviet Union lists the voluminous work which scientists in that country have produced. There have been three major taxonomic publications on the immature stages. Firstly, Lipina (1928) listed all larvae and pupae described up until that date. econdly, there was a key to chironomid larvae by Chernovski (1949) (published posthumously). This key permitted the identification of the majority of known Russian larvae, particularly those from standing waters, and research into the chironomid fauna of reservoirs proliferated. Thirdly, Pankratova (1970) produced a key to orthocladiine larvae and pupae, describing or redescribing 218 larvae and placing them in genera according to the prevailing concept. Unfortunately the generic key does not always work adequately and there are discrepancies between the characters used in the key and the descriptions and figures of these characters elsewhere in the text. There are few original figures since most are taken from previous western European publications, even where these are less than adequate for species recognition. At the specific level there are many species included which are described from the larva only and there are many larvae which are not placed in genera. Chernovski, Lipina and Konstantinov all gave specific names to unreared larvae. Shilova (1971) gives a timely warning that "it should be remembered that not all that defies easy identification represents a new species ... so called "new species" described by the larvae in most cases turn out to be described long ago by the imago".

In Britain the foremost worker on the Chironomidae, F.W. Edwards, published many papers between 1916 and 1941, but although he reared larvae through to adults, he apparently rarely kept the immature stages. The only exception was when he retained the larvae and pupae of Cardiocladius which were described by Saunders (1924).

The next taxonomic work published on the Orthocladiinae in Britain was by Hobart, in Bryce and Hobart (1972). In the key the Orthocladiinae, Clunioninae and Corynoneurinae are considered as subfamilies. This part of the publication is apparently based on earlier descriptions and there is some confusion over the nomenclature used in the earlier works, resulting in inconsistent generic names. There is also no distinguishable generic concept in this key and it is essentially a key to certain of the known species of Orthocladiinae. It is unfortunately not made clear that the key characters used to arrive at a specific name may apply to many species not included in the key.

ii. <u>The schism between nomenclatural systems</u>

Thienemann and the early workers in his school were not taxonomists of the adult stage and sent examples of the adult midges which they had reared to specialists for identification.

The usual person who identified this material was J.J. Kieffer who published from 1884 to 1929. Kieffer usually published the descriptions of the species sent to him separately from the descriptions of the early stages. The adult descriptions are often inadequate for recognition, the type material is frequently lost and Kieffer often appears to have placed the same species in different genera. Kieffer also described new species based on most insignificant differences in the adult.

The problems raised by the identification of Kieffer are still apparent in chironomid nomenclature, but in the first three decades of this century they were the source of much confusion. Thienemann found that the systematic arrangement and generic limits shown by the larvae and pupae did not correspond with the classification of Kieffer, and later, Edwards and Goetghebuer.

Kieffer, Edwards and Goetghebuer based their classifications predominantly upon the adult stage whilst Thienemann worked predominantly with the early stages. Edwards (1929) used large genera (which allowed generic placement of the females as well as the males) which he subdivided into subgenera and species groups mainly based on characters of the male particularly the genitalia. There are many similarities between his classification and that of Goetghebuer (1932) although the latter preferred to elevate Edwards' subgeneric concepts to generic status. Kieffer, on the other hand, described a plethora of genera, often based on quite tenuous characters, the result being an inconsistent classification difficult to use.

Since museum taxonomists tended to look only at the adult midges, while the Thienemann school dealt with the immature stages, there resulted two distinct systems of nomenclature within the family Chironomidae. In Britain and North America the system of Edwards, with large genera and many subgroups, was used in identifying adults. Those who atte pted to identify larvae using the keys of Thienemann or Hennig (1968) often found it difficult to relate the name attained in these works with any name on the ritish list. In North America Johannsen looked at all life-history stages of the Chironomidae and noted the relationships of the larvae and pupae to those described in Europe. espite this awareness of the nomenclature of the Thienemann school, Johannsen used a nomenclature very similar to that of Edwards, apparently disregarding systematic information available from his studies of the metamorphosis.

The disparity between the two systems of nomenclature must have caused much confusion for limnologists not deeply involved in the taxonomy of the family, and was an important reason for the lack of progress in chironomid research in Britain as noted earlier.

iii. <u>The reconciliation of the nomenclatural system</u>

In 1956 Brundin made the first atte pt to reconcile the two systems of nomenclature and revised most of the genera of northern European Orthocladiinae. Based on a knowledge of the larvae, pupae and adults Brundin was able to examine critically most of the genera of Orthocladiinae. New characters were found in the adults which showed that genera previously defined on the immature stages were also valid for the adults. Brundin did not accept in entirety the genera based on the immature stages. For example several genera had been proposed for species Brundin recognised as belonging to the large genus <u>Orthocladius</u>. Although Brundin clearly had a detailed knowledge of the larvae of the genera he discussed, there are no larval descriptions, and any mention of larval characters believed to be of generic value is brief. Despite this, it is a seminal work in the study of Orthocladiinae within a modern generic framework.

Brundin (1956) produced a major work on the subfamilies Podonominae and Aphroteninae from throughout the world, and Fittkau (1962) revised most genera of Tanypodinae. The large subfamily Chironominae has not been revised at the generic level. The confusion evident in the Orthocladiinae prior to Brundin's work is less apparent in the Chironominae for genera have been based more often on all life stages.

iv. <u>The state of chironomid taxonomy in Britain</u>

The pioneering work of F.W. Edwards on the British Chironomidae was of great importance in directing the course of research on the family in Britain. The availability of his key in English made it possible to identify adults relatively easily, but those who studied the immature stages still had to use German keys published in a wide range of journals. As noted in the previous section the identification reached for the adult was different from that reached for the immature stages, particularly at the supra-generic level.

When the Chironomidae were dealt with by Coe (in Coe, Freeman and Mattingly, 1950) the key was taken almost directly from Edwards (1929) with a few minor alterations and additions. There were no alterations to the supra-generic rankings to reflect contemporary European work.

Bryce and Hobart (1972) in recognising the need for a means of identification for larval Chironomidae were aware of the disparity between the classifications of the British and European workers and attempted to relate the names used. However the apparent absence of a generic concept (at least in the Orthocladiinae) did not help in the re-assessment of the generic placement of the species in their key.

In the same year Murray (1972) in adding one hundred and seventeen species to the Irish list placed all two hundred and sixteen species known to occur in Ireland into genera corresponding with those used in contemporary European literature. The classification followed that of Fittkau, Schlee and Reiss (1967) except where modified by more recent publications up to 1971.

With the decision to revise the Checklist of British Diptera (Kloet and Hincks, 1976) it became necessary to bring the classification of all the recorded British Chironomidae into line with that of current European workers using genera based on all known stages of the life history. In the case of the Orthocladiinae this entailed following the classification of rundin (1956) with a number of modificati ns especially those of Hirvenoja (1973). The Checklist and Murray's work on the Irish fauna means that for the first time immature stages and adults can both be identified to the same genera and the classification of British Chironomidae can be compared directly to those of elsewhere in the world.

In 1978 Pinder produced a key to the adult males of British Chironomidae, a timely publication superseding the out-of-print and out-of-date key by Coe mentioned above. The classification used by Pinder closely follows that of Kloet and Hincks (1976) and allows identification of the vast majority of recorded British species. The species omitted from the key are those of dubious species where no specimens exist to confirm the record.

The pupae have not b en ignored and a number of unpublished keys to enera and species in all subfamilies have been prepared by Langton. The classification followed in these works is very similar to that both of Pinder and of Cranston in Kloet and Hincks, although several species and a few genera new to the ritish list have been added based upon the intensive sampling of pupal exuviae throughout Britain.

At present there is considerable agreement amongst British workers regarding the generic placement of the species on the British list, and this agreement extends to the uropean wo kers. This does not indicate that there are no problems at the generic level to be resolved. There are, for example, a number of monospecific genera in all subfamilies which are based sol ly upon the distinctive adult stage and the immature stages are eith r unknown or poorly described. xamination of the immature stages may reveal that these genera are unwarrant d. Similarly closer examination of the adults of monospecific genera erected for aberrant larvae may also result in the synonymizing of these genera.

CHAPTER 3

METHODS AND MATERIALS

1. Introduction

When this research was commenced in 1975 the collections of the British Museum (Natural History) contained no more than 100 chironomid larvae belonging to some 15 species. These larvae were mainly collected by A. Thienemann and D. Bryce and if any of them had been reared, the larval skin, and pupa and/or adult had not been retained.

A few larvae from other collectors existed but unfortunately it seems that although he reared adults from larvae, the most eminent student of the British Chironomidae, F.W. Edwards, did not keep the immature stages.

A visit to Munich to examine material in the Thienemann collection showed that the position in the B.M.(N.H.) was not unique. Although there are many slides of larvae and pupae in the collection it is clear that Thienemann and his students described larvae from unreared material. It is likely that a dish of what appears to be one species may in fact contain more and the possibility of confusion between the stages is apparent. The chances of error were increased by the practice of sending reared adult midges to either J.J. Kieffer or M. Goetghebuer for identification. Beside the possibilities of misassociation inh rent in this system, Kieffer was renowned for not retaining material he described and also for frequently redescribing species, not always in the same genus.

Thus it was apparent from the onset of this work that it would be necessary to rear larvae individually and to prepare slides of all three stages, larva, pupa and adult in order to be sure of the correct identity of the larva and association of the stages

ii. Collection

The problem of collecting and rearing Chironomidae occupied a large proportion of the time, with about 125 species of freshwater Orthocladiinae to be covered. The varying ecological requirements and geographical distribution of these species meant that many sites throughout the country were visited. These sites are listed in part vi of this chapter.

In running waters, sites which dominated in this work, sampling was qualitative using a Surber sampler. The benthos was sampled both by kicking the substrate upstream of the sampler and by washing larger stones in the entrance of the net. The mesh size of the sampler was 300 um which permitted the retention of most of the smallest fourth instar larvae (*Corynoneura* spp.) and many second and third instar larvae. In standing waters the urber sampler proved equally effective in gathering larvae from marginal habitats by kicking up the substrate and pulling the sampler through the disturbed area. A grab sampler was used in Malham Tarn at depths of 1.5 m and deeper.

It was found necessary to sort live Orthocladiinae in the field, for several reasons. As the distance back to the Museum was always long, the movement of particles of substrate in the container damaged or killed the larvae in transit. Secondly any predatory Chironomidae particularly the Tanypodinae can decimate the numbers of the smaller Orthocladiinae such as *Eukiefferiella* and *Corynoneura* and must be removed before transport. Finally, the oxygen tension in a container may fall below lethal limits for sensitive species if much organic detritus and plant matter is included. Thus although sorting of samples is much easier in the laboratory field sorting was essential.

Many species of orthocladiines are cold stenotherms and are rapidly killed by a rise in temperature from that of their environment. This is particularly true of the lotic species. The use of a wide-necked Thermos flask, half filled with water from the area of collection, for transport to the Museum proved very effective in keeping the larvae alive for the necessary period. In most cases larvae collected on one day were not put into rearing dishes until the next day, while in several cases larvae remained in the Thermos flask for up to three days, with no apparent increase in mortality.

iii. Rearing

A problem with some of the previous published work on Chironomidae is that more than one larva had been reared in a single dish and its association with the appropriate adult was not always certain. Also adults obtained by rearing by Thienemann and his students were separated from the immature stages for identification by Kieffer and the adult midges were often lost.

There have been several methods recommended for rearing Chironomidae from larvae. There are further suggestions for breeding chironomids involving provision of space for mating. These methods work with varying degrees of success. Some techniques are only satisfactory for producing a few adults from the numerous larvae resulting from one egg mass, but with high mortality.

By trial and error a method was evolved during the course of the present studies which gave consistently acceptable levels of adult emergence. Initially 100 mm diameter disposable plastic petri dishes were used, but 50 mm diameter dishes were found easier to handle and the larval and pupal skins were more readily found in the smaller dish.

The factors found to be of greatest importance to the success of rearing larvae were temperature and oxygen tension. Many orthocladiine larvae are cold stenotherms and few, mainly Cricotopus, can survive the 20-25° room temperature in the Museum. An optimum incubation temperature of 14-16°C for summer collected larvae and 10-12°C for larvae collected in cooler waters was maintained in a Gallenkamp cooled incubator. A 2-3°C rise in temperature was used when certain fourth instar larvae did not pupate within a month. This sometimes induced pupation in these larvae.

Adult emergence from larvae collected as third or fourth instar generally took place within a fortnight, the longer the period the less likely the species was to emerge. Most premature death was in the pupa, and death as a larva was rare.

The rearing dishes had to be checked every two days for the emerged adult. The adult will live for at most two or three days, and if it falls back onto the surface film and drowns decomposition is fairly rapid rendering identification difficult or impossible. The larval skin and head capsule, as well as the pupal exuvium can be collected with the emerged adult. Even should the pupa die, recognised by the failure of the pupa to move when gently touched, the larval skin and pupa can still be removed since the pharate adult (dissected from the pupa) or the pupa itself can be used for identification.

All material was preserved in 80% alcohol until mounted on slides.

iv. Slide preparation

For accurate identification of larval chironomids, it is necessary to examine many features at a magnification of 400 times, and some must be examined under oil immersion (1,000 times magnification). At the start of the project several larval head capsules were examined by electron microscope to ascertain the nature and relationship of the sensory setae on the labrum and the maxillae. No features of potential taxonomic importance were seen which could not be seen adequately on an optical microscope fitted with phase contrast.

In the early part of the study larvae were mounted in Euparal but it was found that Berlese mountant was preferable. As several formulae for this mountant exist (e.g. Eastop in van Emden, 1972; Lewis in Smith ed., 1973) the formula used is as follows:

Gum arabic	180 gms.
Chloral hydrate	540 gms.
Glacial Acetic acid	75 mls.
50% w/v glucose syrup	75 mls.
Distilled water	550 mls.

The ingredients are dissolved with regular stirring at room temperature then filtered. The very liquid mountant is then evaporated at about 30°C until the appropriate consistency is reached.

Berlese mountant has several advantages when dealing with large amounts of material. Firstly specimens can be mounted directly from water, alcohol or, as in this study, from acetic acid. Secondly the mountant clears specimens as the slide is dried in a 40°C oven. Most of the small orthocladiine larvae do not need to be boiled in KOH to clear before mounting in Berlese since the mountant itself clears the head capsule adequately. Thirdly Berlese fluid is water soluble and specimens which have been roughly mounted for cursory examination can be readily soaked off and properly mounted if necessary.

This water solubility and the fact that Berlese fluid crystallises when dried means that for permanent preparations the coverslips must be ringed with Euparal and dried again in the oven. In order to ring the slide it is necessary to chip off the crystallised Berlese from around the coverslips where the excess mountant has dried in the three to four weeks in a 40°C oven.

The argument over whether to preserve adult Chironomidae dry (pinned or point mounted) or in alcohol and slide preparation is still unresolved. It is probably undisputed that for adequate description of all stages of the Chironomidae the specimens should be mounted on slides. It is the problem of preservation of material prior to mounting which is a matter of debate. Freeman (1955:7), who followed Kieffer, Goetghebuer, Townes and many others in preserving material dry, listed seven criticisms of alcohol conservation, used by the Thienemann school and most limnologists dealing with large numbers of specimens. Schlee (1966:169-173) refuted Freeman's seven points against alcohol preservation, but although some of Schlee's comments are pertinent there are others which are certainly less valid. Most important of these is that specimens which have been in alcohol for long periods do not macerate well in KOH and make poor slides in which fine details of setae and details of the delimitation of antennal flagellomeres and palp segments are difficult or impossible to see. Perfect slides can be made from century old pinned material from the Walker collection for example, yet specimens of Thienemann in alcohol for fifty years and Brundin (thirty years) make very poor slides. Whether this is a general criticism of alcohol preservation or a result of poor preservation technique (addition of glycerol, allowing the alcohol to become dilute or dry out) is unclear.

Despite these reservations, if the material is to be slide-mounted as soon as possible 80% alcohol is a suitable preservative. It is suggested however for large collections of adult Chironomidae that some specimens be retained dried, particularly if there is likely to be some delay in preparing slides.

In this study as specimens were mounted on slides within a matter of days or a week at most all material was preserved in 80% alcohol.

With the Orthocladiinae, usually with relatively small adults, all three stages of the life-cycle should be mounted ideally on a single slide. This prevents the risk of misassociation if separate slides of each stage are made. It is possible to put eight 10 mm. coverslips on a single slide, but this is usually more than is strictly necessary despite the recommendations of Schlee (1966).

An attempt was made to arrange all parts systematically on the slide for ease of comparison. The scheme is shown in Fig. 1a . Usually only one coverslip is necessary for the larval skin and head capsule even when the mandible is dissected off. When the pupa emerges the larval head capsule is split from the occipital margin through the postmentum to the mentum, and with only slight pressure the clypeus and labrum become detached from the rest of the head. The head capsule is thus already partly dissected and all that remains is to position the parts and separate the mandible so that it is not covering the maxilla. This dissection is done in a drop of Berlese fluid on the slide so that the small parts can be moved around without risk of loss.

The pupal skin is mounted under one coverslip with the abdomen dorsal side uppermost, and the separated cephalothorax mounted ventral side up. The cephalothorax is split dorsally to allow emergence of the adult and it is only necessary to complete the dorsal split to allow complete opening of the cephalothorax.

The adult is dissected so that the wings and halteres (if removed) are under one coverslip, the head and separated antennae (including the scape) under another, and the thorax (laterally), abdomen (dorsal side up) and legs under three further coverslips. It may be necessary to remove the top of the thorax and display this dorsal side up to see the thoracic setae, though these are usually visible in lateral view when properly cleared.

In cases where the pupa died, the pharate adult within was dissected out with varying degrees of success. It was usually possible to separate the head and antennae and the hypopygium; features which usually allowed identification.

No problems have been encountered with vertical storage of slides prepared in this manner. Slow drying mountants such as anada alsam, and to a lesser extent Euparal cannot be stored vertically for several years until fully dried because the specimens can still move underneath the coverslips.

v. Measurements

Although few measurements are necessary in defining the genera of Orthocladiinae, this is far from true at the specific level. It is not possible to describe adequately a species in any stage of the life history without giving the range of variation in lengths and ratios of taxonomically important characters. There are several problems with numerical methods which have not been adequately discussed in chironomid research, although the problems are apparent when reading many early descriptions.

Firstly there are several methods for measuring any feature. Few authors state which two points mark the extremes of the character measured, and differences between workers can be large. An example is the measurement of the antennal segments of the larva. The ratio of antennal segment lengths is often of specific value but there has been no consistent method for measuring the lengths of the segments and this means that previously published ratios are of limited value.

The antennal ratio is defined as the length of the basal antennal segment divided by the sum of the individual lengths of the remaining antennal segments. Frequently in the past it appears that the divisor in this ratio has been taken to be the distance between the apex of the basal segment and the tip of the terminal segment. This gives quite a different value because it includes the lengths of all the intersegmental membranes which vary greatly according to the preparation technique.

The second problem lies in the number of characters to be measured. Should only measurements known to be of specific value be made, or should they include a range of features which may prove later to be of either taxonomic or phylogenetic value?

Defects in older descriptions including the use of characters later shown to be of limited value and the omission of those now felt to be of importance has led to the feeling that a greater range of characters than those simply necessary for specific identification should be measured. It is also clear that not all species are known as larvae and the characters necessary to discern a new larva may not be apparent from a bare description of the "important" specific characters of the known relative.

Thus although the measurement of a range of characters may be without direct benefit to the study undertaken, it was felt necessary to take this course for future work.

In this conclusion the author concurs with Saether (1976:4) who "... includes a number of seemingly superfluous measurements which, in most cases, are not strictly necessary to identify the species. These measurements have, however, proved to be necessary in this case to establish species variation and phylogenetic relationships."

In accepting that many measurements should be taken in a systematic manner it was found to be useful to work with a data sheet on which the required characters for measurement were listed. This working sheet is shown on page . The list is not comprehensive but includes all the features examined on all specimens. Further measurements of characters with a restricted distribution within the orthocladiine genera were taken where appropriate.

The following measurements were taken: (all except the body length (mm.) are taken in um.)

Body length (Fig. 1b). A measurement from the most anterior point on the body to the most posterior (usually the posterior parapod). This is usually measured as the length of the thorax and abdomen, plus the head capsule length. This measurement is not of great taxonomic value, but is cited partially as a field identification aid. Certain genera are recognisable in the field, at least partially on size characters - e.g. *Corynoneura* and *Thienemanniella* are distinctly smaller than any other chironomid larvae.

Head Capsule (Fig. 1c). Length on dorsal surface from occipital margin to the labrum. This measurement is subject to some difficulties in judging the anterior end but this matters little since the character is cited only to ensure that gross errors of identification can be avoided by indicating overall size of the larva.

Antenna (Fig. 3a). As previously mentioned the lengths of the sclerotised part of each segment was measured, excluding intersegmental membranes. Sometimes the first antennal segment was asymmetrical and here the maximum length was measured. It was often necessary to use phase contrast to see features of the antennal spine, subsidiary spine and Lauterborn organs. Features of the antenna were frequently used at the generic and specific levels.

Mandible (Fig. 3b). The length was taken to be the maximum distance in a straight line measured from the apex of the apical tooth to the point of articulation at the basal end. Other features that were measured were the length of the subdental seta where present, and the number of filaments in the seta interna, if present. The relative length of the apical tooth of the mandible to the width of the remaining inner teeth is often of generic value.

Labrum (Fig. 2b). As well as a standard description of the features on the labrum the labral setae were measured where possible. Frequently these setae do not lie in a fully horizontal plane, and measurement is not possible. The number of teeth and maximum length of the premandible is an important specific character.

Mentum (Fig. 4b). The width was measured on the flattened mentum, between the outsides of the outer mental teeth. The mentum must be flattened since the shape in life is very variable. The mentum of many terrestrial Orthocladiinae is strongly curved and the mentum appears much narrower than it really is.

The extension of the ventromental plates beyond the mentum is also affected by whether or not the mentum was flattened. The ventromental plates of Bryophaenocladius are normally shown to extend well beyond the outer teeth of the mentum (vide Strenzke, 1942, 1954 & 1957). Flattening the mentum shows that the plates do not extend beyond the mentum (Figs. 8d & 8e). The width of the ventromentum beyond the outer teeth of the mentum was measured as the maximum width, and where the length was measured (Nanocladius) this was taken at right angles to the width measurement.

Abdomen (Fig.5a&b). Some of these measurements were restricted when measuring the larval skin. Anal tubules and posterior parapods were liable to collapse in such a way that they cannot be measured, and this might happen with prepared larvae also. The means of measurement are all shown in the Figure, the only problem arose when the procercus was asymmetrical with the posterior margin longer than the anterior. As is usual the maximum measurement was taken.

vi. Collecting Sites

The intention of this research was to rear Orthocladiinae larvae from as many aquatic species as possible, to produce material for the production of generic and specific keys. Collecting sites were selected with the intention of taking larvae from as wide a range of ecological types, but not necessarily reflecting geographic extremes. A map of collecting sites (Page , Appendix) is included. Each 10 km square blacked in represents at least one site visited in the area, but, especially in the South-East and Malham area there are many sites within each 10 km square.

Squares marked in red are those from which I have received further material cited in the text. The sources of these records and specimens are cited in the distributional data but where the material is my own only the site number is given.

Limitations of time and equipment meant that lake Orthocladiinae have been relatively neglected in this survey, with only Malham Tarn being examined in any detail, while two other small collections were made in the eutrophic Slapton Ley and the oligotrophic Loch Muick. The scarcity of material from oligotrophic water bodies is recognised, but the inherent problems of scarcity, access, low abundances of larvae suggest that this habitat would warrant separate study. The fauna of such lakes outside Britain is relatively well known from studies in the Alps, Scandinavia and Arctic Canada.

The majority of sites visited were lotic, and this was intentional. There is more limnological work in Britain on flowing waters, especially in relation to pollution and water extraction, and it is this area that identification of chironomid larvae is most needed.

Sites are listed in chronological order and the data is presented as: locality and national grid references and the date. Altitude is given for sites over 250 metres above datum. As much ecological information as is available is given for each site. Where the site is a grade 1 or 2 National Nature Reserve data was obtained from "A Conservation Review" (editor - Ratcliffe, published jointly by the Institute of Terrestrial Ecology and the Nature Conservancy).

DETAILS OF COLLECTING SITES

Site 1. KENT: nr. Rye, Peasmarsh, 51/8823, 28.ix.1978.
Wooded stream with silt and decaying leaves.
Many Micropsectra tubes.

Site 2. WARWICKSHIRE: Four Oaks, 42/1198, 4.x.1975. Garden pond with Nuphar.

Site 3. GWYNEDD: nr. Dollgellau, R. Helygog, 23/7918, 300-350 m.o.d., 10.x.1975. Fast mountain river running through open moorland. Water peaty with some submerged Fontinalis.

Site 4. GWYNEDD: nr. Dollgellau, Helygogfach, 23/786 198, 235 m.o.d., 9.x.1975. Stream one kilometer from spring source. Medium flow rate over gravel/sand bed with some overflow onto marginal grass.

Site 5. GWYNEDD: W.Ffestiniog, Nant-y-groes, 23/758 410, 400 m.o.d., 12.x.1975. Fast mountain stream running over flat bed-rock of Cambrian shales.

Site 6. GWYNEDD: Cors-y-Sarnau, 23/969 387, 11.x.1975. Stream running through acid valley mire. Shaded by marginal alder carr.

Site 7. DEVON: Cullompton, R. Culm, 31/028 075, 16.xi.1975. Lowland river, rich agricultural land surrounding. Silt and sand bed.

Site 8. KENT: nr. Westerham, Spring Shaw, 51/447 535, 22.ii.1976. Spring source of R. Darent, rising in Lower Greensand. Some cattle disturbance.

Site 9. EAST SUSSEX: Ashdown Forest, Broadstone Stream, 51/4132, 29.ii.1976. Wooded, acid stream with iron addits. Bed of silt with decaying leaves and covered with iron bacteria.

Site 10. KENT: Otford, R. Darent, 51/523 593, a: 28.iii.1976. b: 15.x.1977. Lowland chalk stream with heavy growth of Potamogeton, Chara etc. Rises at Site 8 and flows over Upper Greensand to Chalk.

Site 11. DEVON: Gidleigh Common, 360 m. o.d., 20/655 875, 16.iv.1976. Slow flowing ditch blocked by macrophytes. Bedrock of granite.

Site 12. HERTFORDSHIRE: nr. Letty Green, R. Lea, 52/282 100, 8.v.1976. Medium flow river running on Chalk. Abundant macrophytes, some cattle disturbance.

Site 13. STAFFORDSHIRE: Cannock Chase, Sherbrook Valley, 33/988 187, 30.v.1976. Alder lined stream running over Bunter Sandstone beds. Sandy bed with Potamogeton.

Site 14. WORCESTERSHIRE: Wyre Forest, Dowles Brook, 32/746 762, 31.v.1976. Tree lined stream on Coal Measures. Acidic with stony bed.

Site 15. DEVON: Dartmoor, Green Combe, 20/694 829, 380 m.o.d., 13.iii.1977. Muddy seepage beside stream flowing through mire.

Site 16. DEVON: R. East Dart, 20/645 791, 336 m.o.d., 13.iii.1977. Fast flowing upland river. Unshaded; bed of gravel and larger stones.

Site 17. NORTH YORKSHIRE: Malham Tarn, 34/895 672, 380 m.o.d. 28.iii-12.iv.1977. Upland marl lake of 62 hectares, maximum depth 4.4 m.. $CaCO_3$ 62-142 p.p.m.. Benthos of calcareous mud. Chara dominates in the deeper parts, Fontinalis on the stony wave exposed shores.

Site 18. NORTH YORKSHIRE: Aire Head, 34/902 622, 200 m.o.d., 28.iii-12.iv.1977. Calcareous spring with muddy bed.

Site 19. NORTH YORKSHIRE: Gordale Scar, 34/915 640, 250 m.o.d., 28.iii-12.iv.1977. Torrential stream on Carboniferous limestone where Gordale Beck falls through Scar. $CaCO_3$ 130-210 p.p.m., nitrate low. Substrate of limestone bedrock covered with algae.

Site 20. NO TH YORKSHI : Upper Gordale Beck, 34/911 657, 380 m.o.d., 28.iii-12.iv.1977. Higher up Gordale Beck than Site 19, but physical characteristics similar. Slo er flow rate, but still fast.

Site 21. NO H YORK HI : Northern Inflow to Malham Tarn, 34/ 63 677, 380 m.o.d., 28.iii-12.iv.1977. Stream 50-150 m. from spring source and with upwellings throughout the bed of the stream. Calcareous.

Site 22. NORTH YORKSHIRE: Malham Cove, 34/897 641, 200 m.o.d., 28.iii-12.iv.1977. Upwelling of underground river after course through limestone.

Site 23. NORTH YORK HIRE: Fountains Fell Tarn, 34/868 713, 650 m.o.d., 10.iv.1977. Exposed Tarn at 700 m. a.s.l. on Millstone grit overlying limest ne.

Site 24. NO TH YORKSHIRE: Malham Tarn Outflow, 34/895 660, 380 m.o.d., 11.iv.1977. A one kilometre stretch of stream between the Tarn and disappearing down a sink. $CaCO_3$ 70-80 p.p.m. and low nitrate. Slowest flow rate of any stream examined in the area with more macrophytes (*Potamogeton*, *Fontinalis* and *Rorippa*). Bed of stone and ravel.

Site 25. E T USSEX: Chuck Hatch, 51/474 330, 1.viii.1977. Shaded acid stream.

Site 26. E T U SEX: nr. Marsh Green, 51/461 332, 1.viii.1977, (a), 17.iv.1978 (b). Partially shaded, broad, gravel bedded stream with some cattle disturbance. Richest stream examined in Ashdown orest.

Site 27. AST USSEX: nr. Coleman's Hatch, Newbridge, 51/456 326, 1.viii.1977. ravel bedded stream, partially running through concrete bedded ford.

Site 28. EAST SUSSEX: nr. Maresfield, 51/4726, 2.viii.1977. Stream running from lake outflow.

Site 29. WARWICKSHIRE: Sutton Park, 42/103 977, 30.x.1977. Stream emerging from pine wood 600 m. after outflow from lake. Flowing on Bunter sandstone and pebble beds with some macrophyte growth.

Site 30. GRAMPIAN: Aberdeenshire, Loch Muick, 37/299 842, 400 m.o.d., 5.x.1977. Oligotrophic loch beneath Lochnagar on granite. Substrate on wave-swept shore of gravel and sand. No algae visible.

Site 31. GRAMPIAN: Kincardineshire, Cowie Water, 37/806 883, 6.x.1977. Lowland tree-lined river. Fast, non-turbulent flow, benthos boulders with few smaller stones apparent. Apparently frequent spates: no macrophytes.

Site 32. KENT: nr. Chiddingstone, R. Eden, 51/512 464, 15.x.1977. Recently dredged, slow flowing lowland river on clay. Unshaded, broad and shallow.

Site 33. HAMPSHIRE: New Forest, Matley Wood Bog, 41/334 078, 22.xi.1977. Mire surrounded by oak trees.

Site 34. SOMERSET: Exmoor, Tarr Steps, R. Barle, 21/867 321, 225 m.o.d., 21.xi.1977. Rich, shaded river running through sandstone, bed of gravel and sand with some _Fontinalis_ covered stones.

Site 35. WEST SUSSEX: S.W. East Grinstead, 51/375 345, 2.iv.1978. Sheltered stream, silt bed with many _Gammarus_.

Site 36. WE T U SEX: nr. Ardingley, 51/353 297, 9.iv.1978. Pool in slow stream. Deep silt benthos with many *Ephemera danica*.

Site 37. EA T U SEX: e t of Fore t Row, 51/414 347, 17.iv.1978. Sheltered stream. Benthos of algal cover d stones, gravel and some sand.

Site 38. DEV N: River Bovey, 20/780 800, 1.vi.1978. Medium to fast flow, shaded, sandy substrate river running through Millstone grit. No macrophytes.

Site 39. DE N: lapton Ley, 20/827 442, 2.vi.1978. Eutrophic freshwater shingle bar lagoon formed by a dammed river delta. $CaCO_3$ 60-80 p.p.m., salinity varies from 30-5200 p.p.m.. Benthos sand and silt, collections up to 2 m. depth and in *Phragmites* at margin.

Site 40. DEVON: nr. Chagford, R. Teign, 20/694 779, 150 m.o.d., 3.vi.1978. road, shallow, open river flowing on east side of Dartmoor. Substrate stony, many ma rophytes.

Site 41. NORTH YORK HIRE: Grassington, R. Wharfe, 44/002 634, (165 m.o.d.), 2.vii.1978. Medium to fast flowing, bro d river rising on Chalk. Solid clay bed with a few marginal algal covered stones. Some macrophytes at margin.

Site 42. .T F RD HI : Ilam, R. Manifold, 43/130 505, 8.vii.1978. rea of emergence of R. Manifold after 11 km. channel through limestone, although base of submerged river is on sandstone. Benthos fine sand with *Potamoget n* present. Water temperature cold.

Site 43. EAST SUSSEX: Crowborough, 51/489 304, 26.vii.1978. Darkly shaded stream of riffles and pools. Benthos of silt and stones with many leaves.

Site 44. *STAFFORDSHIRE : illdale, R. Dove, 43/139 547, 28.viii.1978. Limestone river, fast flowing, with sand and silt deposits at the margins.
*River forms county boundary of taffordshire and Derbyshire.

Site 45. KENT: nr. Goudhurst, tributary of R. Teise, 51/728 359, 3.ix.1978. Weed filled ditch. Some cattle disturbance.

Site 46. KENT: nr. Fordecombe, R. Medway, 51/527 404, 17.ix.1978. Broad, shallow river below weir. Benthos of sand and silt with some macrophytes.

Site 47. EAST SU EX: nr. Newick, R. Ouse, 51/4421, 30.ix.1978. Deep, steep banked (? dredged) Chalk river, enthos of clay without macrophytes.

Site 48. POWY : Elan Village, R. lan, 22/9365, 200 m.o.d., 6.x.1978. Moderate flowing, shallow river fed from oligotrophic Caban Coch reservoir. Bed thickly encrusted filamentous algae covering all stones. Open site.

Site 49. POWYS: 11 kms North of Rhayader, R. Wye, 22/921 739, 240 m.o.d., 6.x.1978. Upland, base-poor river running over shales. Low in both Nitrate and Phosphate. Subject to spate. Benthos of stones, some encrusted with algae and Fontinalis. Open site.

Site 50. POWYS: nr. Builth Wells, R. Duhonw, 32/020 474, 220 m.o.d., 6.x.1978. Deeply shaded river rising on Old Red Sandstone. No macrophytes and poor algal growth on stones. Substrate mainly sand and gravel with silt in marginal deposits.

CHAPTER 4

MORPHOLOGY AND TERMINOLOGY

Saether (1971:1237) succinctly pointed out an important problem which faces all potential students of Chironomidae when he observed "The anatomical terminology used in taxonomic papers on chironomids is often confusing, arbitrary, incorrectly applied, in contradiction with general terminology of dipteran morphology, and, in addition, different authors frequently do not use corresponding terms". These problems apply equally to the larva as to the pupa or adult.

For several reasons it was not intended in this study to review critically the varying terminologies of all previous authors who have published on chironomid larvae. The first of these is that the necessary anatomical studies, involving both histological and embryological analysis, are outside the scope of this work and would probably have involved as much effort as the taxonomic work. Secondly several recent workers have reviewed part of the terminology of the larvae. Hirvenoja (1973:34-44) in a detailed survey of many previous works came to many of the same conclusions about the terminology as had Saether (1971:1237). Saether did not attempt a detailed morphological review, but concentrated on those terms with most inconsistencies in their use. Other authors have also published works with some terminological reviews including Mozley (1970) and Soponis (1977). Although there are some inconsistencies in the terms used by these authors many are not in dispute.

Since stability of terminology is important if studies of the Chironomidae are to be encouraged the terminology followed in this work is that of Saether (1971 and expanded in 1976, 1977 and 1977a). For reasons of stability this terminology will also be used in the forthcoming "Generic key to the larvae of the Holarctic Chironomidae", although some usages may eventually prove to be morphologically incorrect. The terms used are listed with equivalents in parentheses and briefly discussed below:

HEAD CAPSULE

Dorsal features (Fig. 2a)

The dorsal median sclerite, the frontal apotome (frontalapotom) extends from the point of dorsal contact of the lateral genae just anterior to the occipital margin (anale Rand) as far as the interantennal sulcus. The frontal apotome is separated from the genae by a line which fractures during ecdysis, and the sclerite bears the dorsal seta pairs 4 and 5.

The interantennal sulcus, the suture which separates the frontal apotome from the labrum is a suture lying on the line between the antennae just behind the dorsal seta pair 3. The labrum (Stirnfeld, Sinnesfeld) is the anterior dorsal part of the head capsule bounded anteriorly by the labral margin (margo labralis, torma in the sense of authors including Saether (1971) but not Strenzke (1960) or Reiss (1969) who used the term for the premandible). The labrum bears five pairs of sensory setae in the anterior half, and the dorsal seta pairs 1 to 3 posterior to these. In some genera, as in many Chironominae, the constituent sclerites of the labrum can be distinguished (vis. Brillia Fig. 7b).

The sensory setae SI to SIV a & b are normally distributed in the following way: SI are the anterior pair and may be plumose, palmate, branched, bifid or simple or intermediate between these states. Lying posterior to these are the normally simple SII, which are rarely bifid, and in *Epoicocladius* they may be elongate and terminally plumose. The SIII usually lie internal to the SII and are very rarely other than simple (terminally bifid in *Eukiefferiella ilkleyensis* group). The most posterior S setae are the pair of SIV which lie outside the SII and are usually very small "bisensillae" (Fittkau, 1968a: Fig. 20). It appears that these setae are strongly developed in *Epoicocladius*.

The anterior margin of the labrum is frequently covered with non-sensory cuticular projections termed the labral spines and chaetae (see discussion of terms under palatum, page 46).

A further feature of taxonomic importance on the labrum is the labral lamella which lies between the bases of the SI setae and may be anteriorly divided. The anterior margin is variable shaped, often plumose or divided into spines. Labral lamellae are present in many of the more plesiomorphic genera, particularly in the Metriocnemini.

Lateral features including the antenna (Fig. 3a)

The lateral sclerite of the head which bears the antenna, the larval eyes and the setae 6 to 10 is the gena (parietal plate or lobe). The larval eyes (Augen), usually multiple, are of taxonomic significance and were often used by earlier workers. However the eyes cannot be seen on the larval head capsule after pupation, and they are also readily lost if the head capsule is treated with KOH or mounted in Berlese fluid. This greatly restricts their usefulness, and they have been disregarded in this work.

Lying at the dorsal anterior end of the gena is the antenna (Antenne) a sensory, segmented structure. The antenna consists of a basal segment (Basalglied) and a variable number of further segments (Endglieder, Geissel, flagellum). The first antennal segment bears a circular, weakly sclerotised structure, the ring organ, the position of which may be of taxonomic value.

The antennal ratio, an important distinguishing feature, is calculated as the sum of the lengths of the terminal antennal segments divided into the length of the basal segment. Hirvenoja (1973) used the reciprocal of this ratio. For further details of the calculation see Chapter 3.v..

On the membranous apex of the first antennal segment, adjoining the base of the second segment, is the antennal spine (Antennenborste, blade of first antennal segment). This spine may be bifid with the inner branch (Nebenstift) shorter than the outer. The outer branch is of variable length relative to the antennal flagellum, and this length is frequently of taxonomic value.

Frequently, on the apex of the second antennal segment, there are the sensory Lauterborn organs, normally paired and lying each side of the third antennal segment. In one genus (Heterotanytarsus) they are alternate, the proximal rising in the middle of the second segment, the distal organ apical on the segment as normal.

There is frequently a subsidiary spine on the second antennal segment, often arising subapically. It seems that this spine, when well developed, has been mistaken for a Lauterborn organ (e.g. Parakiefferiella, Brillia). Since this spine has only been found on the second apical segment its presence in Brillia helped in the determination of the number of antennal segments in this genus (see page 80). The subsidiary spine is sometimes distinct when Lauterborn organs are present (e.g. Parametriocnemus and Eukiefferiella) but often attains its maximum development when they are absent.

The number of antennal segments is not easy to determine since, particularly in the more plesiomorphic genera of Metriocnemini, there can be a fine terminal segment, visible only under oil immersion with phase contrast. When this terminal segment is noted it is referred to in the description and key as vestigial. There are similar difficulties in determining the number of segments in the antennae of the more apomorphic genera of Metriocnemini where the antenna is strongly reduced.

Palatum and premandibles (Fig. 2b)

There is much confusion about the terminology of the cuticular sculpturing in the Diptera. Saether (1971:1251) notes that Richards (1951:268) recognises five types of cuticular sculpturing but observes that the different kinds of setae intergrade in such a way that there can be no sharp delimitation between types.

While it is here accepted that the terms chaeta (from Greek), seta (Latin), chaetula, scale and spine may often be synonymous and may not always give the correct information about the sensory nature of the structure, it is felt that there is value in retaining this terminology where it is well founded in the literature. In view of the problems noted already concerning the use of different terms for equivalent structures in chironomid taxonomy it is surprising to find a unanimity about the terms pecten epipharyngis, labral chaetae, chaetulae laterales and chaetulae basales. It is proposed in this work that these terms should be retained for those specific cuticular extensions of the head capsule which they have been used for unambiguously in the past. The alternative of providing new, neutral terms is rejected.

The palatum (Mundfeld, epipharynx) is the ventral surface of the labrum, anteriorly delimited by the labral margin. This consists of two sclerites - the anterior ungula (U-sclerite, piece en U) with a posterior basal sclerite (Basalsklerit, piece trapezoidale). Lying within the U shaped ungula are several setae of taxonomic importance. Amongst the most anterior of the setae can usually be distinguished a central group, the pecten epipharyngis (not equivalent to Strenzke's (1960) Epipharynxkamm) and, lying on each side of the pecten epipharynx, a variable number of chaetulae laterales. The setae of the pecten epipharyngis and chaetulae laterales may be either simple or serrate. Lying posterior to these, or below the chaetulae laterales, on the ungula, are up to two chaetulae basales, which also may be serrate.

On either side of the ungula, articulating behind the labral margin, is a movable structure. These were termed premandibles (pramandibelen) by Goetghebuer (1912:9), but his postulation of second metameric (premandibular segmental) origin has not always been accepted, often by those who did not believe that dipterous larvae should have retained an appendage which is lost in other less specialised Orders. Many other terms have been used for these appendages including "armature of the undersurface of the labrum", messores, messorials and tormae in the sense of Strenzke (1960) and Reiss (1969) but not Saether (1971) who uses the term for the labral margin.

Substantial evidence has accrued showing that these structures may be of premandibular origin, starting with Zavrel (1931) who examined the musculature and confirmed Goetghebuer's interpretation of the innervation from the "tritocerebrum" of the brain. Cook (1949) confirmed the homology of the "messores" of the Chironomidae, the mouth-brushes of larval Culicidae and the fans of larval Simuliidae, but rejected their premandibular origin. Saether (1971:1253) summarises evidence for the presence of premandibles in several families of Nematocera based on embryological studies but notes that Craig (1969) showed the labral origin of the brushes of Aedes aegypti (Culicidae). In using the term premandible in this study it is accepted that further embryological study is necessary to confirm the use of this term.

Mandible (Fig. 3b)

The mandible (mandibel) articulates on the anterior lateral margin of the gena. It tapers to a rounded or pointed apical tooth which may be longer or shorter than the combined width of the variable (1 - 4) number of inner teeth. The relationship of the length of the apical tooth to the combined width of the inner teeth is often of taxonomic value. There is no outer tooth to the mandible as is often found in the Chironominae: all the teeth are in a straight line in the same plane, with the exception of Corynoneura (see page 100).

Just inside the innermost tooth of the mandible is a seta subdentalis and, in the middle of the basal third, just above the point of insertion of the adductor muscle, is a single broad seta, the seta interna. This seta is divided into a number of branches and each branch may be simple, plumose or serrate. Sometimes either the seta subdentalis or the seta interna may be missing - a feature of taxonomic significance. Care must be taken not to confuse the adductor muscle with the seta interna, and the seta is best seen on a detached mandible. Errors have been made in descriptions apparently based on the intact mandible.

Maxilla (Fig. 4a)

The terminology used in describing the maxilla is that of Saether (1976:Fig. 20a, 23 a-g). Although the maxilla has been frequently figured in this work the value of the appendage as a taxonomic feature has been disappointing. However there may well be features of phylogenetic importance in the maxilla as in the prementohypopharyngeal complex illustrated by Saether (1971:1257).

The maxilla lies below the mandible on the anterior margin of the gena. Although the maxilla has been figured in the literature from many angles it will be described here as drawn in this study (e.g. Fig. 4a). This is a ventral view of the left hand maxilla, such that the inner edge is beside the outer teeth of the mentum and the outer edge is adjacent to the base of the antenna, or the mandible where it has not been dissected off. This is the normal view of the maxilla when the larval head capsule is flattened with the mentum upwards.

The maxilla consists of two parts, the outer palpiger (stipes, stipalsklerit) and the inner galea (galeolacinia, cardo). At the base of the palpiger may lie a number of scales, the tetrahedral lamellae of the palpiger. On the palpiger itself there is usually a distinct ring organ lying on the more heavily sclerotised base of the palpiger. There are a number of setae on the palpiger including at least one bisensillum and a distinctive apical "a" seta. At the inner end of the row of tetrahedral lamelles of the palpiger, sometimes starting behind the palpiger, there may lie a row of galear lamellae of variable shape. At the inner corner of the galea, at the inner end of the row of galear lamellae, are a group of setae the maxillary setae. Separate from these setae are a paraxial seta, lying outside and slightly above the remaining maxillary seta, and lying inside and below the other maxillary setae, an antaxial seta. Frequently these setae are indistinguishable from the remaining maxillary setae, any or all of which may be simple, serrate or plumose.

On the upper surface of the galea there are usually two bisensillae of variable lengths, and there may be a pecten galearis running between the two bisensillae. A third sensory structure on the galea may be a multilobate sensilla.

Frequently obscured by the mentum, on the inner margin of the galea there may be an appendix - a long, sometimes serrate, spine. The absence of the appendix in figures in this work should not be regarded as definite because it may be obscured by the mentum. In a study of the comparative morphology of the maxillae of the Orthocladiinae it would be necessary to dissect the maxilla from the gena to prevent obscuring by the mentum or the mandible.

The ventral surface of the head (Fig. 4b)

The terminology of this part of the head capsule has been more confused than any other feature. In accepting the interpretation of the toothed plate as the mentum in the sense of Tokunaga (1932), Saether (1971:1254) summarised much evidence of homology outside the Chironomidae. Primary among these is Craig (1969) who showed that this structure is the mentum in Simuliidae and that the area posterior to it is the submentum. In the Chironomidae the submentum extends from the tentorial pits on the occipital margin forward to the mentum, which is rarely distinctly separated from the submentum (only in Potthastia and some Tanypodinae according to Saether loc.cit.). Saether thus believes that mentum should be used in place of labial plate, hypostomal plate, hypostomium, submentum sensu auctt., endolabium or hypochilum used by previous authors.

Saether (loc.cit.) also reinterprets the structures lying lateral to the mentum, particularly evident in the Chironominae, as ventromental plates (paralabial plates, submental plates, submentum (sensu Tokunaga, 1932)). Saether interprets the mentum as a double structure. The ventromentum or ventral plate of the mentum is the ventral wall of the median teeth and extends out, sometimes beyond the lateral mental teeth, to form what has been called the paralabial plates. The dorsomentum forms the dorsal wall of the median teeth, and all of the lateral teeth. There may be setae (beard)arising from lateral of the dorsomentum, appearing below the ventromental plates where the ventromentum extends beyond the dorsomentum. The striated ventromental plates of the Chironominae may be interpreted as an incorporation of setae into the ventromentum.

The extent of the ventromental plates, and the occurrence of setae beneath, are of taxonomic significance, often at the generic level.

BODY SEGMENTS (Figs. 1b, 5a, 5b)

The body consists of three thoracic segments and ten abdominal segments. The thoracic segments are recognised in the fourth instar larvae by the swelling ("thoracic packing") caused by the developing adult thorax, wing buds and legs within these segments. In *Corynoneura* and *Thienemanniella* there appear to be only two thoracic segments with the second and third fused.

Frequently there are setae distributed on the body segments and these may be of taxonomic value. *Epoicocladius* and the Arctic genus *Abiskomyia* are densely covered in stout setae, and finer but sometimes longer setae are found in *Eukiefferiella*, *Paralimnophyes* and some *Limnophyes*. These genera usually have simple setae (with the exception of *Abiskomyia* which has some plumose setae and a *Eukiefferiella* with a few forked setae) but there are others with complex setae. Many *Cricotopus* have the posterior lateral setae (l_4 of Hirvenoja, 1973) developed into a setal brush on abdominal segments I - VI or VII. *Synorthocladius* has alternating lateral setae (l_2 & l_4) developed as stellate setae.

Abdominal segment IX normally carries on the dorsal side a pair of protruberances the *procerci* (*Borstenträger*, or *preanal Borstenträger*, *preanal papillae*). The procerci bear apically a number of setae of variable lengths. These may be of taxonomic importance, as is the absence of procerci in certain genera of Metriocnemini. The procerci bear two lateral setae, one of which may be more strongly developed (e.g. *Eukiefferiella*). The tenth abdominal segment may bear supra-anal setae which may extend beyond the body, and in *Corynoneura* and *Thienemanniella* there is a strongly developed subanal seta. The tenth segment may sometimes not be visible, or may be bent ventrally through 90 degrees such that the posterior parapods point vertically downwards and the procercal setae point backwards.

In those larvae with *parapods* (*fussstummel* (anterior), *nachschieber* (posterior), *prolegs*) these are on the first thoracic segment and on the tenth abdominal segment. In most genera the parapods are separate and bear terminal claws, but in *Heterotanytarsus*, *Abiskomyia*, *Heterotrissocladius* and *Paratrissocladius* there are additional groups of spines at the bases of the anterior parapods. In other genera the anterior parapods are fused for some or all of their length and this may also be the case with the posterior parapods. Several genera in the Metriocnemini may have any or all of the procerci, anterior parapods, posterior parapods or anal setae missing.

Also on the tenth abdominal segment above the bases of the posterior parapods there are usually two pairs of *anal tubules* (*anal papillae*, *analpapillen*, *analkiemen*). These organs are absent in marine species of Orthocladiinae, and in some genera there are only one pair of tubules. The relative lengths of the anal tubules to the posterior parapods is often of taxonomic use, and the genus *Georthocladius* appears to have been erected largely upon the distinctive, long, frequently constricted anal tubules of the larvae.

CHAPTER 5

KEY TO THE GENERA OF ORTHOCLADIINAE

1. Introduction to the key

Many of the genera of Orthocladiinae, although distributed throughout the world, are only known in their larval stage from the Palaearctic and to a lesser extent the Nearctic regions. Even in these areas only a limited proportion of the larvae are known in many genera. This relatively scanty knowledge of the genera on a worldwide basis makes the construction of a larval generic key difficult if its use is not to be transient.

For the key to remain useful beyond the discovery of new life-cycles it is necessary to find characters in the known species of a genus which are likely to be present in other, as yet undescribed, members. The discovery of these characters is the basis of phylogenetics and keys using these characters may be termed "natural" as opposed to "artificial". These terms are, however, relative. It is not possible to construct a totally natural key without knowing the complete evolutionary history of a group and most artificial keys contain some phylogenetic information whether deliberately imparted or not.

There seems to be a number of advantages in attempting to construct a natural key for groups in which the taxa are inadequately known as in the generic key which follows.

The first, and most important, advantage is that such a key has a higher probability of having a predictive value for character states possessed by as yet undescribed larvae. In the construction of a natural key it is necessary to search for character states which can be postulated as advanced (apomorphic) in each taxa. When the necessary allowances are made for possible evolution of apomorphic characters in parallel or convergence the sharing of apomorphic characters in different taxa (synapomorphy) can be used to propose relationships between the taxa involved. By the postulated evolution of apomorphic characters phylogenies can be proposed for the group under study and a key can be prepared based upon these characters. (For further discussion of these problems, see Chapter 7).

If a genus is defined by unique apomorphic characters in the known adult males, as is often the case in the Chironomidae, and there are also apomorphic characters of the known pupae which confirm this generic homogeneity, there is a high probability that apomorphic characters found in the known larvae will be present in as yet undiscovered larvae in the genus. The discovery of synapomorphic characters can be seen to have a potential predictive value.

In a group where most or all taxa to be included are fully described there can be no objection to the production of an artificial key which uses some plesiomorphic (primitive) characters. These characters are invalid for assessing phlogenetic relationships since they may be retained in a number of divergent lines which are not closely related. Since these characters are often retained in unrelated taxa they cannot have any predictive value and will be of limited use in a natural key.

A second reason for preferring a natural key is the amount of information contained in such a key about the relationships of the taxa included is much greater than in an artificial key. The latter in fact need contain no information on the relationships of the taxa included.

A third advantage of the production of a natural key is the need to examine critically all characters used, and the necessity for systematic comparison of these characters in all taxa examined. Although time-consuming this procedure avoids many of the problems of inadequate descriptions associated with some artificial keys.

For the reasons outlined above it was felt desirable to compile a natural key to the genera of Orthocladiinae. An initial attempt was made (Cranston, 1976 unpublished) but unfortunately one of the problems with a natural key was encountered. Certain characters believed to be apomorphic were found to be present in unrelated taxa having evolved either in parallel or by convergence. Therefore multiple choice couplets were necessary to exclude taxa and this led to some lengthy couplets with a number of "either/or" choices. In practice there is often difficulty in using such a key. Because of these problems the key was rearranged, making it easier to use, but losing some of the phylogenetic basis of the sequence of genera.

It was also felt that the key should be expanded to include genera from outside Britain. The predominant reason for this decision was the discovery of additional generic records based upon the pupae (Wilson, 1977; Langton pers. comm.) and larvae (this survey). The list of orthocladiine genera based on the adults was thus shorter than that for the immature stages. It is very likely that, as the taxonomic basis for the identification of the immature stages improves, further new generic records will be made. As noted on the opening page of this chapter it is hoped that the key will remain useful despite the discovery of new life histories and the same applies to the discovery of new genera to the British and Irish faunas.

A further reason for the extension of the key is the intended inclusion of some of the research in this study in a collaborative key to the Holarctic genera of Chironomidae (to be edited by Fittkau). Genera not so far found in Britain were examined for the purposes of the latter key (in co-operation with Oliver and Saether) and the descriptions were therefore included in the present study. Also included only at the generic level are those genera which are mainly or exclusively terrestrial, both for the possible occurrence of any of these taxa in aquatic habitats and for completion of the generic diagnoses and phylogenetic discussions.

The generic key which follows is based upon examination of all the species mentioned in the text of Chapter 6, many published descriptions cited in the text and two unpublished working keys of Oliver and Saether. The opportunity to examine material in the Staatssammlung der Bayerischen Staates, Munich, particularly the collections of Thienemann and Strenzke, assisted in keying out the genera not yet recorded from the British Isles. These genera are marked by an asterisk (*) after the generic names in the text of the key.

This key, like the unpublished 1976 version, has been widely circulated to taxonomists and limnologists for comment and to encourage people to send material presenting difficulty. Changes have been made in the key accordingly.

11. Key to Holarctic Genera

1 Anal end without procerci although there may be procercal setae arising from the body wall. Anterior parapods often fused for part of their length (Fig. 33d) 2
Procerci present with variable number of procercal setae. Anterior parapods nearly always separate for all their length 13

2 Preanal and anal segments and posterior parapods bent at right angles to the axis of the rest of the body (Figs. 8g and 33e) 3
Preanal and anal segments on same axis as rest of body (Fig. 5a) 4

3 Posterior parapods divided into two parts, the anterior part with small claws (Fig. 33e). Anal tubules absent. One procercal seta present ... Gymnometriocnemus Goetghebuer
Posterior parapods undivided (Fig. 8g); No procercal setae. Anal tubules present ... Bryophaenocladius Thienemann

4 Anal tubules absent; marine species 5
Anal tubules present, although sometimes small; terrestrial, semiterrestrial and occasionally aquatic species 7

5 Procercal setae single, S1 broad and apically feathered, S11 similar (Fig. 12b) .... Clunio Haliday
Two or three procercal setae, S1 and S11 not as above ... 6

6 Premandible with four teeth .... Tethymyia Wirth*
Premandible with two or three teeth ....
.... Thalassosmittia Strenzke & Remmert

7 Premandible absent, mandible with spine-like teeth. Ectoparasitic on Ephemeroptera .... Symbiocladius Kieffer & Zavrel*

Premandible always present, mandibular teeth rounded or subtriangular as usual 8

8 SI, SII both bifid (Fig. 9b) 9

SII never bifid 10

9 Posterior parapods, procerci, anal setae and anal claws all absent. Terminal antennal segment as long as that preceding (Fig. 9a). Premandible with 3 teeth (Fig. 9b) .... Camptocladius Wulp

Anal claws and posterior parapods present; if absent (P. simplex Strenzke) the terminal antennal segment is at least 3 times as long as that preceding and there are two apical and two inner premandibular teeth (Fig. 71b) .... Pseudosmittia Goetghebuer

10 Anal tubules long with many constrictions. Anterior parapods separate .... Georthocladius Strenzke*

Anal tubules short without constrictions. Anterior parapods fused 11

11 Mandible without seta interna. SI simple .... Mesosmittia Brundin

Mandible with seta interna. SI palmate 12

12 Antenna very reduced, four segmented but with the final two segments difficult to discern. Antennal blade extends beyond end of antenna .... Parasmittia Strenzke*

Antenna not usually reduced, four or five segmented with 3&4 or 3-5 small. Antennal blade not extending beyond end of antenna (Fig. 75a) .... Smittia Holmgren

13 Anterior parapods with apical and preapical claws. (Fig. 36e). Antenna mounted on tubercle as in Tanytarsiini (Fig.36a) 14

Claws of anterior parapods usually in a single group. Antenna never mounted on tubercle 15

14 Antenna subequal to the length of the head, with two large Lauterborn organs alternating on second antennal segment (Fig.36a). Body setae short, simple ....Heterotanytarsus Sparck

Antenna shorter than head, but longer than mandible. Lauterborn organs smaller. Strong body setae, some plumose .... Abiskomyia Edwards*

15 Antenna as long as or longer than half the length of the head 16

Antenna shorter than half the length of the head 17

16 Antenna four segmented, longer than the head (Fig. 13b) .... Corynoneura Winnertz

Antenna five segmented, slightly longer than half the head length (Fig.77a) .... Thienemanniella Kieffer

17 One of the setae on the procercus as long as ¼ the body length (Figs.38f & 70e) 18

No procercal setae as long as ¼ body length 19

18 Mentum with four pairs of lateral teeth (Fig. 70d). Premandible with one apical tooth. Procercal setae point backwards in same axis as rest of body because preanal segment projects over anal segment (as in *Paraphaenocladius*)(Fig.60g) .... *Pseudorthocladius* Goetghebuer

Mentum with six pairs of narrow, needle-like, lateral teeth (Fig. 38e). Premandible with two apical teeth. Procercal setae directed normally .... *Krenosmittia* Thienemann

19 Mentum with at least sixteen teeth 20

Mentum with fifteen teeth or less 24

20 Mentum strongly arched, giving the impression of only 6 central teeth; laterals visible on compression of the mentum (Fig. 24d). Anal tubules either absent or at most one pair 21

Mentum not as above. Two pairs of anal tubules 22

21 Premandible with five apical teeth. Pecten epipharyngis of 3 spines. Body without strong brown setae .... *Baeoctenus* Saether*

Premandible with two apical teeth. Pecten epipharyngis of 8-10 fine spines (Fig. 24b). Body covered with strong brown setae (Fig. 24f) ...... *Enoicocladius* Zavrel

22 Ventromentum distinct from dorsomentum and extending to cover the dorsomentum. Dorsomentum with 13 lateral teeth on each side, ventromentum with three medium teeth. Mandible without seta interna..*Phycoidella* Saether*
Mentum of more normal construction. Dorsomentum with 10 or fewer pairs of lateral teeth. Mandible with seta interna 23

23 Mentum with 10 pairs of lateral teeth. Premandible with four apical teeth ....
.... *Lapposmittia* Thienemann in Edw.Kr. & Th.*
Mentum with 8 or 9 pairs of lateral teeth. Premandible with one terminal tooth ....
.... *Orthocladius* (*Euorthocladius*) (part)
(*rivulorum* Kieffer, *suspensus* Tokunaga*)

24 Preanal segment extends backwards over anal segment, procercal setae directed backwards along main axis of body (as *Pseudorthocladius*) (Fig. 60g) ....
.... *Paraphaenocladius* Thienemann
Preanal and anal segments normal 25

25 Ventromental plates conspicuous, occasionally with two pairs of plates, never with setae beneath. S1 never bifid 26
Ventromental plates weak or absent; if conspicuous then either with setae below or S1 bifid, or both ... 33

26 All S1 setae simple, fine and often difficult to see (Fig. 43b). Ventromental plates elongate and relatively narrow (Fig. 43c) .... Nanocladius Kieffer

S1 setae never simple, usually distinct. Ventromental plates broader and less elongate 27

27 Labral lamellae present between, or below S1 setae. Antenna five segmented .... Chaetocladius Kieffer (? part)

No labral lamellae. Antenna four to seven segmented.. 28

28 Antenna seven segmented, seventh vestigial 29

Antenna at most six segmented, with sixth very fine . 30

29 Premandible simple. Pecten epipharyngis of three dark spines (Fig. 62b). 4 pairs of lateral mental teeth (Fig. 62d) .... Paratrissocladius Zavrel

Premandible bifid. Pecten epipharyngis of three pale, weak, serrate scales (Fig. 37b). 5 pairs of lateral mental teeth .... Heterotrissocladius Sparck

30 A single wide median mental tooth. S1 finely plumose with more than 30 branches ....Oliveria Saether*

Mentum with paired median teeth. S1 with less than 20 branches 31

31 Mentum with the two median teeth distinctly lower than first pair of laterals. Blood red larvae ....Trissocladius Kieffer

Mentum with the two median teeth as high, or higher than first pair of laterals .... Hydrobaenus Fries*

32 Ventromental plates with setae beneath, occasionally fine and sparse 33

Ventromental plates without setae 42

33 S1 setae simple 34

S1 setae bifid, plumose or palmate 36

34 Median tooth of mentum small, overreached by first pair of lateral teeth. Seta interna of mandible absent .... Parorthocladius Thienemann*

Median tooth or teeth level or distinctly higher than first pair of laterals. Seta interna present 35

35 Median teeth paired, greatly overreaching the first pair of laterals (Fig. 76f). Each abdominal segment with a pair of plumose setae alternating with simple setae on each side (Fig. 76g)..Synorthocladius Thienemann

A single, broad mental tooth more or less level with first pair of laterals. Abdominal segments with a single long simple seta on each side .... Paracricotopus Thienemann & Harnisch

36 S1 bifid, sometimes with fine feathering, at times giving the impression of up to four branches in Acricotopus (Fig. 6b) 39

S1 plumose or palmate 40

37 Seta interna of mandible absent. S1 often with fine feathering (Fig. 6b) ....Acricotopus Kieffer

Seta interna present. S1 not as above 38

38 Procercus often with posterior spur (Fig. 72d). Mentum with two median teeth sometimes each with a small closely appressed lateral and five pairs of lateral teeth ...... Rheocricotopus Thienemann & Harnisch

Procercus without posterior spur. Mentum with one central tooth and six pairs of lateral teeth. Setae beneath mentum only visible with difficulty 39

39 Anal tubules present. Lauterborn organs distinct (Fig. 56a). Median mental tooth sometimes pale and at least twice as wide as first lateral tooth (Fig. 56d) .... Paracladius Hirvenoja

Anal tubules absent. Lauterborn organs faint or absent. Median mental tooth dark, narrower than twice the width of the first lateral tooth .... Halocladius Hirvenoja

40 S1 palmate with 3-10 subequal teeth (Figs. Premandible simple. Procercus with at least one sclerotised spur at base (Fig. 63f) .... Psectrocladius Kieffer

S1 plumose with unequal size teeth. Premandible bifid. 41

41 Ventromentum elongate with many long setae beneath. Mandible with four inner teeth ..... Diplocladius Kieffer

Ventromentum shorter with fewer weak setae beneath. Mandible with three inner teeth .... Zalutschia Lipina

42 Inner margin of mandible usually with spines (Fig. 29b) and S1 simple (S1 split into fine setae and mandibular spines may be missing in _E. verralli_ group (Fig. 38g)). Oral seta on procercus long and strong (except _E. cyanea_). Mentum often with distinct striations of lighter sclerotization; abdominal segments frequently with long setae. Premandible always simple .... _Eukiefferiella_ Thienemann

At most one spine present on inner margin of mandible. Oral seta of procercus less strong 43

43 S1 simple, no sclerotised plates between S1 and S11 . 44

S1 bifid, palmate or pectinate; if simple then sclerotised plates present between S1 and S11 46

44 Conspicuous tufts of setae present on abdominal segments of larvae .... _Cricotopus_ v.d. Wulp (part: _brevipalpus_ Kieffer, _elegans_ Johannsen (?=_obnixus_ Walker))

These tufts of setae not present 45

45 S1 thick and heavily sclerotised (Fig. 10d). Procerci very reduced with two procercal setae stronger than remainder .... _Cardiocladius_ Kieffer

S1 normal. Procerci not reduced .... _Tokunagaia_ Saether*

46 S1 bifid, no scales or labral lamellae on labrum 47

S1 palmate or pectinate, if simple or bifid then scales or labral lamella present on labrum 59

47 Mentum with paired median teeth, weakly divided from each other (Fig. 39d). Antennal blade extends well beyond fifth antennal segment .... ? Limnophyes Eaton (part)

Mentum with a single central tooth. Antennal blade not reaching as far as tip of fifth antennal segment... 48

48 Abdominal segments bearing either plumose setae or tufts of setae (Fig. 19f) .... Cricotopus Wulp (part: all of subgenus Isocladius Kieffer, part of subgenus Cricotopus)

Abdominal segments with only simple setae 49

49 Mentum with more than six pairs of lateral teeth ....Orthocladius Wulp (subgenus Euorthocladius Thienemann, part)

Mentum with, at most, six pairs of lateral teeth 50

50 Head capsule brown to dark brown or black 51

Head capsule yellow to yellowish brown 53

51 Antenna with four segments and Lauterborn organs poorly developed (Fig. 55a) .... Orthocladius (subgenus Pogonocladius Brundin)

Antenna five segmented, Lauterborn organs better developed, usually quite distinct 52

52 Head capsule reddish-brown to dark tan coloured .... Orthocladius (subgenus Eudactylocladius Thienemann)

Head capsule lighter brown .... Orthocladius (subgenus Euorthocladius Thienemann)

53 First pair of lateral mental teeth bulbous, broader at the middle of the tooth than at the base (Fig. 61b) .... Paratrichocladius Santos-Abreu
First pair of lateral mental teeth subtriangular or if rounded the greatest width of the tooth is at the base 54

54 Mentum with only five pairs of distinct lateral teeth, the first laterals may have at most a weak lateral notch (Fig. 20e)...Cricotopus (Cricotopus) trifascia group
Mentum with six pairs of lateral teeth, sometimes the second laterals indicated by a distinct lateral notch on the first pair of laterals 55

55 Mandible with distinct spines on the inner margin (Fig. 18c) ... Cricotopus (Cricotopus) bicinctus (?group)
Inner margin of mandible smooth 56

56 Lauterborn organs distinct, as long as third antennal segment (Fig. 51a).......Orthocladius (Orthocladius) part
Lauterborn organs weaker, appreciably shorter than the third antennal segment 57

57 Mandible with strong crenulations on the outer margin. Premandible with two teeth ....
.... Cricotopus (Cricotopus) fuscus group
Mandible with at most weak crenulations on the outer margin. Premandible usually simple, rarely bifid 58

58 Basal antennal segment four to five times as long as wide and antennal blade extending to tip of fifth antennal segment Antenna clearly more than half as long as mandible .... *Cricotopus* (subgenus *Cricotopus*) *tremulus* group
Basal antennal segment between two and four times as long as wide and antennal blade not surpassing the end of the fifth antennal segment. Antenna not more than slightly longer than half the length of the antenna .... *Orthocladius* (subgenus *Orthocladius*, part)

59 Labral lamellae present, elongate, pectinate lobes lying nearly contiguously between the bases of S1 and pecten epipharyngis (Fig. 7c) 60
Labral lamellae, if present eith r simple, or if pectinate then not elongate and widely separated, lying between the bases of S1 61

60 Antenna with four segments, the second apparently divided into two (Fig. 7a) .... *Brillia* Kieffer
Antenna with four segments, the second undivided, longer than the third .... *Eurycnemus* Wulp

61 No labral lamellae or scales 62
Labral lamellae or scales present 69

62 Antenna not reduced, antennal blade extends beyond tip of fifth antennal segment by the same length again (Fig. 35a). Two median mental teeth divided by a J-shaped notch (Fig. 35c) .... *Heleniella* Gowin

Antennal blade only overreaches final antennal segment by as much as this when the antenna is strongly reduced. Median mental teeth divided by a V-shaped notch 63

63 Some setae on the abdomen as long as the length of the abdominal segment bearing the setae 64
No setae as long as this 65

64 Each abdominal segment bearing four long, thin setae. Premandible with four apical teeth... <u>Paralimnophyes</u> Brundin
Premandible with two or three teeth .... <u>Limnophyes</u> Eaton (part)

65 Mentum with a single median tooth with the first pair of laterals closely fused to the median tooth, giving the impression of a trifid median tooth (Fig. 57d) .... <u>Parakiefferiella</u> Thienemann
Mentum not as above 66

66 Mentum with a broad, paler median area. This may be either one broad tooth or several weakly separated teeth. Procercus with a strong dorso-anal spur .... <u>Propsilocerus</u> Kieffer*
Mentum evenly sclerotised with two median teeth. Procercus usually without spur 67

67 Double median tooth of mentum much higher than the first pair of lateral teeth. A small point or tooth is present at the side of the base of the mentum (Fig. 40c) .... <u>Limnophyes</u> Eaton (part)

Median mental teeth at most only slightly higher than first lateral teeth, sometimes (Metriocnemus) much lower 68

68 Antenna subequal in length to the mandible. Lauterborn organs distinct, at least as long as the third antennal segment (Fig. 59a). Ventromental plates present but not extending beyond the flattened mentum (Fig. 59d) .... Parametriocnemus Thienemann

Antenna reduced, less than half the length of the mandible, Lauterborn organs indistinct. Ventromental plates very small to absent .....Metriocnemus Wulp (part)

69 Antenna reduced, no longer than half the length of the mandible .... Metriocnemus Wulp (part)

Antenna normal, subequal in length to the mandible .. 70

70 Lauterborn organs distinct, as long as third antennal segment ....Chaetocladius Kieffer (part)

Lauterborn organs weak and indistinct 71

71 All setae of the seta interna of the mandible broad and plumose. Procerci without a spur. Mentum with paired median teeth much lower than first laterals .. .. Thienemannia Kieffer

At least one seta of seta interna simple. Procercus sometimes with a spur. Median mental teeth lower than, subequal to or higher than first pair of laterals........................Metriocnemus Wulp (part)

British genera with undescribed larvae:

Acamptocladius Brundin, 1956 (submontanus (Edwards)).

Orthosmittia Goetghebuer, 1943 (albipennis (Geotghebuer) and brevifurcata (Edwards))

CHAPTER 6

BIOSYSTEMATICS OF THE LARVAL ORTHOCLADIINAE

1. Introduction

In this chapter all the genera of larval Orthocladiinae which have been recorded from the British Isles are dealt with in alphabetic order of the genera. All species found in the freshwater sites listed in Chapter 3.vi. are described, several for the first time and most in greater detail than hitherto. Original keys to the species are provided within the aquatic genera with more than one British species included. Where an adequate larval description exists for species with aquatic larvae known to be present in Britain from adult records but not found in this survey, the species is included in the key but not described further. The keying of these species must be treated with care since many earlier larval descriptions are inaccurate or erroneous. This is frequently due to the description of larvae with a worn mentum and mandibles or misinterpretation of the structure of the antenna.

Certain genera, notably *Chaetocladius*, *Limnophyes* and *Metriocnemus* are often described as having larvae which are semiterrestrial (living in mosses, *Sphagnum*, damp earth, river banks and the hygropetric zones for example), as well as some which are fully aquatic. The scarcity of larvae from these genera in this survey is surprising in view of the abundance of adults which may be found, but examination of previous surveys of aquatic ecosystems (e.g. Lehmann (1971) and Lindegaard-Petersen (1972)) shows that larval and pupal records of these genera are similarly infrequent. It seems possible that there are fewer aquatic species in these genera than indicated in Fittkau & Reiss (1978) which is based on the opinions of Thienemann in his numerous publications.

These genera are treated in this study in the same way as those genera of terrestrial and marine Orthocladiinae. These are described as fully as possible based upon previously published descriptions, on re-examination of this "historic" material where possible, and examination of the limited material available in the collections of the B.M.(N.H.). From published records it seems that most orthocladiine genera may occur in aquatic habitats however infrequently. For this reason representative species of terrestrial and semiterrestrial genera are illustrated to enable identification with the generic key. In all these cases however the larvae have not been reared and the identity is not therefore confirmed.

For each genus reference is given to the original author of the genus followed by any recent revision containing adequate larval descriptions. The generic diagnosis is based on the British material examined but account is taken of non-British material based on descriptions and examination where possible. Following the generic diagnosis comments are made on related genera and on the postulated phylogeny of the genus. The description of the fourth instar larvae follows the key where there is more than one species in the genus.

In the description all measurements except the body length, which is in mm, are in um. The mean is given first with the range following in parentheses. Where there are numerous specimens a selection were measured including those with the largest and smallest head capsules representing the extremes.

For each species the distributional information is summarised, both within Britain and outside the country. Ecological information is assessed and the evidence from the British material collected in this study is compared with the available information from European studies. Where an author has recently summarised the available distributional and ecological information for a particular species only this reference and more recent data is cited.

ii. *Acricotopus* Kieffer

Acricotopus Kieffer, 1921:90, Hirvenoja, 1973:81.

Type-species *Acricotopus grandis* Kieffer, 1921:90

(= *lucens* Zetterstedt, 1850), by original designation.

GENERIC DIAGNOSIS

Medium sized larvae, up to 8 mm long, head capsule up to 650 um long.

Antenna. Five segmented with segments consecutively smaller and antennal spine not extending to fifth antennal segment. Lauterborn organs present but indistinct. Ring organ weakly indicated in basal third of first antennal segment.

Labrum & palatum. SI basically bifid with the outer branch further divided into three or four fine spines. The inner branch is apparently simple. Other S-setae simple. Pecten epipharyngis of three spines. Labral chaetae and spinulae numerous. Chaetulae laterales and basales simple. Premandible with one sharp tooth and indications of broad, blunt inner tooth.

Mandible with apical tooth slightly longer than combined width of three inner teeth. Seta subdentalis present, seta interna absent.

Mentum with six pairs of lateral teeth. The broad, paler central area can be seen in unworn specimens to consist of four, indistinctly divided median teeth (unlike Fig. 38 (1) of Hirvenoja, 1972: 87). Ventromental plates extend beyond outer mental teeth with distinct setae beneath.

Maxilla. Lamellae on palpiger and galea, a few of the latter are complex, the remainder simple and pointed. Palpiger with distinct sensillae and apical seta. Pecten galearis present. Numerous maxillary setae, some feathered apically. Fine, simple appendix present.

Abdomen. Procercus with 6 or 7 apical setae, lateral procercal setae weak. Anal tubules present and short. Claws of fore parapod serrate, claws of hind parapod simple.

COMMENTS AND PHYLOGENY

Hirvenoja (1973:66) suggests that Acricotopus is the sister group of Paratrichocladius within the group of genera associated with Cricotopus. It is difficult to sustain this belief in view of the presence of a seta interna in Paratrichocladius, contrary to the observations of Hirvenoja (see page 265). Acricotopus has a number of plesiomorphic characters including the wide ventromental plates with setae beneath (resembling Rheocricotopus in this feature) and the long apical tooth of the mandible but the apomorphic characters necessary to determine the relationships of the genus are few. The structure of the SI seta appears to be derived from the bifid SI seta rather than directly from the presumed primitive plumose seta and the absence of the seta interna is also probably apomorphic. However this is of limited use as a generic character since the seta is lost in certain species in several genera including obvius in Psectrocladius and frigidus in Orthocladius. Characters in the adult males and females as well as the pupae indicate that Acricotopus is plesiomorphic within the Cricotopus series of genera and apomorphic amongst the non-Metriocnemini genera. Evidence from larval characters does not refute this but with the larvae from only one species examined it is not possible to examine the relationships in any further detail

Acricotopus lucens (Zetterstedt)

Acricotopus lucens (Zetterstedt, 1850:3574), Hirvenoja 1972:82.

DESCRIPTION OF 4TH INSTAR LARVA (n = 9)

Body length 6.7 mm (5.1-7.8), head capsule length 605 um (550-650). Preserved colour green, head capsule yellow with dark brown or black occipital margin, mentum and apical third of mandible. Premandible brown.

Antenna (Fig. 6a). Five segmented with lengths 81, (74-89); 16, (14-19); 7.7, (6-8); 5.4, (4-6); 4, (3-5). Antennal ratio 2.38, (2.2-2.6). Antennal spine 27, (24-31), subapical spine on 2nd antennal segment 8 - 10 long. Ring organ and sites of antennal spines indistinct.

Labrum & palatum (Fig. 6b). SI 29, (21-34) long, SII 31, (29-34) long, SIII 11, (8-14) long and SIV 8.1, (6-9) long. Simple labral chaetae and spinules present. Chaetulae laterales simple, six or seven present. Two chaetulae basales present. Premandible 112, (108-118) long, with indication of divided apical tooth and long relatively broad inner tooth.

Mandible (Fig. 6c). Length 203, (179-216). Apical tooth slightly longer than inner three teeth. Seta subdentalis 17.6, (16-21) long, characteristically shaped with apical hook. Seta interna absent.

<u>Mentum</u> (Fig. 6d). Flattened mentum width 172, (147-190). Six pairs of laterals and central tooth weakly divided into four teeth. Ventromental plates extend beyond outer mental teeth, setae beneath.

<u>Maxilla</u> (Fig. 4a). Palpiger with long apical seta and distinct sensillae. Galea with simple, pointed lamellae and a few scattered complex lamellae. These are widely distributed in the Orthocladiinae and appear to consist of basally fused setae. Pecten galearis present. 8-10 maxillary setae, the outer two on the row terminally serrate. Small fine appendix present.

<u>Abdomen</u>. Procerci wider at base than apex, and the maximum width greater than the height. Width 51, (34-63), height 47, (30-61). Lower lateral seta stronger than the upper, (but both weak), 114 long, (80-135). 5-7, usually 6, apical setae. Body setation fine and simple. Hind parapod 248 long, (230-265). Anal tubules bluntly oval 124 long, (95-148), and 94 (74-106) wide. Claws on posterior parapod simple, those on anterior parapod serrate with the apical tooth on the smallest claw twice the length of the inner tooth.

<u>MATERIAL EXAMINED</u>

CAMBRIDGESHIRE: Madingley Brick Pits, 29.iii.1978, leg. and det. S.D. Howard. 9 4th instar larvae, 3 3rd instar larvae.

<u>DISTRIBUTION AND ECOLOGY</u>

Hirvenoja (1972:87) summarises the distribution of the species as widespread in Northern and Central Europe extending as far east as Siberia. In Britain the species (based on adults) is widespread.

The species is described by Hirvenoja (loc.cit.) as ubiquitous in small bodies of standing water, and has once been recorded from the marine shore (Kreuzer, 1940:465). Adults fly from March to August.

iii. Brillia Kieffer

Brillia Kieffer, 1913:34; Spärck 1922:70-77.

Type-species Brillia bifida Kieffer, 1913 (= modesta (Meigen, 1830)) by original designation.

GENERIC DIAGNOSIS (Based on reared British modesta and published descriptions of longifurca).

Medium to large sized larvae, up to 8 mm long.

Antenna. Four segmented, the second segment apparently divided with a band of weaker sclerotization in the basal third. No Lauterborn organs at the apex of the second antennal segment , but a subsidiary spine is present subapically on the second segment. Antennal blade extends beyond terminal antennal segment. Ring organ distinct.

Labrum & palatum. SI plumose, remaining S setae simple. Pectinate, elongate labral lamellae present, resembling some Chironomini. Beneath these lamellae, but above the pecten epipharyngis there seem to be a row of blunt teeth (modesta). Pecten epipharyngis of three equal sized scales. Four to six chaetulae laterales on each side. Premandible with two apical teeth and smaller inner tooth.

Mandible. Apical tooth shorter than four inner teeth. Seta subdentalis long, extending beyond third inner tooth. Seta interna present, all branches feathered.

Mentum. Two large median teeth with a small tooth usually between these teeth. Five pairs of lateral teeth with the outer two teeth often closely apressed, and when worn appearing as a single tooth. Ventromental plates absent but a tooth is present basally on the outer mental tooth. Postmental setae withdrawn further basally than usual.

Abdomen. Anterior and posterior pa apods separated and with only simple claws. Two pairs of anal tubules present, shorter than posterior parapods. Procercus higher than wide bearing apical setae.

COMMENTS AND SYSTEMATIC STATUS

The larvae of Brillia modesta, upon which this generic description was largely based has a combination of plesiomorphic and apomorphic characters. The indistinguishable ventromental plates and absence of setae beneath these plates, together with the four segmented antenna (if this is correctly interpreted) are all apomorphic character states within the Orthocladiinae. The structure of the labral setae especially the plumose SI is plesiomorphic and the clear separation of the sclerites of the frontoclypeus and labrum (as in some Chironomini vide Reiss, 1974) is here believed to be plesiomorphic within the Orthocladiinae.

In the absence of further information on the other potentially closely related Orthocladiinae (based on the adult stages) (Eurycnemus, Propsilocerus etc.) the phylogenetic relationships of Brillia must be left open.

KEY TO SPECIES

longifurca Kieffer has not been reared in Britain to the author's knowledge although the adult is almost as frequent as modesta. The characters used by other authors to separate the two species are cited here, but in the author's opinion must be treated with caution since the colouring on the postmentum varies according to the age of the larva, and a pale postmentum may be present in *modesta* shortly after moulting.

1 Dark circular patch on the postmentum (Fig. 7b) ....
.... *modesta* (Meigen)
Postmentum the same colour as surrounding area of head ...
....*longifurca* Kieffer

Brillia modesta (Meigen)

Brillia modesta (Meigen, 1830:256); Spärck, 1922:70-73 (as *bifida* Kieffer).

DESCRIPTION OF 4TH INSTAR LARVAE (n = 10)

Body length 6.5 (4.8-8.5) mm, head capsule length 740 (686-800) um. Head capsule yellow with black mandibles, mentum and occipital margin. Postmentum brown (Fig. 7b). Premandibles and labral margin pale to dark brown.

Antenna (Fig. 7a). Five segmented with lengths 93 (87-97); 7.6 (7-8); 27.5 (24-29); 16.5 (14-18); 5.3 (5-6). Antennal ratio 1.62 (1.58-1.73). The problem of whether there are four segments with a divided second segment (as in *Heleniella* Fig. 35a) or five segments (many authors) is resolved here by the presence of a subsidiary spine on what is assumed to be the second of four antennal segments. In most (? all) cases where a subsidiary spine is present it is on the second segment. This spine may have been confused with a Lauterborn organ by previous workers, but its subapical origin on the segment resembles a spine more than a Lauterborn organ. Antennal spine 64 (61-71) long, subsidiary spine 8 (6-9) long and ring organ 13.7 (12-15) from base of first antennal segment.

Labrum, frontoclypeus & palatum (Figs. 7 c & d). Fronto-clypeus clearly divided into sclerites with differential sclerotisation, resembling Chironomini. SI setae plumose 22 (20-24) long. SII simple c. 26 long, SIII simple c.18 long, SIV present. Labral lamellae distinct with row of blunt teeth beneath and above three scales of pecten epipharyngis. Premandible with two apical teeth and one broad inner tooth, 109 (105-113) long in total.

Mandible (Fig. 7e). 214 (184-234) long with three distinct inner teeth and a fourth tooth less clearly delimited. Seta subdentalis 32 (29-34) long. Seta interna with 6 or 7 feathered branches.

Mentum (Figs. 7 b & f). Two broad median teeth with a small tooth between these. Five pairs of lateral teeth with the outer two closely apressed, the outermost usually higher than the inner. Ventromental plate absent.

Maxilla (Fig. 7g). Strongly developed sensillae on the galea. The shape of the maxillary seta (shaded in Fig. 7g) with fine serration is unusual.

Abdomen. Procerci twice as high as wide, 68 (63-79) high and 31 (21-37 wide, bearing apically (7-) 8 setae maximum length 622 (530-678). Hind parapods 309 (243-392) Anal tubules approximately 100 long by 60 wide. Lateral seta of procercus c. 130 long, supra-anal seta 270 (169-353) long. All claws simple, yellow to light brown.

MATERIAL EXAMINED

Sites 4 (reared), 27 (3 reared), 31 (2 reared, 2 larvae). Also Site 9 .vi.1974 leg. A. Hildrew, KENT: R. Teise, 2½ miles E. Tunbridge Wells, 51/629 385, 6.vii.1975, leg. R.W. Crosskey, 'ex cocoon of Simulium ornatum'; KENT: 1½ m. SSW Lenham, 51/889 504,.1.1976, leg. R.W. Crosskey.

DISTRIBUTION AND ECOLOGY

Brillia modesta is widespread in Northern and Central Europe as well as the Balkans and Siberia. Within Britain it is apparently found very frequently throughout the country.

Thienemann (1954:389) says that it is a characteristic species in springs but it is also found throughout the course of rivers. Lindegaard-Petersen (1972:476) found it at all stations in the Danish lowland stream Linding Å, and Lehmann (1971:478) says that this coldstenothermic rheophilic species attains its highest abundance in the rhithral zone of the Fulda. Although Thienemann (1954:335) notes the species from the hygropetric it has not been seen in standing waters.

iv. Bryophaenocladius Thienemann

Bryophaenocladius Thienemann, 1934:38.

Type-species Spaniotoma muscicola Kieffer, 1906:332 by original designation.

GENERIC DIAGNOSIS (Based on unreared British material, and original material of Strenzke from Stuttgart Museum).

Medium to small sized larvae, up to 6 mm long.

Antenna five segmented with the segments of varying relative lengths. Either the second longer than the first and the fourth longer than the third (Fig. 8a), or the first and second subequal and the third and fourth subequal (Fig. 8b). The antennal spine may extend beyond the fifth antennal segment but is usually somewhat shorter. Lauterborn organs present but not seen to be longer than the third segment. Ring organ present and distinct on first antennal segment.

Labrum & palatum (Fig. 8c). SI simple, often quite dilate or lanceolate. SII shorter but similarly shaped. SIII lying inside SI setae, more anterior than usual. SIV present. Structure of epipharynx difficult to see on specimens examined but apparently as in Fig. 8c. Premandible with three distinct teeth, often darkened.

Mandible (Fig. 8f). Apical tooth shorter than three inner teeth. Seta subdentalis, if present at all, short and blunt. Seta interna absent.

Mentum. Either one broad (Fig. 8e) or two broad (Fig. 8d) median teeth and four pairs of lateral teeth. Ventromental plates distinct, heavily sclerotised, but not extending beyond flattened mentum. Sometimes an indistinct second pair of ventromental plates can be seen. The length and thickness of the setae on the postmentum appears to be of specific value in the genus.

Abdomen (Fig. 8g). Anterior parapods fused without claws but with fine bristles. Posterior parapods present, simple, bearing a variable number of claws, these claws absent in ? *xanthogyna* Edw.. Two pairs of short, broad anal tubules present. Anal tubules and posterior parapods are capable of retraction into the posterior segments of the body, and these segments are at right angles to the axis of the rest of the body. Procercus absent and in most species there are no setae at the posterior end of the body. However in *nidorum* (Edw.) and *nitidicollis* (Goet.) there are spines similar to those of *Gymnometriocnemus* (Fig. 33e).

COMMENTS AND SYSTEMATIC STATUS

Bryophaenocladius and *Gymnometriocnemus* are difficult to separate as larvae and pupae, although the adults are apparently distinct. Strenzke (1952) suggested that because the larva of *Bryophaenocladius nidorum* Edw. showed apparently intermediate characters between *Bryophaenocladius* and *Gymnometriocnemus*, the two genera should be synonymised. Strenzke had overlooked the division of the posterior parapods in *Gymnometriocnemus* which separates all described *Gymnometriocnemus* larvae from *Bryophaenocladius*. This does not necessarily invalidate his suggested synonymy - the character may not be of generic value. The question must remain unresolved until a full revision of the two genera takes place, preferably taking into account species from outside the Palaearctic. Species in these genera are frequent in the South-east Asian tropical forest.

The systematic placement of the genus will be considered along with *Gymnometriocnemus* since they are so closely related. The tendency in both genera for the fourth antennal segment to be longer than the third, as well as the reduction in size of the procerci (absent) and posterior parapods, and the fusion of the anterior parapods clearly place these genera in the Metriocnemini. The reduction in characters of the posterior end of the larva (apomorphic characters) are also found in *Smittia* and the marine Orthocladiine genera as well as *Mesosmittia*, *Pseudosmittia* and *Camptocladius*. The two genera here discussed however retain some apparently plesiomorphic characters within the group of genera mentioned, namely the well developed ventromental plates and the well developed, clearly five segmented antenna. In the latter character the genera resemble *Smittia* more than any other considered genus.

The extension of the preanal segment over the anal segment, and the ability to retract the posterior parapods and anal tubules into the preanal segment also occurs in *Paraphaenocladius*, but since this genus possesses procerci it is believed that the character has risen in parallel and does not indicate a close relationship to *Bryophaenocladius* and *Gymnometriocnemus*.

DISTRIBUTION AND ECOLOGY

No *Bryophaenocladius* were found in aquatic ecosystems in Britain although Strenzke (1942) records *subvernalis* (Edwards) from the shores of Lunzer Unter- and Mittersee. Fittkau and Reiss (1978) note other species from aquatic habitats as well as the more usual terrestrial habitats. *nidorum* (Edwards) is recorded from nests of birds and larvae associated with adults of *xanthogyne* (Edwards) were found in Epping Forest leaf litter (A. Seddon pers. comm.).

v. Camptocladius Wulp

Camptocladius Wulp, 1874:133; Strenzke, 1940:118.

Type-species *Tipula byssinus* Shrank, 1803:76 (= *stercorarius* (Degeer, 1776)) by subsequent designation of Coquillett, 1910:518.

GENERIC DIAGNOSIS

Medium sized larvae up to 5 mm long.

Antenna. Very reduced with only three segments. Antennal blade extending well beyond terminal antennal segment. Ring organ and Lauterborn organs absent or indistinct.

Labrum & palatum. SI and SII bifid, rest simple. Premandible trifid.

Mandible. Apical tooth shorter than four inner teeth. Seta interna absent, seta subdentalis very small.

Mentum. Broad median tooth and four pairs of lateral teeth. Ventromentum indistinct.

Abdomen. Anterior parapods fused, with minute claws. Posterior parapods, procercus, procercal setae and anal setae absent. Anal tubules present.

COMMENTS AND SYSTEMATIC STATUS

The extreme reduction of the antenna and the loss of the procercus and procercal setae as well as the posterior parapods are all apomorphic characters suggesting that this genus belongs in the Metriocnemini, close to genera such as Pseudosmittia, Parasmittia, Mesosmittia and the marine Orthocladiines. Camptocladius shares several apomorphic characters with Mesosmittia including the loss of the seta interna, but many of the apparently apomorphic characters of the larval Camptocladius are a result of the specialised habitat chosen by this genus: cattle dung. The relationships of this genus with those of the other apomorphic Metriocnemini is therefore uncertain.

Camptocladius stercorarius (Degeer)

Camptocladius stercorarius (Degeer, 1776:388); Strenzke, 1940:118.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 6).

Small to medium sized larvae, up to 5 mm long. Head capsule 348 (296-409), yellow with mentum and mandibles brown. Occipital margin deeper yellow than rest of capsule.

Antenna (Fig. 9a). Three segmented with segment lengths 13.2 (11-15); 6.3 (6-7); 2 (1.5-2.5). Antennal ratio 1.62 (1.49-1.80). Ring organ 3-4 from base of first antennal segment. Spine 22 (21-24) long.

Labrum & palatum (Fig. 9b). SI and SII both broad and bifid. SIII and SIV normal. Pecten epipharyngis of three broad scales, other chaetulae (laterales and basales) not visible in any preparation. Premandible trifid 66.7 (62-72) long.

Mandible (Fig. 9f). 106 (92-118) long, combined lengths of four inner teeth greater than outer tooth. Seta subdentalis short, no more than 5 long. Seta interna absent.

Mentum (Fig. 9e). 94 (84-108) wide. Median tooth as broad as wide as the four pairs of lateral teeth. Ventromentum not extending beyond outer lateral tooth.

Maxilla (Fig. 9g). The palp is divided into an outer and an inner part both bearing sensillae. In this feature *Camptocladius* resembles the Tanytarsini (Mozley, 1971, Fig. 4).

Dorsal surface of head. As shown in Fig. 9a there is a heavily sclerotised projection lying outside the base of the antennae in the flattened head capsule. In an unflattened head capsule this projection points ventrally and lies inside the base of the mandible (Fig. 9c - shown as a dark structure anterior to the eye). The function of the structure is unknown, and has not been seen in any other species.

Abdomen (Figs. 9c & d). Anterior parapods fused with fine spines. Posterior parapods, procerci and procercal setae absent. Anal tubules present 30 - 35 wide by 50 - 60 long. No body setae present.

MATERIAL EXAMINED

CAMBRIDGESHIRE: Cambridge, 25.viii.1922, L.G. Saunders, B.M. 1922-403 (5 larvae), No data except "old dung"- believed to be from B.R. Laurence (4 larvae).

DISTRIBUTION AND ECOLOGY

Camptocladius stercorarius is a widely distributed species occurring throughout Europe. It is also found in Greenland, Alaska and many states of the U.S.A. The larva is usually found in cow pats (Strenzke, 1950:361, Laurence, 1951, 1954).

vi. Cardiocladius Kieffer

Cardiocladius Kieffer, 1912:22; Saunders 1924:227-231.

Type-species Cardiocladius ceylanicus Kieffer, 1912 by original designation.

GENERIC DIAGNOSIS

Medium to large larvae, up to 11 mm long.

Antenna five segmented with segments consecutively shorter, or three and four subequal. A single Lauterborn organ present on the second antennal segment. Antennal blade extends up to or beyond fourth antennal segment. Ring organ distinct.

Labrum. All S setae simple. Pecten epipharyngis with three scales, the median one larger than the outer two. Premandible distinctive, heavily sclerotised with a trace of two blunt apical teeth and stout triangular inner tooth. Labral margin heavily sclerotised.

Mandible. Apical tooth shorter than four (always ?) inner teeth. Seta interna and seta subdentalis present. On some specimens there appears to be a plumose spine on the inner edge of the mandible.

Mentum. One broad median tooth with five pairs of lateral teeth. The outer part of the mentum is heavily sclerotised. Ventromental plates weakly sclerotised and may extend beyond mentum.

Abdomen. Anterior parapods fused basally with two crowns of claws. Procerci very small bearing two long and a variable number of smaller apical setae. Anal segment reduced so that procerci are placed just above the anal papillae. Anal papillae shorter than the well developed posterior parapods.

COMMENTS AND SYSTEMATIC STATUS

The larvae of Cardiocladius are strongly modified for living in fast flowing waters and resemble the Diamesinae in several characters notably the reduction of the procercus to a sclerotised ring, and the shortened antennae, while the inferred predatory nature of the larva (on Simuliidae) may explain the irregular heavy sclerotisation on the mentum, premandible and labrum.

For the reasons stated above the phylogeny of the genus is difficult to ascertain and Saether (1977:86) suggests that the simple SI seta is a synapomorphy for the genera Cardiocladius, Eukiefferiella and Tokunagaia. The premandibles in these three genera are similar being broad and blunt, and the seta on the mandible in Cardiocladius might be homologous with the spines present in many Eukiefferiella, but more positive proof of the relationships must rest with other stages, particularly the pupae which show greater similarities.

KEY TO SPECIES

(Note: fuscus description is based upon four specimens all of which show distinct signs of wear, while capucinus is based on a single larva. This key is therefore highly tentative)

1 First antennal segment less than 60 µm long, antennal ratio below 2. Mentum somewhat squared off with first laterals subequal to broad median tooth (Fig. 10e) .... fuscus Kieffer

First antennal segment greater than 60 µm long and antennal ratio greater than 2. Mentum more triangular in shape with the first laterals lower than the broad median tooth (Fig. 10f) ....capucinus (Zetterstedt)

Cardiocladius fuscus Kieffer

Cardiocladius fuscus Kieffer, 1924:72; Saunders 1924:229; Thienemann 1932:82-84.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 4) (Based on larvae associated with pupae and adults reared from these larvae by F.W. Edwards)

Body length 8.6 (8.3-8.9) mm, head capsule 586 (572-604) µm. Head capsule yellow brown with dark brown to black mentum, mandible, premandible and labral margin.

Antenna (Fig. 10a). Five segmented with lengths 55 (50-58); 13.8 (13-15); 6; 6 (5-6); 4.8 (4-5). Antennal ratio 1.8 (1.67-1.93). Ring organ 7 - 10 from base of first antennal segment. Antennal spine 26-29 long. Lauterborn organs present.

Labrum & palatum (Fig. 10d). All S setae simple, SI more heavily sclerotised than usual about 25 long. Pecten epipharyngis of three scales, the median one twice the length of the two laterals. Premandibles heavily sclerotised with trace of second apical tooth and distinct triangular inner tooth. Length of premandible 94 (89-98).

Mandible (Fig. 10b). 159 (150-168) long with the outer tooth shorter than the inner four combined. Sometimes the innermost tooth is less distinct. Seta interna with common base extending for half the length and five plumose setae apically. Seta subdentalis 7 (5-10) long. On the inner margin of the mandible in three of the four specimens examined there is a 25 µm long serrate margined seta. In all specimens the mandible is worn and this seta may be lost rather easily.

Mentum (Fig. 10e). 150 (140-158) wide, subrectangular in shape (though all specimens are more or less irregularly worn). One broad median tooth with five distinct lateral teeth (unlike Saunders 1924: Fig. 6; Pankratova 1970:126 based on a symmetrically worn specimen). Postmental setae apparently absent.

Abdomen. Unusual in the Orthocladiinae known to the author in that the anal segment is vestigial or absent, and the procerci lie directly above the anal tubules and posterior parapods. The procerci are very small, broader than high, and bear two strong setae and two or three finer setae. It is not possible to distinguish a lateral procercal seta. Hind parapods 344 (286-380), anal tubules 100 - 150 long by 65 - 90 wide. Maximum length of the procercal setae 258 (233-296). All claws simple. Anterior parapods fused basally but separate groups of claws at the apex.

MATERIAL EXAMINED

BUCKINGHAMSHIRE: near Denham, River Colne, no date, F.W. Edwards (4 larvae).

DISTRIBUTION AND ECOLOGY

Both species of Cardiocladius recorded from Britain will be dealt with here since the data for both are very similar, and inadequate distributional information exists to warrant separation.

Adult fuscus are only known in Britain from the locality cited above from whence it was reared by F.W. Edwards. In Europe it is only known from a few sites in western Europe, including the River Fulda (Lehmann 1971:478). capucinus is known in Britain from the larval site in Devon and Durham, and as adults from Yorkshire: Whernside and three localities in Perthshire. In Europe the species is more widely distributed with further records from Scandinavia and the Alps. Tokunaga (1939) records both capucinus and fuscus from Japan.

Thienemann 1954:58 notes that many of the larval records of Cardiocladius are in association with Simulium colonies and surmises that all Cardiocladius may be so associated. Although not noted by Edwards (1924) or Saunders (1924) there are many head capsules of Simulium incorporated into the larval and pupal cases of both species described by these two authors, and they do note that the immatures occur in regions of high flow rate where one would expect to find Simuliidae. The apparent absence of this genus from any collections seen by the author is unexpected unless the genus is rare, and not restricted simply by the presence of simuliid larvae. Tokunaga (1939:310) records capucinus from torrents in Japan, and it may be that the genus is restricted to faster flowing water than is usually encountered in most of Britain.

Cardiocladius capucinus (Zetterstedt)

Cardiocladius capucinus (Zetterstedt 1850:3499); Saunders 1924:229, Tokunaga 1939:310).

DESCRIPTION OF 4TH INSTAR LARVA (n = 1, larva associated with pharate pupae reared by F.W. Edwards). As fuscus except: Body length 6.8 mm, head capsule length 520 µm. Head capsule yellow with brown to dark brown mentum, mandible, labral and occipital margin and premandibles.

Antenna. Five segmented like fuscus but segment lengths 71; 16; 6; 6; 5, antennal ratio 2.5. Antennal spine 27 long, ring organ 8 from base of first antennal segment.

Labrum. As in fuscus, premandible 92 long.

Mandible (Fig. 10c). 182 long apparently thicker than fuscus but specimen is slightly tilted. No seta is visible on the inner margin, although Tokunaga (1939) may be describing this, or the seta interna.

Mentum (Fig. 10f). More triangular in shape than fuscus. Width 118.

Abdomen. As in fuscus. Longest procercal seta 233. Procercus bearing two strong and two or three finer setae.

MATERIAL EXAMINED

DEVON: River Dart, 2.vi.1920, F.W. Edwards (1 larva associated with pupae).

DISTRIBUTION AND ECOLOGY

See under fuscus Kieffer (Page 90).

vii. Chaetocladius Kieffer

Chaetocladius Kieffer, 1921:182.

Dyscamptocladius Thienemann, 1921:833.

Type-species Dactylocladius setiger Kieffer, 1908:36 (= perennis Meigen) by subsequent designation of Thienemann, 1938:90.

GENERIC DIAGNOSIS (based on unreared larvae cited below in Material Examined)

Medium sized larvae, up to 9 mm long.

Antenna.(Fig. 11a). Five segmented with the fourth segment subequal to, or longer than the third. Antenna frequently shorter than the mandible but never strongly reduced. Distinct Lauterborn organs present. Antennal blade frequently extends beyond the fifth segment. A distinct ring organ present and often a clear mark of setal insertion on the first segment.

Labrum & palatum (Figs. 11 b & c). SI setae plumose, the remainder simple. SIV well developed. Distinct labral lamellae present between or below the bases of the SI setae, these lamellae can be either pectinate (Fig. 11b) or simple (Fig. 11c). Numerous, frequently serrate labral chaetae. Pecten epipharyngis of three subequal spines. Four or five simple chaetulae laterales, two simple chaetulae basales, often not extending beyond the overlying chaetulae laterales. Premandible with (? always) two apical teeth with one or two blunt inner teeth and no premandibular beard.

Mandible (Fig. 11d). Apical tooth shorter than the combined width of the three or four inner teeth. Seta subdentalis present. Seta interna with five or six fairly strong branches, each terminally serrate.

Mentum (Fig. 11e). One or two median teeth, if paired these are only weakly divided. Five pairs of laterals. Ventromental plates distinct, often extending beyond the outer lateral mental teeth, without setae beneath.

Maxilla (Fig. 11f). Apparently quite variable in structure. Palpiger with strongly developed sensillae. Lamellae on palpiger and galea simple, but there may be a few complex setae on the galea. Maxillary seta (? always) simple. Pecten glaearis present only in dentiforceps (Edwards) of those species examined.

Abdomen. Procerci distinct, higher than wide and bearing apically six or seven setae. These setae are often no longer than the posterior parapods. Anterior and posterior parapods present, fully divided and bearing usually simple claws. Lateral seta of procercus short, supra-anal seta long. Two types of anal tubules observed in the genus. In some species the anal tubules are subequal to the anterior parapods, medially constricted and terminally pointed, in others the tubules are short and rounded. No long body setae.

COMMENTS AND SYSTEMATIC STATUS

Chaetocladius appears to be a well defined genus in the adult stage but the larvae and pupae are too poorly known to state whether this is the case in these stages. The four species examined as larvae show quite large variation in labral lamellae, maxillae and anal tubules and the genus may be more variable in the larvae than in the adults. One of the problems with defining the genus is that they possess many plesiomorphic characters including the plumose SI, distinct labral lamellae, distinct ventromental plates, strong procerci and fully separated parapods. No unique apomorphic character has been found for the larval *Chaetocladius* examined which makes the generic diagnosis difficult.

The antennal structure with the elongate fourth segment relative to the third indicates that the genus belongs in the Metriocnemini and the plesiomorphic characters mentioned in the preceding paragraph indicate that the genus is amongst the more primitive genera in this tribe. *Chaetocladius* can be separated from all *Metriocnemus* and *Thienemannia* by the distinct ventromental plates and the absence of a beard on the premandibles. There may also be differences in the structure of the labral lamellae: in *Chaetocladius* they lie between the SI and the labral margin while in *Metriocnemus* they lie between the SII and SI, or between the SI setae. Those *Chaetocladius* with pectinate labral lamellae can be separated from all other plesiomorphic Metriocnemini with distinct labral lamellae by the structure of the labral lamellae but those *Chaetocladius* with simple labral lamellae may be confused with *Hydrobaenus*. The only character suggested for separation is on the relatively large sized lamellae in *Chaetocladius*, larger than in *Hydrobaenus*.

For comments concerning the scarcity of larvae of *Chaetocladius* in the aquatic habitats samples in this study see page 72. It is clear that the taxonomy and ecology of the genus is in need of detailed study, although no species appear to be frequent in aquatic habitats.

MATERIAL EXAMINED

dentiforceps (Edwards); larvae "associated" with adults by J.P. Ducrotoy

dissipatus (Edwards); larvae determined by D. Bryce.

perennis Meigen; larva determined as *pentachaetus* (Kieffer) by A. Thienemann.

suecicus (Kieffer); larvae determined by Thienemann.

sp. indet. Site 33. 2 unreared larvae.

All larvae unreared.

viii. Clunio Haliday

Clunio Haliday, 1855:62; Strenzke, 1960 :13.

Type-species *Clunio marinus* Haliday, 1855:62 by monotypy.

GENERIC DIAGNOSIS

Medium sized larvae, up to 6 mm long.

Antenna (Fig. 12a). Five segmented, the first segment about as high as wide, the second subequal in height to the first but narrower. The fourth segment subequal to or longer than the third. Antennal spine divided, the outer spine not extending to the fifth segment, the fine inner spine only slightly shorter than the outer. Small subsidiary spine on the apex of the second segment. Lauterborn organs very small and indistinct. Distinct ring organ in apical half of the first segment.

<u>Labrum & palatum</u> (Fig. 12b). SI seta plumose with ten or more branches. SII finer, also plumose with fewer branches. SII and SIV normally developed. Labral lamellae present, weakly sclerotised, each divided into a number of spines. Both serrate and simple labral chaetae present. Pecten epipharynx of three small basally fused scales. Four or five simple chaetulae laterales with one broad one overlying the bases of the others. Two serrate chaetulae basales present. Premandible with a blunt apical tooth and a broad blunt inner tooth.

<u>Mandible</u> (Fig. 12c). Apical tooth shorter than combined width of three inner teeth. Seta subdentalis present. Seta interna with five or six strong plumose branches.

<u>Mentum</u> (Fig. 12d). One domed median tooth twice the width of the first laterals. Four pairs of laterals evenly decreasing in size. Ventromental plates present, weak, not extending beyond the outer teeth of the flattened mentum.

<u>Maxilla</u> (see Strenzke, 1960:Fig. 27). Two strong setae on apex of palpiger. Sparse simple lamellae on palpiger and galea. Maxillary setae weakly serrate. No pecten galearis. Galear sensillae weak. Distinctive setose appendix present.

<u>Abdomen</u> (Fig. 12e). Anterior parapods partially fused basally. Posterior parapods separate with several simple claws. Procercus absent, but in their place a single strong seta on each side. Anal tubules absent. Supra-anal seta present.

COMMENTS AND SYSTEMATIC STATUS

Clunio, together with most of the genera of marine Chironomidae, such as _Thalassosmittia_, _Eretmoptera_, _Belgica_, _Tethymyia_, _Thalassomya_, _Telmatogeton_, _Paraclunio_, and _Halirytus_ were placed in a subfamily the Clunioninae by most authors until Strenzke (1960). Strenzke showed that these genera previously placed in the Clunioninae were not closely related but were divisible into two groups. Wirth (1949) had already reached the same conclusion and named the e groups the Telmatogetonini (_Paraclunio_, _Halirytus_, _Telmatogeton_ and _Thalassomya_) and the Clunionini (the remaining genera cited above). Strenzke went further than Wirth in recognising that the characters of the adult stage which apparently united the two groups were related to their marine habits and examination of the immature stages showed that the "Clunionini (inae)" were in fact the sister group of the terrestrial genus _Smittia_, and thus did not warrant supra-generic ranking. Although the observations of Strenzke have not been disputed the nomenclatural conclusions have not been accepted by all workers. An example of the confusion prevalent is Hashimoto (in Cheng, 1976) who, in a review of marine Chironomidae, referred to a subfamily Clunioninae and a subfamily Orthocladiinae with the genus _Thalassosmittia_ excluded from the tribe Telmatogetonini within the Orthocladiinae.

Saether (1977:86) concurs with Strenzke's (loc.cit.) conclusions about the phylogeny of the groups centred on _Clunio_ but adds little substantial phylogenetic evidence of the relationships within the group. Two suggested synapomorphies for the group are the absence of anal tubules and the marine nature of the larvae, but this is likely to be the same trend since anal tubules are usually lost in marine species. It is however likely that a single marine ancestor has given rise to the present "Clunio-group".

Clunio marinus Haliday

Clunio marinus Haliday, 1855:62; Strenzke 1960b:13.

The single British species can be recognised from the generic description and figures. The larvae are frequent in rockpools in the mid-littoral zone of shores in the south and west of Britain.

ix. Corynoneura Winnertz

Corynoneura Winnertz, 1846:12.

Type-species Corynoneura scutellata Winnertz, 1846, by designation of Coquillett (1910:528).

GENERIC DIAGNOSIS

Small larvae, no more than 3 mm long.

Antenna (Fig. 13a). Four segmented, third segment longer than the second and the fourth minute. Second and third segments frequently darkened. Lauterborn organs indistinct or absent and antennal spine narrow and weak. Ring organ distinct with a darkened central spine. Distinct marks of origin of two setae on the first antennal segment. Whole antenna subequal to, or longer than head capsule.

Labrum (Fig. 14a) and palatum (Fig. 14b). SI setae strongly developed simple, arising from a distinct socket. All other S setae simple. Labral chaetae indistinct or absent. Pecten epipharynx of five subequal spines. Only two pairs of chaetulae laterales, strongly modified. The anterior pair are large and strongly plumose, the posterior (and inner) pair are large and serrate. No chaetulae basales. Premandible (Fig. 14c) with up to twelve minute apical teeth and a strongly developed but translucent beard which can be seen to extend laterally from the premandible

Mandible (Fig. 13c). Apical tooth lying outside the line of the remaining four inner teeth and scarcely longer than any of the inner teeth. Seta subdentalis absent. Seta interna absent, but a group of setae lying on the dorsal side of the palpiger look like the seta interna until the mandible is detached from the head capsule.

Mentum (Figs. 15 a-e). Triangular shaped with either two or three median teeth and five laterals. Ventromental plates absent, no setae beneath.

Maxilla (not figured). Very small and difficult to interpret. Palpiger with normal sensillae. Maxillary setae numerous and apparently simple. Dorsal side of palpiger with fine, translucent setae resembling a seta interna, but apparently attached to the maxilla when the mandible is removed.

Abdomen. Two thoracic segments, the meso- and metathoracic segments being fused. Procerci small bearing four apical setae. Anterior parapods elongate, relatively longer than in any other Orthocladiinae examined. Posterior parapods also elongate. Anal tubules shorter than the posterior parapods, tapering to a point. A variably developed seta (Fig. 13d) arises from the ventral basal side of the posterior parapod. This seta is usually basally plumose, sometimes dark brown and up to half the length of the posterior parapod.

COMMENTS AND SYSTEMATIC STATUS

The larvae of Corynoneura and Thienemanniella are very similar and all stages of these two genera (and the doubtfully distinct non-British Corynoneurella) are quite distinct from the other Orthocladiinae. These differences have in the past led to their placement in a separate subfamily the

Corynoneurinae or tribe Corynoneurini. Since rundin (1956) the "*Corynoneura*-group" has been recognised as the most apomorphic group of the Orthocladiinae. This finding was confirmed by chlee (1968) using phylogenetic analysis and later also by Saether (1977:86).

Larval *Corynoneura* have not been adequately described before and the apparently distinctive characters of the mentum have not been noted previously. Many of the characters found useful in other genera including the labrum, mandible and palatum have not been found to be valuable in this genus and have not been figured for each species.

Of potentially great im ortance in the genus is the modification of the chaetulae laterales of the palatum and the premandibular beard into broad very finely divided branches. This may be indicative of filter feeding in the larvae of this genus. Further investigation including electron microscope studies of the very small parts involved is necessary before any further conclusions can be drawn.

KEY TO THE KNOWN SPECIES OF LARVAL *CORYN NEURA*

1 First lateral teeth of the mentum strongly reduced (Figs. 15 a, c & e) 2

All lateral mental teeth subequal (Fig. 15 b & d) ... 4

2 Only two median mental teeth (Fig. 15a). First antennal segment greater than 200 um ...*coronata* Edwards

Three median mental teeth (Figs. 15 c & e). First antennal segment less than 200 um 3

3 Central median mental tooth small (Fig. 15c). First antennal segment more than 130 um long ....lobata Edwards

Central median tooth larger (Fig. 15e). First antennal segment less than 120 um .... species A.

4 Second and third antennal segments strongly darkened. Median of three mental teeth distinct (Fig. 15b) .... lacustris Edwards

All antennal segments pale. Median of three mental teeth very small, sometimes absent (Fig. 15d) ....scutellata Winnertz

celeripes Winnertz may be separable on the position of the ring organ very low on the first segment, unlike the higher position in all the species examined in this study.

The larvae of the British species carriana Edwards, celtica Edwards and edwardsi Brundin are unknown, and the species fuscihalter Edwards and minutissimus Meigen are doubtfully valid.

gratias Schlee has been seen by the author (S.D. Howard coll.) but has not yet been added to the British list, nor has the larva been described.

Corynoneura coronata Edwards

Corynoneura coronata Edwards, 1924:187.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 10).

Small larvae 1.7 - 2.0 mm (n = 3), head capsule 307 (270-334) um, pale brown with the occipital margin scarcely darkened and the mentum, labral margin, basal premandible and apical part of the mandible darker brown. First antennal segment yellow, second pale brown, third and fourth dark brown. Sculpturing on dorsal and lateral sides of head as in Fig. 14d resembling scales with uneven anterior edge slightly raised.

Antenna. Four segmented, lengths 210 (190-219); 81.7 (77-85); 95.4 (90-103); 2.7 (2-4). Antennal ratio 1.18 (1.15-1.25). Site of insertion of proximal seta 116.7 (108-127) and dorsal seta 145.3 (130-159) from base of first antennal segment. Weak antennal spine about 40 long. Ring organ 98 (84-106) from base of first segment.

Labrum & palatum (Fig. 14b). As in generic diagnosis. No specific differences observed. Premandible 29 - 35 long with up to 10 fine teeth.

Mandible. 58.7 (55-63) long with an outer tooth and four inner teeth. Seta interna and seta subdentalis absent.

Mentum (Fig. 15a). Flattened width 33.6 (30-36). Two median teeth and five pairs of laterals. The first pair of laterals are strongly reduced compared with the second.

Abdomen. Procercus 10 (9-11) long by 11 (8-13) wide bearing apically four setae of maximum length 234 (212-318). Hind parapods 195 - 212 (n = 2) bearing simple yellow claws. Anterior parapods bearing yellow claws with apical serrations. Anal tubules 77 (66-95) long by 19 (16-25) (n=3), apically pointed. Seta on base of posterior parapod 72 (69-79) long, strongly plumose at the base, but quite variably developed.

MATERIAL EXAMINED

Site 32 (1 reared); Site 40 (8 larvae, 5 reared); 44 (1 reared).

DISTRIBUTION AND ECOLOGY

Schlee (1968:26) notes that specimens are known only from England, Germany and Sweden and believed the species to be rare. In Britain the species is only known from the type series from Suffolk and Bedfordshire.

Brundin (1949:503) found the species in humic lakes of maximum depth 16 metres and no larger than 1 square kilometer. The finding of this species in slowly flowing lowland rivers suggests that the species may have been overlooked in lotic surveys and may be more frequent than previously believed.

Corynoneura lacustris Edwards

Corynoneura lacustris Edwards, 1924:187.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 7)

Body length unmeasured (all exuviae), head capsule 336 (318-345), pale yellow brown, occipital margin dark brown with head capsule somewhat darker towards the occipital margin. Mandible, mentum and labral margin dark brown. First antennal segment yellow, second and third dark brown. Apex of third segment and fourth segment very pale. Sculpturing on dorsal head capsule weak stippling.

Antenna. Four segmented, lengths 263 (246-290); 135.5 (132-143); 143.1 (127-153); 2.6 (2-3). Antennal ratio 0.94 (0.91-0.98). Site of insertion of proximal seta 148 (137-159) and dorsal seta 203 (182-220) from base of first antennal segment. Ring organ 140 (132-151) from base of first segment. Antennal spine weak, about 45 long.

Labrum (Fig. 14a) & palatum. As in generic diagnosis, no specific differences noted. Premandible (Fig. 14c), 31 - 34 long with up to 12 minute teeth.

Mandible (Fig. 13c). 61.7 (56-66) long with a single outer tooth and four inner teeth. Seta interna and seta subdentalis absent.

Mentum (Fig. 15b). Three median teeth, the central one only slightly smaller than the outer two. Five pairs of lateral teeth, subequal in size.

Abdomen. Procerci 11 - 13 high by 11 - 13 wide bearing apically four setae of maximum length 240 (212-270). Parapods not measured in exuviae, all claws yellow and simple. Anal tubules unmeasurable. Seta at base of posterior parapod 60.7 (58-63) long, basally plumose. Translucent body setae on body up to 53 long.

MATERIAL EXAMINED

Site 41 (5 all reared); Site 45 (1 reared); Site 47 (1 reared).

DISTRIBUTION AND ECOLOGY

Schlee (1968:24) states that the species is only known with certainty from Britain, Germany and Sweden. In the British Museum (Natural History) there are specimens from North Wales, Scotland and Northern England. The species appears to be restricted to standing water or slowly flowing rivers, particularly in marginal stretches with almost stationary water.

Corynoneura lobata Edwards

Corynoneura lobata Edwards, 1924: 86.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 10).

Small larvae, no more than 4 mm long. Head capsule 282 (259-297), pale yellow to pale brown. Occipital margin darkened, mentum, mandibles and labral margin brown.

Second to fourth antennal segments evenly dark brown or black.

Antenna (Fig. 13a). Four segmented, lengths 159 (134-172); 76 (72-80); 83 (76-91); 4.3 (4-5.5). Antennal ratio 0.98 (0.85-1.10). First seta inserted 88 (84-95) and second seta inserted 128 (110-145) from base of first antennal segment. Ring organ 81 (74-87) from base of first segment. Antennal spine weak, frequently damaged, 35 - 45 long. No subsidiary spine present.

Labrum & palatum. As in generic diagnosis. No specific characters noted. Premandible 27 - 31 long, with a single apical tooth.

Mandible. Apical tooth no longer than the first inner tooth and slightly displaced outwards. Four inner teeth. No seta subdentalis, apparent seta interna is on the dorsal surface of the maxilla.

Mentum (Fig. 15c). Flattened width 30.7 (29-33). Three median teeth, the middle tooth smaller than the other two. The first laterals reduced in size compared with the second of five laterals. Ventromental plates absent without setae beneath.

Abdomen. Procerci small, 8 - 10 high by 6 - 9 wide with small, fine lateral setae and bearing apically four setae of maximum length 166 (137-188). Anterior and posterior parapods long but not measurable in exuviae. Claws simple, yellow. Seta at base of posterior parapod (Fig. 13d) 60 (51-64) long. Translucent setae on the body 59 (48-68) long.

MATERIAL EXAMINED

Site 4 (2 reared); Site 29 (1 reared); Site 35 (7 reared); Site 43 (1 reared); Scotland, R. Endrick, leg. P. Maitland (3 larvae); Site 9, no date, leg. A. Hildrew (many larvae).

DISTRIBUTION AND ECOLOGY

Schlee (1968:47) records the species only from England and Germany. The type-series in the British Museum (Natural History) comes from Devon, Hertfordshire, Cambridgeshire, Arran, and North Wales. Lehmann (1971:492) found the species in the river Fulda from springs down to the metarhithral, and Schlee (loc.cit.) noted that the species was not found in any of the intensive surveys of north German and Swedish lakes. All the sites in which *lobata* was found in this survey are lotic and in most streams and small rivers *lobata* was the most abundant *Corynoneura*.

Corynoneura scutellata Winnertz

Corynoneura scutellata Winnertz, 1846:13.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 6).

Body length 2.4 mm (n = 1), head capsule 336 (312-360) um (Fig. 13b), yellowish brown, occipital margin scarcely darkened, mentum, apical part of mandible, labral margin and basal part of premandible darker brown. All antennal segments yellow, no apical darkening. Head capsule sculpturing of regularly arranged stippling (Fig. 14e).

Antenna. Four segmented, lengths 264.7 (240-291); 119.4 (111-130); 125.0 (116-130); 2.9 (2-4.5). Antennal ratio 1.08 (1.00-1.16). Site of insertion of proximal seta 145.5 (138.153) and dorsal seta 192 (188-198) from base of first antennal segment. Ring organ 130 (127-135) from base of first segment. Antennal spine weak, not measured.

Labrum and palatum. As in generic diagnosis, with no specific differences noted. Premandible 39 (37-41) long with up to 12 small teeth apically and the beard more distinct than in other species examined.

Mandible. 71.2 (68-76) long with an outer tooth and four inner teeth.* Seta interna and seta subdentalis absent.

Mentum (Fig. 15d). Flattened width of mentum 45.6 (45-47). Either two or three pairs of median teeth, if three the central one is weakly developed. All five pairs of lateral teeth subequal in size.

Abdomen. Procerci 10 - 11 by 11 - 12 (n = 2) bearing apically four setae of maximum length 301 (280-339). Hind parapod 232 - 238 long (n = 2), all claws yellow and apparently simple. Anal tubules not measurable. Seta at base of posterior parapod strongly plumose at base and 72 (63-79) long. Longest body seta 55 long.

MATERIAL EXAMINED

Site 17 (5 larvae, 4 reared); Site 30 (1 reared).

DISTRIBUTION AND ECOLOGY

Fittkau and Reiss (1978:415) indicate that this is the most widely distributed of the Palaearctic Corynoneura with records from most zones of the Palaearctic and also from Greenland. Records from prior to Schlee's (1968) revision must be treated with caution, however this does appear to be a common species in Europe and there are specimens from throughout Britain in the British Museum (Natural History).

The species appears to be restricted to lenitic habitats including Lunzer See and Bodensee (Reiss 1968:246).

Corynoneura species A.

Corynoneura species A.

DESCRIPTION OF 4TH INSTAR LARVA (n = 1 exuvium)

Body length not measurable in exuvium. Head capsule 249 long, yellowish brown, occipital margin slightly darker, mentum, mandible, labral margin and apical part of premandible brown. Head capsule smooth.

Antenna. Four segmented, lengths 100; 45; 64; 2.5. Antennal ratio 0.90. Site of insertion of proximal seta 53 and of distal seta 76 from base of first antennal segment. Ring organ 42 from base of first segment.

Labrum & palatum. As in generic diagnosis with no specific differences observed. Premandible 27 long with ten apical teeth and a fine beard extending laterally from the premandible.

Mandible. 47 long with one outer tooth and four inner teeth. Seta interna and seta subdentalis absent.

Mentum (Fig. 15e). Flattened width 26. Three median teeth with the central tooth only slightly smaller than the outer ones. Five pairs of lateral teeth with the first pair of laterals smaller than the rest.

Abdomen. Procerci 8 high by 8 wide, bearing apically four setae of uncertain length (all broken). Seta below posterior parapod 39 long, basally plumose. Longest body seta 66, thin and dark.

MATERIAL EXAMINED

Site 50 (1 reared).

COMMENTS

The adult male Corynoneura reared from this larva appears to be undescribed using the key of Schlee (1968). There are only ten antennal flagellomeres and the final flagellomere is as long as the three preceding flagellomeres. The internal structure of the hypopygium which is of considerable value in species determination in the genus, is different from any specimens examined, or figured by Schlee (loc.cit.).

The larval antenna is quite different from any other larvae seen and it is suggested that this may be an undescribed species of *Corynoneura*.

x. *Cricotopus* v.d. Wulp

Cricotopus v.d. Wulp, 1874:132; Hirvenoja, 1973:131.

Trichocladius Kieffer, 1906:356 (nomen dubium Brundin, 1956:114) (partim)

Isocladius Kieffer, 1909:44.

Eucricotopus Thienemann, 1936:200.

Type-species *Chironomus tibialis* Meigen, 1804:16 designated by Coquillett, 1910.528.

GENERIC DIAGNOSIS (modified from Hirvenoja, 1973:131).
Medium sized larvae up to 8 mm long, head capsule up to 700 um long.

Antenna. Five segmented with the third and fourth segments subequal. Lauterborn organs variably developed, often distinct, absent when the first antennal segment is strongly reduced (*brevipalpis*). Antennal blade usually not extending beyond the fifth antennal segment. ubsidiary blade usually distinct. Ring organ on the basal third of the first antennal segment.

Labrum. SI seta bifid, rarely simple (*obnixus* and *brevipalpis*), other S setae simple. SIII often as long as SII. Pecten epipharyngis either three subequal smooth scales (subgenus *Cricotopus* s.s. Fig. 19b) or one fused plate (subgenus *Isocladius* Fig. 23b). Labral chaetae numerous, simple or serrate. Chaetulae laterales often numerous, either simple or terminally toothed, sometimes (e.g. *Cricotopus* (*I.*) *trifasciatus* Fig. 23b) the first pair of chaetulae laterales are broad and resemble the fused scales of the pecten epipharyngis. Premandible with one or two apical teeth and there may be a brush on the inner margin.

Mandible. Apical tooth shorter than combined width of three inner teeth. Seta subdentalis present, seta interna present in all species except brevipalpis. Outer margin of mandible frequently with crenulations. Inner margin smooth, or with spines (bicinctus and species A).

Maxilla. Hirvenoja (loc.cit.) shows that the distribution and shape of the lamellae on the galea and the antaxial setae are of taxonomic importance in this genus. A feature not noted by Hirvenoja is that the pecten galearis is always absent.

Mentum. One median tooth of variable width and six pairs of lateral teeth rarely reduced to five. Ventromental plates very small mostly without setae beneath but some specimens show a few fine setae.

Abdomen. Parapods present, anal tubules of variable lengths. Claws on anterior parapods often with teeth, the shape of which can be taxonomically important. Procercus about as high as wide, bearing apically six or seven setae.

All species of Isocladius and most species of Cricotopus have a complex setal brush on the abdominal segments I-VI or VII. The relative lengths and distribution of the setal brush is an important character in larval identification.

COMMENTS AND SYSTEMATIC STATUS

Hirvenoja (1973) carefully examines the relationships of the genera centred on Cricotopus and there is no evidence available to contradict his finding that Cricotopus is the sister group of Halocladius and that Paracladius is the sister group of these two genera combined.

One problem which is not discussed by Hirvenoja is the separation of those Cricotopus species without the l_4 seta developed into a setal brush from both Orthocladius and

Paratrichocladius. As mentioned on page 266 Paratrichocladius has a seta interna and this character used by Hirvenoja is not valid. n the generic key it has proved necessary to key out the problem species individually: no unique characters have been found in the larval stage to unite these species at generic level.

KEY TO THE KNOWN LARVAE OF THE BRITISH SPECIES OF CRICOTOPUS

1 Pecten epipharyngis of three subequal length scales, unfused. l_4 seta either simple or developed into a setal brush .... subgenus Cricotopus 2

Pecten epipharyngis of three fused scales (beware broad blunt chaetulae laterales on either side of the pecten epipharyngis which may resemble a pecten epipharyngis of three scales). All species with the l_4 developed into a strong setal brush ....subgenus Isocladius 13

2 First, second and sixth pairs of lateral mental teeth strongly reduced, the sixth may be absent .... trifascia Edwards

Mentum not as above. Sixth laterals never strongly reduced 3

3 Inner margin of mandible with three spines. l_4 seta weakly developed or absent 4

Inner margin of mandible smooth. l_4 variably developed, but may be absent 5

4 Median mental tooth rounded. First antennal segment no more than 65 um long .... _bicinctus_ (Meigen)
Median mental tooth triangular. First antennal segment more than 70 um long .... species A

5 Ratio of width of median mental tooth to width of whole mentum less than 0.16 6
Ratio of width of median mental tooth to width of whole mentum greater than 0.16, usually 0.20 or more 9

6 l_4 either simple or at most a weakly developed setal brush 7
l_4 a distinctly developed setal brush 8

7 Premandible with one apical tooth. Second lateral mental teeth reduced in size compared with the irst and third laterals .... _tremulus_ (Linnaeus)*
Premandible with two apical teeth. All lateral teeth subequal .... _fuscus_ Kieffer

8 Premandible with two apical teeth .... _tibialis_ group*1
Premandible with one apical tooth....._annulator_ Goetghebuer

9 Ratio of width of median mental tooth to width of whole mentum 0.20 - 0.22 10
Ratio of width of median mental tooth to width of whole mentum 0.23 - 0.25 11

10 First antennal segment no more than 45 um .... _albiforceps_ (Kieffer)
First antennal segment greater than 50 um .... _triannulatus_ (Macquart)

11 First antennal segment less than 45 um. Second lateral teeth smaller than the others......flavocinctus (Kieffer)*
First antennal segment greater than 55 um. All lateral teeth subequal .... pulchripes Verrall

12 SI simple, and with either two blunt chaetulae laterales on either side of the conical pecten epipharyngis, or both the chaetulae laterales and pecten epipharyngis very short and tooth shapes 13
SI bifid, as usual for the genus. Chaetulae laterales never as above 14

13 Antenna wider than long. Lauterborn organs and seta interna of mandible absent ....brevipalpis Kieffer
Antenna more than twice as long as wide. Lauterborn organs and seta interna present .....(?) obnixus (Walker)*

14 Premandible with two apical teeth 15
Premandible with one apical tooth 18

15 l_4 developed into a setal brush on abdominal segments I to VII .... ornatus (Meigen)*
l_4 developed into a setal brush only on segments I to VI 16

16 The smallest claw on anterior parapod bearing more than one tooth has the apical tooth scarcely stronger than the inner teeth of that claw (Fig. 22e) ....
.... sylvestris (Fabricius)

The smallest claw on anterior parapod bearing more than one tooth has the apical tooth distinctly stronger than the inner teeth of that claw (Fig.23e)..17

17 Antennal ratio higher than 1.8 ...... _trifasciatus_ Meigen
Antennal ratio lower than 1.75 .... _tricinctus_ Meigen*

18 l_4 setal brush on abdominal segments I - VII with 10 setae, the longest double the length of the segment .. .. _laricomalis_ Edwards*
l_4 setal brush on abdominal segments with usually more than 20 setae the longest of which is no longer than the segment length 19

19 l_4 setal brush on abdominal segments I - VII with between 20 and 50 setae .... _reversus_ Hirvenoja*
l_4 setal brush on abdominal segments I - VI or I - VII of 20 to 30 setae, but on segment VII generally less than 10 .... _intersectus_ (Staeger)

* Keyed on basis of Hirvenoja's (1973) description, but not examined in this study

1 _C.(I) ephippium_ (Zetterstedt) and _C.(I.) polaris_ Kieffer both belong to the _tibialis_ group, but are undescribed.

Species with undescribed larvae:
C.(C.) pilosellus Brundin; _C.(C) similis_ Goetghebuer; _C.(C.) festivellus_ Kieffer; _C.(C.) pallidipes_ Edwards; _C.(C.) lygropis_ Edwards; _C.(I.) pilitarsis_ (Zetterstedt); _C.(I.) speciosus_ Goetghebuer).

<u>Cricotopus</u> (<u>Cricotopus</u>) <u>albiforceps</u> (Kieffer)

<u>Cricotopus</u> (<u>C</u>.) <u>albiforceps</u> (Kieffer in Thienemann & Kieffer, 1916:533); Hirvenoja, 1973:234.

DESCRIPTION OF 4TH INSTAR LARVA (n = 2).

Body length not measured (Hirvenoja states 6mm). Head capsule 380 (n = 1), yellow with occipital margin scarcely darkened. Mentum and apical third of mandible dark brown.

<u>Antenna</u> (Fig. 16a). Five segmented with length of segments; 44.5 - 45.5; 11; 5 - 5.5; 3; 3 - 4.5. Antennal ratio 1.91 - 1.98. Antennal spine 30 - 31, extending beyond fifth antennal segment. Ring organ 7 - 8 from base of first antennal segment. Subsidiary spine 7 long, Lauterborn organs weak (? absent).

<u>Labrum and palatum</u>. Typical for subgenus <u>Cricotopus</u> (see <u>pulchripes</u> Figure 19b). Branches of bifid SI subequal or inner branch slightly shorter than the outer. Five or six chaetulae laterales, three lying above the others and quite broad. Two terminally bifid chaetulae basales. Premandible simple, 74 - 76 long.

<u>Mandible</u>. 132-135 long with apical tooth shorter than combined width of the three inner teeth. Seta subdentalis 12 long. Seta interna of six simple branches. Outer margin of mandible at most weakly crenulate.

<u>Mentum</u> (Fig. 16b). Width of flattened mentum 119 - 138, width of median tooth 21 - 25, ratio of median tooth to mental width 0.18. Six pairs of lateral teeth subequal.

<u>Maxilla</u>. Palpiger and sensillae on galea typically well developed. Maxillary setae all simple or very finely serrate apically. Several quite strongly developed simple lamellae on galea, fewer complex lamellae. Appendix simple.

<u>Abdomen</u> (n = 1). Procercus 21 high by 16 wide bearing apically six setae of maximum length 318. Posterior parapods and anal tubules not measurable in the exuvium. Claws on posterior parapod light brown, simple. Claws on anterior parapod yellow-brown. Smallest claw bearing inner teeth has the apical tooth much longer although scarcely wider than the inner tooth. l_4 seta developed into a strong setal brush on abdominal segments I - VI, of maximum length 158, with more than 25 branches.

MATERIAL EXAMINED

Site 17 (1 reared to a female, identification not as certain as the next); Site 41 (1 reared to male).

COMMENTS

The larvae described above only differ from those described by Hirvenoja on the antennal ratio, a frequent finding in this survey. Recalculation of the A.R. (presented by Hirvenoja as the reciprocal of the A.R. in this and most other works) from the figures of Hirvenoja shows a greater agreement, suggesting that the lengths of each segment calculated by Hirvenoja included the intersegmental membrane. The reasons for excluding this feature in the calculation of the antennal ratio are given on page 30.

DISTRIBUTION AND ECOLOGY

Hirvenoja (1973:234) summarises the distribution as northern and western Europe as well as Italy and Jugoslavia. Within Britain the species is widespread with material in the B.M.(N.H.) from many counties in England as well as Wales and Ireland. Birkett (1957:147) recorded a single specimen from Cumbria.

Citing Thienemann's observati ns Hirvenoja (loc.cit.)

stated that the species lives in lakes and rivers, and that Thienemann found the species to be the most abundant chironomid in the _Schizotrix_ zone of Lunzer Untersee, but was also found in lesser numbers in the _Rivularia_ crust, and still less often in the _Elodea_ zone up to 2 m. deep.

The two localities in which the larvae have been found in Britain in this survey are apparently quite similar. Malham Tarn is an upland naturally eutrophic lake, while the iver Wharfe site is an upland calcareous river, although the collecting site was in a very slowly flowing section with much algal growth on the large stones.

Cricotopus (_Cricotopus_) _annulator_ Goetghebuer

Cricotopus (_C._) _annulator_ Goetghebuer, 1927:52; ? not Hirvenoja, 1973:204 (description of larva of _bituberculatus_ (Goetghebuer)).

DESCRIPTION OF 4TH INSTAR LARVA (n = 6).

Length 4.5 mm (n = 1), Hirvenoja (loc.cit.) says up to 6 mm. Head capsule 450 (424-477) long, yellow-brown with occipital margin, mentum and apical half of mandible brown. Premandible yellow.

Antenna (Fig. 16e). Five segmented, lengths 45.3 (44-47.5); 11.7 (9.5-13); 5.2 (4.5-6.5); 3.2 (3-4); 3.6 (3-4.5). Antennal ratio 1.92 (1.76-2.10). Antennal spine 26 - 28 long, subsidiary spine distinct 9 - 11 long. Ring organ 11 (8-13) from base of first antennal segment. Lauterborn organs indistinct.

Labrum and palatum. Typical for subgenus _Cricotopus_ (see _pulchripes_, Fig. 19b). Branches of bifid SI subequal. 4 or 5 chaetulae laterales two broader than the others. The two chaetulae basales apically bifid. Premandible simple, 83 (74-90) long.

Mandible (Fig. 16d). 144 (138-156) long with the apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 17 (16-18.5) long. Seta interna of six simple branches. Outer margin of mandible without crenulations.

Mentum (Fig. 16c). Flattened width 122 (116-132), median tooth 22 (20-25) wide. Ratio of width of median tooth to width of mentum 0.18 (0.17-0.19). All six lateral teeth subequal.

Maxilla. Palpiger and sensillae on galea typically well developed. Maxillary setae all simple. Appendix fine and simple. Pecten galearis absent. Few lamellae on galea, all simple.

Abdomen. Procercus 22 (16-26) high by 17.5 (13-24) wide, bearing apically six setae of maximum length 424 (379-456), and the longest lateral seta 68 (61-74) long. Posterior parapods and anal tubules not measurable in the specimens e amined. Anterior parapod claws yellow, the smallest claw bearing inner teeth has the apical tooth very strongly developed compared with the inner teeth. Posterior parapod claws simple, pale brown. l_4 seta developed into a setal brush bearing more than 20 branches on abdominal segments I - VI. The longest seta 76 (69-84) long.

MATERIAL EXAMINED

Site 40 (4 reared, 1 larva); Site 44 (1 reared).

COMMENTS

Hirvenoja (1973:206) redescribed the larva of bituberculatus Goetghebuer and suggested that this might be a synonym of annulator Goetghebuer. The adult midges reared from the larva described above are conspecific with annulator as redescribed by Hirvenoja (loc.cit.) but the larva does not appear to be the same as that of bituberculatus. Differences noted include a higher antennal ratio in annulator, different distribution of pigmentation on the mandible, fewer lamellae on the galea and palpiger and a larger l_4 in annulator. It is not easy to decide whether these are specific differences, particularly since there is frequently a disparity between the antennal measurements of Hirvenoja and those of this study.

DISTRIBUTION AND ECOLOGY

Because of the possible confusion over the identity of the larvae described by Hirvenoja, comments can only be made on the distribution and ecology as instanced by the adults. Hirvenoja (loc.cit.) stated that the species is widely distributed throughout north and central Europe with a questionable record from Canada. There are numerous specimens in the B.M.(N.H.) from throughout England and Wales, but none from Scotland.

Hirvenoja states that annulator is associated with running waters and sometimes lakes, and that bituberculatus (Goetghebuer) has been found in springs. The two sites in which the larvae of annulator has been found in Britain are both rhithral zones of rivers, one a chalk river, the other running from the granite of Dartmoor.

Cricotopus (Cricotopus) species A

DESCRIPTION OF 4TH INSTAR LARVA (n = 3)

Body length 5.8 mm (n = 1), head capsule 674 (646-699), yellow-brown with dark brown to black occipital margin, mentum and apical half of mandible. Premandible dark brown.

Antenna (Fig. 17a). Five segmented, lengths 72.3 (71-74); 16.3 (16-17); 5; 3; 3.5 (3-4). Antennal ratio 2.60 (2.55-2.67). Antennal spine 26 (25;27), subsidiary spine 8 - 9, Lauterborn organs distinct. Ring organ 6.3 (5-8) from base of first antennal segment.

Labrum and palatum (Fig. 17b). SI bifid with the inner branch shorter than the outer, remaining S setae simple, somewhat shorter than usual. Labral chaetae simple. Pecten epipharyngis of three subequal spines. Chaetulae laterales of one broad scale overlying two or three finer ones. Two terminally bifid chaetulae basales. Premandible 98 (93-101) long with one apical tooth and a broad inner tooth.

Mandible (Fig. 17c). 198 (195-201) long with the apical tooth shorter than the inner three teeth. Seta subdentalis 16 - 19 long, seta interna with six finely serrate branches. Inner margin of mandible with three distinct spines, outer margin with weak crenulations.

Mentum (Fig. 17d). Distinctive. Width of flattened mentum 150 (148-154) with median tooth 25 (24-26) wide. Ratio of width of median tooth to mentum width 0.16-0.17. Median tooth distinctly triangular, second laterals reduced in size but not appressed to the first. Ventromental plates indistinct.

Maxilla (Fig. 17e). Sensillae on palpiger and galea distinct. Lamellae on galea both simple and complex, few of each. Maxillary setae simple, the outermost broader and somewhat sinuous. No pecten galearis but in this place is an area of small tubercles. Appendix simple.

Abdomen (n = 2). Procercus 26 - 27 high by 32 - 34 wide, bearing apically six setae of maximum length 445 - 466, and laterally a seta 45 - 53 long. The supra-anal seta is 95 - 98 long. Parapods and anal tubules not measurable. Hind parapod claws yellow-brown, simple; anterior parapod claws yellow with the apical tooth scarcely longer than the inner teeth. Largest and smallest claws both simple. l_4 seta simple, very weakly developed.

MATERIAL EXAMINED

Site 26b (2 larvae, 1 reared to pharate female adult).

COMMENTS

This species is distinctive as a larva, having a large, strongly pigmented head capsule with a distinctive shaped mentum. The mentum is rather different from other Cricotopus species, although the aberrant brevipalpis (see Fig.21b) has a similar shaped median tooth. Neither the adult nor the pupa can be placed with any certainty in any of Hirvenoja's species groups, although there are some similarities with the tremulus group. Further pupal and adult material, particularly the adult male, is necessary before the status of this species can be established.

DISTRIBUTIO AND ECOLOGY

The species is only known from a nutrient rich stream in Ashdown Forest, East Sussex collected in April as fourth instar larvae. Further collecting is necessary before any further information can be added.

Cricotopus (Cricotopus) bicinctus (Meigen)

Cricotopus (C.) bicinctus (Meigen, 1818:44); Hirvenoja, 1973: 238; Oliver, 1977:98.

DESCRIPTION OF 4TH INSTAR LARVA (n = 6)

Body length not measurable (Hirvenoja states 6 mm), head capsule 488 (466-498), pale brown with occipital margin light brown and mentum and apical third of mandible dark brown.

Antenna (Fig. 18a). Five segmented, lengths 59.5 (53-64); 15 (13.5-17); 5.3 (4.5-6); 3.3 (3-4); 3.7 (3.5-4). Antennal ratio 2.20 (1.86-2.56). Antennal spine 26 - 28 long, subsidiary 8 - 10 long. Lauterborn organs present, shorter than third antennal segment. Ring organ 7.5 (6-9) from base of first antennal segment.

Labrum and palatum. Typical for subgenus *Cricotopus* (see *pulchripes* figure 19b). Five or six chaetulae laterales, one of which is very broad, the others narrower. Two terminally bifid chaetulae basales. Premandible simple, 92 (85-95) long.

Mandible (Fig. 18c). 165 (159-169) long with the apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 14 (13-15). Seta interna of six simple branches. Outer margin of mandible crenulate, inner margin with three fine spines.

Mentum (Fig. 18b). Flattened width 132 (125-140), median tooth 23 (21-27) wide, ratio of median tooth to whole mentum width 0.18 (0.17-0.20). Six pairs of lateral teeth subequal, first pair somewhat squarer than the remainder.

Maxilla. Sensillae on palpiger and galea typically well developed. Maxillary setae simple or weakly serrate apically. Both simple and complex lamellae on galea, neither strongly developed. Appendix simple.

Abdomen. Procercus 20.7 (16-25) by 24.8 (24-26) bearing apically six setae of maximum length 438 (402-477). Lateral seta 58 (56-61). Posterior parapods and anal tubules not measurable. Claws yellow-brown, anterior ones serrated. l_4 seta simple on all material examined.

MATERIAL EXAMINED

Site 7 (1 larva); Site 9 (2 larvae); Site 10a (2 reared); Site 40 (1 reared); Site 42 (1 larva, 1 reared); Site 46 (2 reared).

DISTRIBUTION AND EC LOGY

Hirvenoja (1973:239) summarises the distribution as widespread in Europe from Scandinavia to the Balkans and also in Afghanistan, Siberia, Canada and the U.S.A. (Florida) and Michigan).

Oliver (1977:102) examined specimens from throughout Canada and from several northern states of the United States. bicinctus (Meigen) is similarly widely distributed in Britain. Birkett (1957:147) found it to be frequent in Cumbria and Hall (1961:181) recorded it from southern English chalk streams.

Hirvenoja states that the species is known from running waters with two records from brackish water. Although Reiss (1968:235) found pupae and adults in Bodensee the larva has not been found in lakes. Lehmann (1971:479) described bicinctus as a eurythermic, eurytopic species found particularly on stones. In the River Fulda Lehmann found the species in the helokrene and rheokrene but found the highest abundance in the potamal zone.

Cricotopus (Cricotopus) fuscus (Kieffer)

Cricotopus (C.) fuscus (Kieffer, 1909:46); Hirvenoja, 1973:174.

DESCRIPTION OF 4TH INSTAR LARVA (n = 9)

Body length 5.6 (5.1-6.1) (n=3), head capsule length 489 (424-540), pale yellow brown with occipital margin slightly darker and mentum and apical third of mandible darker brown. Premandible yellow.

Antenna (Fig. 18d). Five segmented, lengths 52 (45-58); 12.5 (12-13); 5.1 (4.5-5.5); 3.7 (3-5); 4.0 (3.5-4.5). Antennal ratio 2.07 (1.88-2.22). Antennal spine 25-27 long, subsidiary spine 5 - 6 long. Lauterborn organs distinct but small. Ring organ 10.3 (7-13) from base of first antennal segment.

Labrum and palatum. Typical for subgenus *Cricotopus* (see *pulchripes*, Figure 19b) with SI bifid with inner branch shorter than the outer. Labral chaetae simple. Two broad chaetulae laterales lying over five or six finer scales. Two terminally bifid chaetulae basales present. Premandible 90.7 (83-100) long, terminally bifid and with a broad inner tooth.

Mandible. 165 (145-206) long, the apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 16 - 17 long, seta interna of six very finely serrate branches. Outer margin of the mandible distinctly crenulate.

Mentum (Fig. 18e). Flattened width 138 (129-148), median tooth 19.6 (18-22). Ratio of median tooth to mentum width 0.14 (0.13-0.17). Six pairs of laterals, subequal in size. Ventromental plates small but present, without setae beneath.

Maxilla. Sensillae on palpiger and galea typically well developed. Numerous small simple and complex lamellae on galea and base of palpiger. Maxillary setae numerous and simple. Appendix with terminal short branches.

Abdomen. Procercus 31.7 (26-39) high by 33.5 (25-39) wide and bearing apically six setae of maximum length 623 (487-752). Lateral seta 99 (79-121) long, supra-anal seta 90-105 long. Posterior parapod 183 (174-190) long, anal tubules extend beyond posterior parapod, without constrictions. l_4 seta simple, 40 - 111 long. Posterior parapod claws yellow-brown, simple; anterior parapod claws yellow with the apical tooth scarcely longer than any of the inner teeth. The longest and smallest claws bear no inner teeth.

MATERIAL EXAMINED

Site 10a (1 reared); site 21 (1 reared, 6 larvae); site 42 (1 reared); WEST SUSSEX: Rogate, River Rother, .vii.1975, leg. P.S. Cranston (1 larva, 1 reared).

DISTRIBUTION AND ECOLOGY

Hirvenoja (1973:175) notes that the species is widely distributed throughout Europe and the U.S.S.R. as far West as Siberia. British records under _Cricotopus biformis_ are questionably accepted as _fuscus_ but in this work the synonymy is confirmed, on the basis of the immature stages. British records are from a number of English localities predominantly in the south-east although Birkett (1957:154) found adults (as _biformis_) in Cumbria and North Yorkshire, and Morgan and Waddell (1960:63) record the species (again as _biformis_) from Scotland for the first time.

Hirvenoja (loc.cit.) records the larvae from all types of water although less frequently from ponds and pools. In this survey all the localities are slowly running streams or rivers.

Cricotopus (_Cricotopus_) _pulchripes_ Verrall

Cricotopus (_C._) _pulchripes_ Verrall, 1912:22.

DESCRIPTION OF 4TH INSTAR LARVA (n = 1 exuvium)

Size not measurable, head capsule 693, yellow. Occipital margin, mentum and apical half of mandible dark brown.

Antenna (Fig. 19a). Five segmented, lengths 61; 14.5; 5.5; 4; 4.5; Antennal ratio 2.14. Antennal spine 34 long, ring organ 20 from base of first antennal segment. Lauterborn organs distinct, as long as the third segment.

Labrum and palatum (Fig. 19b). SI bifid with the inner branch shorter than the outer. Remaining S setae as usual for the genus. Labral chaetae simple. Pecten epipharyngis of three unfused spines. Chaetulae laterales three simple scales. Chaetulae basales and ungula not visible. Premandible 74 long, simple.

Mandible (Fig. 19d). 191 long, apical tooth longer than usual in the genus but still shorter than the combined width of the three inner teeth. Seta subdentalis 20 long with apical hook. Seta interna of six fine simple branches. Outer margin weakly crenulate.

Mentum (Fig. 19c). Flattened width 154, median tooth 37 wide, ratio of width of median tooth to mentum width 0.24. Six pairs of laterals subequal in size. Ventromental plates small, no setae beneath.

Maxilla (Fig. 19e). Apparently no lamellae on palpiger and few on the galea. Three complex lamellae and three simple ones in the specimens examined. Five serrate maxillary setae. Pecten galearis absent. Appendix divided apically into three short branches. All sensillae on galea and palpiger well developed.

Abdomen. Procercus 33 high by 32 wide, heavily sclerotised on half of the procercus. Apically with six setae of maximum length 640. Lateral procercal seta strongly developed, 117 long. Supra-anal seta not measured, anal tubules and posterior parapods not measurable on the exuvium. l_4 setal brush with up to 25 branches (Fig. 19f), longest 80, apparently only present on abdominal segments I to V. Claws on anterior parapods yellow and with some inner teeth, posterior claws brown and simple.

MATERIAL EXAMINED

Site 3 (1 reared).

NOTES

Hirvenoja placed _pulchripes_ in the _tremulus_ group of species within the subgenus _Cricotopus_, based upon the adult male and female, the pupa and larva being unknown. The larva of _pulchripes_ is atypical for the group in that the median mental tooth is more than three times the width of the first lateral tooth, and would not key to the _tremulus_ group in the key of Hirvenoja (1973:138). A paper dealing with the pupal description and systematic position of the species is in preparation.

DISTRIBUTION AND ECOLOGY

Hirvenoja (1973:190) summarises the distribution based on the adult as Norway, Sweden, Belgium, Germany, Britain and possibly from France. Coe (1950:145), citing records available in Britain from Edwards, described the species as "common in hilly districts", and Macan (1949:177) found _pulchripes_ to be one of the rarer species in Three Dubs Tarn (Cumbria). Birkett (1957:147) recorded specimens from a large swarm at Little Langdale (Cumbria).

On the basis of Macan's observations and other adult finds (the larva is recorded and described for the first time in this work), Hirvenoja suggests that _pulchripes_ lives in standing waters. However the site from which the larva described here originated was a mountain stream with one of the fastest rates of flow amongst those examined. The author has seen a second reared larva from the River Wye (D. Morris collection) and the sites of collection of the British adults suggest that the species is more likely to be lotic, particularly in high, cold waters.

Cricotopus (*Cricotopus*) ?*triannulatus* (Macquart)
Cricotopus (*C.*) *triannulatus* (Macquart, 1826:202); Hirvenoja, 1973:210.

DESCRIPTION OF 4TH INSTAR LARVA (n = 1, unreared)
Body length 5 mm, head capsule length 455, pale brown with occipital margin, mentum and apical half of mandible darker brown. Premandible yellow

Antenna (Fig. 20a). Five segmented, lengths 58; 13; 5; 3; 3. Antennal ratio 2.42. Antennal spine 20 long, subsidiary spine 6 long. Lauterborn organs present, half the length of the third segment. Ring organ present, 5 from base of first antennal segment.

Labrum and palatum. Typical for subgenus *Cricotopus* (see *pulchripes*, figure 19b). SI bifid with branches subequal. Pecten epipharyngis of three subequal spines, five chaetulae laterales less broad than usual, two terminally bifid chaetulae basales. Premandible 101 long, with one apical tooth.

Mandible. 156 long with apical tooth shorter than the three inner teeth. Seta subdentalis 14 long, seta interna with six very finely serrated branches. Outer margin of mandible quite strongly crenulate.

Mentum (Fig. 20b). Flattened mentum 148 wide, median tooth 31 wide. Ratio of median tooth to width of mentum 0.21. Six pairs of lateral teeth subequal, ventromental plates present but not extending beyond outer mental teeth.

Maxilla. Sensillae on palpiger and alea distinct. Numerous simple and complex lamellae on galea, and several lamellae on palpiger base. Maxillary setae simple. Pecten galearis absent.

Abdomen. Procercus 29 high by 20 wide bearing apically six setae of maximum length 551. Lateral seta 45 long.

Posterior parapod 212 long, anal tubules unmeasurable but apparently shorter than the posterior parapod. Claws on posterior parapod yellow-brown, simple; those on anterior parapod with the apical tooth scarcely stronger but longer than any inner teeth Fig. 20c). l_4 seta developed into a setal brush with up to 20 branches of maximum length 90. Present on abdominal segments I - VI.

MATERIAL EXAMINED

Site 10a (1 unreared).

DISTRIBUTION AND ECOLOGY

Hirvenoja (1973:211) summarises the distribution as widespread in Europe from Scandanavia to the Balkans and notes records from Japan and possibly Canada. Within Britain there are specimens in the B.M.(N.H.) from Scotland, northern and south-east England and mid-Wales. Birkett (1957:147) records triannulatus as common in light traps in Cumbria and Morgan and Waddell (1960:63) took a single specimen on Lake Dunmore, Perthshire.

There are larval records of triannulatus from both standing and flowing water and also from brackish water.

Cricotopus (Cricotopus) trifascia Edwards

Cricotopus (C.) trifascia Edwards, 1929:322; Hirvenoja, 1973:246.

DESCRIPTION OF 4TH INSTAR LARVA (n = 5).

Body length 5.3 (5.0-5.6) mm (n=4), head capsule 614 (593-636), pale brown with occipital margin, mentum and apical half of mandible dark brown to black. Premandible brown.

Antenna (Fig. 20d). Five segmented, lengths 76 (69-82); 20.7 (18.5-24); 8.0 (7.5-9); 4.3 (3-4.5); 4.8 (4.5-5). Antennal ratio 2.01 (1.79-2.14). Antennal spine 35 - 37 long, subsidiary 11.7 (10-14) long (longer than usual in the genus). Ring organ 7 (4-8) from base of first antennal segment. Lauterborn organs ? absent.

Labrum and palatum. Typical for the subgenus *Cricotopus* (see *pulchripes*, figure 19b). SI bifid, the inner branch only half the length of the outer branch. Pecten epipharyngis of three subequal spines, the chaetulae laterales consist of three broad scales overlying five or six finer scales. Two terminally bifid chaetulae laterales present. Premandible 119 (111-132) long with a single apical tooth and a slight inner tooth.

Mandible. 192 (181-198) long with the apical tooth shorter than the combined width of the inner three teeth. Seta subdentalis 19 (18-20.5) long, seta interna with seven eakly serrate branches. Outer margin of mandible scarcely crenulate.

Mentum (Fig. 20e). Flattened width 154 (148-159), width of median tooth 36.9 (34-39). Ratio of width of median tooth to width of mentum 0.24 (0.23-0.25). First and second laterals strongly reduced and appressed to road median tooth. Outermost (sixth) laterals very reduced, often absent. Ventromental plates small.

Maxilla. Sensillae distinct but smaller than in many species of *ricotopus* ss.. Only a few small simple lamellae on galea and palpiger base. Maxillary setae and appendix both simple. Pecten galearis absent.

Abdomen. Procercus 26.7 (21-29) high by 24.7 (20-27) wide bearing apically six setae of maximum length 381 (360-424). Lateral seta 55 (50-61) long. Posterior parapod 204 (159-275) (n = 3) long, anal tubules not measured but shorter than posterior parapod. Claws on posterior parapod brown, those on anterior parapod yellow with the apical tooth a little broader and longer than the inner teeth (Fig. 20f).

MATERIAL EXAMINED

Site 10a (1 larva); 10b (1 larva); 12 (2 larvae, 1 unreared).

DISTRIBUTION AND ECOLOGY

Hirvenoja (1973:247 states that trifascia is distributed through central Europe and the U.S.S.R. and northwards to Finland. There are specimens in the B.M.(N.H.) from several localities in England including Dovedale (Derbyshire), Temple Sowerby (Cumbria), Sidmouth (Devon) and Wood Walton Fen (Huntingdonshire). Birkett (1957:147) found the adults to be common in Kendal (Cumbria). Humphries (1951:212) described the larvae and pupa of trifascia from the upper and lower reaches of the River Liffey (Ireland). Mundie (1957:184) caught several males swarming at a London reservoir but they may not have emerged from the standing water, since all records except those of Reiss (1968:239) refer to running waters.

Cricotopus (Isocladius) brevipalpis Kieffer

Cricotopus (I.) brevipalpis Kieffer, 1909:45; Hirvenoja, 1973:335.

DESCRIPTION OF 4TH INSTAR LARVA (n = 4)

Body length 5.7 - 5.9 mm (n = 2), head capsule 523 (477-551) strongly narrowed anteriorly, brown with occipital margin darker brown with apical half of mandible and mentum black.

Antenna (Fig. 21a). Five segmented although strongly reduced. Basal segment 12 - 14 wide by 5 - 6 high with a distinct ring organ. Remaining four segments 18 - 21 long. Antennal spine c. 13 long, subsidiary spine c. 5 long.

Labrum and palatum. SI simple, remaining S setae. Labral chaetae simple. Labrum and palatum curved and somewhat laterally compressed. Pecten epipharyngis of one scale, chaetulae laterales reduced to two pairs of heavily sclerotised scales. ? Chaetulae basales absent. Premandible 67 (64-71) long with a single apical tooth and a broad blunt inner tooth.

Mandible (Fig. 21c). 118 (116-124) long, apical tooth no longer than any of the three inner teeth. eta subdentalis present but very small, seta interna absent. Outer margin of mandible scarcely crenulate.

Mentum (Fig. 21b). 80 (77-85) wide, distinctively shaped with a triangular median tooth no wider than the lateral teeth. Five pairs of lateral teeth, the second pair very strongly reduced. Setae at base of mentum retracted towards occipital margin.

Maxilla. Palpiger shorter than usual in the genus and all sensillae reduced. Lamellae on galea indi tinct, if present. No pecten galearis. All maxillary setae relatively short and simple.

Abdomen. (n = 1). Procercus 11 high by 18 wide bearing apically six setae of maximum length 455. Parapods and anal tubules not measurable. Claws of posterior parapod brown and simple; those of anterior parapod with the apical tooth stouter but scarcely longer than any inner teeth, dark brown. l_4 developed into a setal brush on abdominal segments I - VII, of maximum length 296

MATERIAL EXAMINED

NORTH YORKSHIRE: Malham Fen Pond, 17.viii.1973, leg. R.H.L. Disney, "mining in Potamogeton"; PERTHSHIRE: Kindrogan, 37/047 634, 15.v.1977, leg. ?, "mining in Potamogeton".

DISTRIBUTION AND ECOLOGY

Hirvenoja (1973:335) summarises the distribution of the species as Austria, Belgium, Czechoslovakia, England, Finland, Germany, Holland, Poland and the U.S.S.R.. All larval records except Risbec (1951:219) who found it in rice plants are from mines in the leaves of Potamogeton. The discovery of brevipalpis mining in Potamogeton natans L. in a fish pond (Disney, 1975:173) is only the second record from Britain following a single male taken by Edwards in 1929 in Epping Forest.

Cricotopus (Isocladius) intersectus (Staeger)

Cricotopus (I.) intersectus (Staeger, 1839:574); Hirvenoja, 1973:315.

DESCRIPTION OF 4TH INSTAR LARVA (n = 10)

Body length 5.5 - 6.2 mm (n = 3), head capsule length 550 (530-583), pale brown with occipital margin darker and apical third of mandible and mentum dark brown to black. Premandible golden yellow basally, yellow-brown apically.

Antenna (Fig. 21f). Five segmented with segment lengths 51 (48-55); 14.7 (13-16); 5.7 (5-6.5); 4.8 (4-5); 3.5 (3-4.5). Antennal ratio 7 (6-8) long subapical on second segment. Ring organ 8.9 (7-12) from base of first antennal segment. 10 - 15 from the base of the first segment is a pale, oval scar, not observed in other species of Cricotopus.

Labrum and palatum. Typical for subgenus Isocladius (see trifasciatus Figure 23b). Branches of bifid SI subequal, SII 35 - 40 long, longer than usual, remaining S setae normal. Labral chaetae simple. Pecten epipharyngis of three fused scales. One broad pair of chaetulae laterales overlying three or four pairs of finer, frequently serrate setae. Two terminally serrate chaetulae basales. Premandible 90 (81-95) long, with one apical tooth and a broad inner tooth.

Mandible (Fig. 21e). 173 (161-180) long, apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 8 - 9 long, seta interna of six or seven finely serrate branches. Outer margin of mandible crenulate.

Mentum (Fig. 21d). Flattened mentum width 140 (132-148), width of median tooth 26 (24-28). Ratio of width of median tooth to whole mentum 0.18 (0.17-0.19). Median tooth domed, although this is lost in even slightly worn specimens. Six pairs of laterals, the second pair reduced and fused with the first. Ventromental plates small without setae beneath.

Maxilla. All sensillae typically long and distinct. Simple lamellae on galea and palpiger base numerous and distinct. ? No complex lamellae on galea. No pecten galearis. Maxillary setae broad and simple.

Abdomen. Procerci 27 21-31) high by 34 (29-42) wide bearing apically six setae of maximum length 669 (636-720). Lateral procercal seta 84 (74-98) long. Parapods and anal tubules not measured. Claws on posterior parapods golden-yellow nd simple, claws on anterior parapods yellow. Claw with more than one tooth have the apical tooth narrow but clearly longer than the inner teeth. l_4 seta developed into a setal brush on abdominal segments I - VII, the longest brush 405 (360-434) long. The setal brush on segment VII contains fewer setae and is shorter (221 (180-275)).

MATERIAL EXAMINED

Site 17 (numerous larvae reared and unreared); Site 39 (numerous larvae reared and unreared); CUMBRIA: Sunbiggin Tarn, NY 676 088, 23.vi.1978, C.H.C. Lyal, (4 larvae, 3 reared).

COMMENTS

Adult *Cricotopus* reared from these larvae are clearly *intersectus* (Staeger) according to Hirvenoja (1973) but the pupae particularly more resemble *reversus* Hirvenoja in lacking the pedes spurii B on abdominal segment III. The character used to separate the larvae of *intersectus* and *reversus* (otherwise very similar) is the relative development of the setal brush on abdominal segment VII - the reduction in size of the brush in these specimens indicates that this is *intersectus* despite the anomalous pupa. The larvae of *reversus* have not been recognised in this survey if they are indeed separable from *intersectus* by the character Hirvenoja cites.

DISTRIBUTION AND ECOLOGY

Hirvenoja (loc.cit.) summarised the distribution as Scandanavia, Britain, Germany, Iceland, Italy, U.S.S.R. and Canada. Larval records of *intersectus* (Staeger) (frequently as *dizonias* (Meigen)) are all from standing water bodies, mainly lakes. Brundin (1949:729) found the species to be a characteristic form of the Swedish eutrophic lakes but absent from mountain lakes. Reiss (1968:235) found *intersectus* to be the dominant species in the emergent stone and plant zone of Bodensee.

Cricotopus (*Isocladius*) *sylvestris* (Fabricius)

Cricotopus (*I.*) *sylvestris* (Fabricius, 1794:252); Hirvenoja, 1973:282.

DESCRIPTION OF 4TH INSTAR LARVA (n = 10)

Body length 4.8 - 6.7 mm (n = 3), head capsule 557 (508-593), yellow with occipital margin pale brown. Mentum and apical third of mandible dark brown and premandible yellow becoming browner apically.

Antenna (Fig. 22a). Five segmented, lengths 64 (61-71); 14.9 (13-16); 7.8 (6.5-9); 4.6 (4-5); 4.2 (3-5). Antennal ratio 2.02 (1.73-2.26). Antennal spine 33.4 (29-36) long; subsidiary spine 9.2 (8-10.5) long, inserted subapically on the second antennal segment. Ring organ 11.9 (8-14) from base of first antennal segment.

Labrum and palatum. Typical for subgenus *Isocladius* (see *trifasciatus* Figure 23b). Inner branch of bifid SI clearly shorter than the outer branch. Remaining S setae normal. Labral chaetae finely serrate. One large pair of chaetulae laterales overlying one or two smaller setae which may be finely serrate. Two terminally bifid chaetulae basales present. Premandible (Fig. 22b) 105 (93-111), with two apical teeth and a variably developed, broader inner tooth.

Mandible (Fig. 22d). 184 (159-206) long, with apical tooth shorter than combined width of the three inner teeth. Seta subdentalis 13.6 (13-14.5) long, seta interna of seven finely serrate branches. Outer margin strongly crenulate.

Mentum (Fig. 22c). Flattened width 155 (145-164), width of median tooth 21.8 (21-24). Ratio of width of median tooth to width of mentum 0.14 (0.13-0.16). Six pairs of lateral teeth with the second pair slightly reduced and appressed to the first. Ventromental plates weak, without setae beneath.

Maxilla. Palpiger large, sensillae on palpiger and galea distinct. Lamellae on galea small, few in number and mostly simple. Maxillary setae all simple. Appendix narrow and simple, or weakly divided apically. No pecten galearis.

Abdomen. Procercus 34 (29-40) high by 34 (32-41) wide bearing apically six setae of maximum length 767 (742-816). lateral seta of procercus 70 (42-95) long. Procercus dark brown, heavily sclerotised and apical setae darker brown than usual. Anal tubules shorter than posterior parapods but neither measurable. Claws on posterior parapods golden yellow, those on anterior parapod yellow with apical tooth fine and scarcely longer than inner teeth (Fig. 22e). l_4 developed into a bristle brush on abdominal segments I - VI and of maximum length 304 (238-339).

MATERIAL EXAMINED

Site 2 (numerous reared and unreared larvae); EST SUSSEX: Rogate, River Rother, .vii.1975, leg. P.S. Cranston, (2 larvae); CUMBRIA: Sunbiggin Tarn, NY 676 688, 23.vi.1978, leg. C.H.C. Lyal, (4 larvae, 3 reared).

DISTRIBUTION AND ECOLOGY

Cricotopus sylvestris is widely distributed throughout the Holarctic region including Afghanistan, Formosa, Canada and the United States. It is also known from Java in the Oriental region. Adults of this species have been taken from throughout Britain and it is probably one of the most common British species of *Cricotopus*.

The larvae have been found in all kinds of water bodies from small pools to fast flowing stretches of water and the larvae have also been found in brackish waters with salinities of up to 8 parts per thousand of sodium chloride. Hirvenoja (loc.cit.) summarises all the available information on the ecology of the larvae and notes that the highest larval densities are found in areas rich in vegetation although they are also found on stones and muddy substrates and are tole ant of both polluted environments and drying pools. The larvae found in this survey are from a garden pond, a eutrophic lake and a calcium rich lowland river. All three sites had strong plant growth.

Cricotopus (Isocladius) trifasciatus (Panzer)

Cricotopus (I.) trifasciatus (Panzer, 1813:18); Hirvenoja, 1973:296 (as "Kleinere Form").

DESCRIPTION OF 4TH INSTAR LARVA (n = 10, all exuviae).

Body length not measurable, head capsule 594 (572-657), yellow with occipital margin scarcely darker. Mentum and apical half of mandible dark brown.

Antenna (Fig. 23a). Five segmented, lengths 61.5 (58-66); 13.4 (12-14.5); 6.8 (5.5-8.0); 5.0 (4.0-5.5); 3.7 (2.5-5.0). Antennal ratio 2.12 (1.91-2.29). Antennal spine 27 (21-31), ring organ 12 (5.5-13) from base of first antennal segment. Lauterborn organs distinct but shorter than third antennal segment.

Labrum and palatum (Fig. 23b). Typical for Isocladius with bifid SI, fused pecten epipharyngis and broad chaetulae laterales. Premandible (Fig. 23c) 50.3 (47-56) long with two apical teeth and a broad inner tooth.

Mandible. Typical for the genus. Length 188 (174-196), apical tooth shorter than three inner teeth. Seta subdentalis 12 (10.5-13) long, seta interna with six simple branches. Outer margin of mandible strongly crenulate.

Mentum (Fig. 23d). Width of flattened mentum 149.5 (143-154), median tooth 20 (17-21). Ratio of width of median tooth to mentum width 0.13 (0.12-0.14). Six pairs of lateral teeth, the second pair reduced and appressed to the first. Ventromental plates small without setae beneath.

Maxilla. Maxillary setae more strongly developed than usual, up to 53 long, and weakly serrate. Few lamellae on galea, some developed into pointed spines. Pecten galearis absent. Appendix simple.

Abdomen. Procercus 33.6 (21-37) high by 27.6 (11-35) wide, bearing apically six setae of maximum length 673 (615-795). Lateral seta of procercus 45 (39-53). l_4 seta developed into a setal brush on abdominal segments I - VI, with more than 30 branches and 321 (275-360) long. Posterior parapods and anal tubules not measured on the exuviae. Claws on anterior parapods yellow-brown and with inner teeth (Fig. 23e), finer than the apical teeth. Posterior parapod claws golden-brown.

MATERIAL EXAMINED

Site 45 (6 reared); Site 46 (3 reared); WEST SUSSEX: Rogate, River Rother, .vii.1975, leg. P.S. Cranston (1 reared).

DISTRIBUTION AND ECOLOGY

Hirvenoja (1973:297) summarised the distribution as widespread in Europe from Scandanavia eastwards to East Siberia and Japan and southwards to Italy. Outside the region it is known from Canada, the United States and Java. In the British Museum (Natural History) collections the adults are from a number of localities in Scotland and Wales as well as England.

The larvae are frequently found mining in water plants - Hirvenoja (loc.cit.) cites _Limnathemum_ (_Nymphoides_), _Polygonum_, _Potamogeton_ and _Nuphar_. All the larvae found in this survey were taken from slow flowing water with dominant stands of _Potamogeton_ or _Ranunculus_ although the larvae were not noted to be burrowing in the plants.

xi. _Diplocladius_ Kieffer

Diplocladius Kieffer, 1908:72; Thienemann, 1935:220, Cernovski, 1949:115.

GENERIC DIAGNOSIS (Based on published descriptions, no material examined).

Antenna. Clearly four segmented although there may be a small fifth segment present (not clear from descriptions). Lauterborn organs present, small. Antennal blade shorter than flagellum. Ring organ present in basal quarter of the first segment.

Labrum and palatum. SI plumose, remainder simple. Palatum poorly described, premandible broad and with two apical teeth.

Mandible. Apical tooth shorter than combined width of the four inner teeth. (The innermost tooth is not always clearly separated according to descriptions). Seta subdentalis and seta interna present although the structure of the latter is not stated.

Mentum. Two median and six pairs of lateral teeth all subequal in size and shape. Ventromental plates broad, extending well beyond the outer mental teeth and with numerous fine, long setae beneath.

Maxilla. Not described.

Abdomen. Procercus large, taller than wide and bearing apically six or seven setae. Anterior and posterior parapods present, separate and bearing claws. Anal tubules shorter than posterior parapods.

COMMENTS

Although the larva of Diplocladius cultriger Kieffer has not been described fully there are a number of characters which make the larva easily recognisable in the key. These features are the broad ventromental plates with a strong beard beneath and the subequal mental teeth. The genus has many plesiomorphic features and resembles the Prodiamesinae in the structure of the ventromental plates and SI setae, but can be separated by the non-recessed median mental teeth, the four segmented antenna or the shape of the ventromental plates.

DI TRIBUTION AND ECOLOGY

Adult Diplocladius cultriger Kieffer are known from several western European countries including Belgium, Czechoslovakia, Germany, Britain and both European U.S.S.R. and Siberia. British specimens are known only from a few southern English lowland localities.

The limited ecological information available suggests that the larvae live in small pools and has not been found in running waters.

xii. Epoicocladius Zavrel

Epoicocladius Zavrel, in Sulc & Zavrel, 1974:16.

Type-species Camptocladius ephemerae Kieffer 1924 by monotypy.

Medium sized larvae, head capsule up to 450 um long.

Antenna. Four segmented (Cernovski figures five segments, but this may be an erroneous interpretation of a divided second antennal segment). Fourth segment longer than the third. Lauterborn organ apparently absent, but a subsidiary spine present on the subapex of the second antennal segment. Antennal spine usually extends beyond the apex of the terminal antennal segment by a variable distance.

Labrum. The sensory setae on the labrum are difficult to interpret and relate to those of the other Orthocladiinae. The most likely interpretation is that the SI setae are reduced to fine setae lying just anterior to the labral margin and that the SIII setae are similarly fine, lying posterior to the presumed SI setae. In this interpretation the SIV bisensillae are strongly expanded and are the most posterior of the sensory setae on the labrum, and the elongate setae, arising from even larger sockets than the SIV setae, are the SII setae. Previous workers have interpreted the latter setae as SI setae, but this explanation entails the loss of the SIV setae, and the SIII setae becoming two segmented.

Whichever interpretation is correct, it is clear that the sensory setae of the labrum of Epoicocladius are greatly modified co pared to other Orthocladiinae. This is also true of the pecten epipharyngis which consists of up to nine slender, needle-like spines, with up to four chaetulae laterales lying outside these spines.

The premandible is bifid, without a beard.

Mandible. This has been variously interpreted by different authors, but it seems clear that the apical tooth is much longer than the combined width of the variable number of inner teeth. There are basically three inner teeth of which only the innermost is clearly delimited, the inner two are only separated from the mandible by fine incisions. Seta subdentalis present and distinctively shaped (See Fig. 24c). Seta interna is present with simple branches, although not figured by some previous authors.

Mentum. Strongly curved, such that only the median group of teeth are distinct. When flattened a lateral group of five teeth are visible on each side of the median group of 6 (- ?7) teeth. The median area is somewhat paler than the rest of the mentum. In the flattened mentum the ventromental plates, although still evident, do not extend beyond the most lateral of the mental teeth. There are no setae beneath the plates.

Maxilla. The palpiger is elongate and there are numerous antaxial setae, some (or all) apically serrate.

Abdomen. The thick covering with stout setae is distinctive and almost diagnostic (shared only with Abiskomyia). The procerci are slightly higher than wide, but are larger than in most Orthocladiinae, bearing apically six or seven setae of differing lengths, the longest up to a quarter the body length. There are only one pair of anal tubules which are conical in shape and shorter than the length of the anal parapods.

COMMENTS AND SYSTEMATIC STATUS

The larvae of Epoicocladius have been described by a number of British, European and North American authors, and the descriptions differ in enough details for Saether (1966:107) to suggest there may be more than one species involved. In the generic description above it is pointed out that many of the disparities between descriptions can be ascribed to errors in the examination or drawing of various features and the range of these are no greater than that found elsewhere in the Orthocladiinae. After examination of Zavrel's material it is felt th t there is only one European species and Saether's (1969:137) synonymy with a North American species is accepted.

The phylogenetic relati nships of the genus Epoicocladius are difficult to ascertain based upon the larval stage because of the specialised phoretic habit of the larvae. For example the labral sensory setae, usually so useful in determining the relationships cannot be used in Epoicocladius since they are apparently strongly modified in the genus. The stages in the life history which are not modified by the phoretic habit show a close relationship with Parakiefferiella, particularly in the adult. The pupae show a similar toothed extension of the anal lobe but can be separated by the fringe of hairs on the lateral margins of the abdominal segments in *Epoicocladius*.

The problems of the erection of genera based on a single aberrant stage of the life history is well known in the Chironomidae, and is discussed further in Chapter 7 (pages 337 - 340). This may prove to be a case in point in which the genus *Epoicocladius* was erected by Zavrel for the distinctive larva, but the other stages indicate that the species warrant subgeneric status at most, in a genus which includes those species currently placed in *Parakiefferiella*. This problem can only be resolved when all stages of the species are closely examined including those of the subgenus *Rheosmittia* (genus *Parakiefferiella*) which are not yet recorded from Britain.

Epoicocladius flavens (Malloch)

Epoicocladius flavens (Malloch, 1915:356); Saether, 1969:137 gives full synonymy.

Camptocladius ephemerae Kieffer, 1924:385; (Henson, 1957:25).

DESCRIPTION OF 4TH INSTAR LARVA (n = 4)

Medium sized, body length 3.9 - 4.4 mm, head capsule 340 - 371 um. Head capsule pale yellow with occipital margin dark yellow to brown, mentum (excluding four median teeth and first (broad) laterals) and mandible darker brown.

Antenna (Fig. 24a). Four segmented, lengths 43 (38-46); 13.3 (12-15); 2; 3.2 (3-3.5). Antennal ratio 2.31 (2.24-2.44). Antennal spine 30 (26-34) long, extending beyond terminal antennal segment. Lauterborn organs apparently absent but a short spine present on the subapex of the second antennal segment. Distinct ring organ present 4-5 from base of the first antennal segment.

Labrum (Fig. 24b). As mentioned in the generic description the interpretation of the sensory setae is difficult, but the strong reduction of SI setae suggested does occur in some genera, notably Nanocladius (q.v.), Phycoidella (Saether, 1971: Fig. 12c) and Icthyrocladius (Fittkau, 1974:Fig.11). In this interpretation it is the SII which have long pedicels and are up to 35 long with a plumose apex. The SIII are fine setae lying between and slightly anterior to the bases of the SII setae. The SIV are very distinctive lying most posterior of the sensory setae. The inner setae (SIVa) is a bisensillum, about 16 long, and outside this is a 14 long SIVb.

The pecten epipharyngis consists of nine spines with four chaetulae laterales. The premandible is slender and bifid without a beard and 45 (41-48) long.

Mandibla (Fig. 24c). 90 (85-97) long. All specimens examined have a long apical tooth and three inner teeth. Only the innermost tooth is distinctly separated, the remaining two are weakly incised. Seta interna five or six branched, all simple. Seta subdentalis present, distinctively shaped.

Mentum (Figs. 24d&e). Six pairs of median teeth total width 27 (26-29), five pairs of lateral teeth. Width of flattened mentum about 132. Four median and first lateral teeth pale; outermost median and outermost four pairs of laterals darker. Ventromental plates present, weak and not extending beyond outermost lateral teeth on flattened mentum.

Maxilla. Apical seta on palpiger elongate, 9 - 10 long. 6 antaxial setae ? all terminally serrate. All sensillae on galea distinct.

Abdomen (Fig. 24f). Procerci 65 (52 - 80) high by 42 (37-48) wide, deep yellow bearing apically six setae of varying lengths. The longest apical seta is 780 (720-826) long, there are usually two this length, two intermediate and two much smaller. The lateral setae of the procercus are subequal, quite strong and 73 (47-95) long. Posterior prolegs about 200 long, one single pair of anal tubules, somewhat conical in shape, only half the length of the posterior parapod, and distinctly darkened in some specimens.

The claws of the anterior parapod are finer than usual in the Orthocladiinae and are apically serrate. There are two types of claw on the posterior parapod; up to five are broad, simple and blunt while the others are similar to those on the anterior parapods.

The body is covered in distinct setae, are more distinct than those found in Eukiefferiella and are only otherwise found in such profusion in the non-British Abiskomyia. The longest setae on each segment is 148 - 160 long.

MATERIAL EXAMINED

EAST SUSSEX: Ashdown Forest, .xi.1976, leg. J. Francis (3 larvae), NORTH YORKSHIRE: Upper Gordale Beck, 20.iv.1973, "ex-Ephemera danica", leg. H. Disney (1 larva) (This is my site 20).

Also seen: CZECHOSLOVAKIA: no further data, leg. J. Zavrel (2 larvae, 1 pupa). This material, which may be part of that examined by Zavrel for his description (Sulc and Zavrel, 1924), is identical with the British material described here.

DISTRIBUTION AND ECOLOGY

This species is recorded from much of central and northern Europe as well as Siberia and North America (Ontario to Illinois). Most of these records are based on the distinctive larvae, and the B.M.(N.H.) is probably not unusual in possessing only six adults, four of them reared by Henson. The adults are probably frequently identified as Parakiefferiella spp..

Most of the larval records are based on larvae found living on the nymphs of Ephemera danica Muller. The relationship of Epoicocladius has been variously described as epizosis (Sulc & Zavrel, 1924), phoresis (Henson, 1957) or commensal (Bryce & Hobart, 1972; Disney, 1975:173) and as symphoresis for the similar relationship between Nanocladius (Plecopteracoluthus) and Plecoptera (Saether, 1977).

The larvae are always found on the abdomen behind the wing buds in association with the gills of the nymph and it therefore seems unlikely that the relationship is commensal since the larvae appear to graze on the surface of the nymph. Since all instars are found on the Ephemera (Henson, 1957) the description of the relationship as phoretic is doing no more than stating the obvious since Ephemera are mobile. The question is what do the Epoicocladius gain by such a close association with the may-fly nymph? The habitats in which Ephemera nymphs are found are not always conducive to the larvae of Orthocladiinae particularly where the substrate is very fine. It is possible that attachment to the nymphs dwelling in such places permits the Epoicocladius to enter these relatively inhospitable habitats where the movement of the gills of the nymph gives increased aeration of the burrow, and the weight of the nymph gives more protection against the movement of the fine particles.

It is clear from all observations that Epoicocladius is not a parasite as are several species throughout the world placed in the genus Symbiocladius. These larvae are parasitic on Ephemeroptera and eat the gills. This genus is not yet recorded in Britain although the species rhithrogenae Zavrel is found as near to Britain as central France.

xiii. Eukiefferiella Thienemann

Eukiefferiella Thienemann, 1926:325; Zavrel 1939b:1-29.

Type-species: Dactylocladius longicalcar Kieffer, 1911 sensu Thienemann, 1926 (misidentification = gracei Edwards, 1929) by original designation.

GENERIC DIAGNOSIS

Small to medium sized larvae up to 7 mm long. Head capsule yellow to dark brown, body colour in life very variable from yellow through blue-green to violet. Body colour is apparently often of specific value.

Antenna. Normally five segmented (four in claripennis and species A). Fourth antennal segment subequal to, or longer than third. Antennal spine never extends beyond terminal antennal segment. Ring organ present, Lauterborn organs present.

Labrum. SI seta normally simple, terminally branched in the calvescens group. SII simple, SIII simple, bifid in ilklevensis and species B. SIV normal. Pecten epipharyngis of three spines, usually broad. Lateral chaetae often serrate edged. Premandible always with one broad blunt apical tooth.

Mandible. Apical tooth always shorter than combined width of inner teeth. Usually three inner teeth although several species from the U.S.S.R. have four. Seta interna and seta subdentalis present. Inner edge of mandible usually with spines.

Mentum. One or two median teeth of variable width (a specific character) and with four to six pairs of lateral teeth. Ventromental plates absent, no setae present. The presence of paler, less sclerotised striations on the mentum is characteristic in Eukiefferiella.

Abdomen. Parapods well developed, anal tubules present. Procerci either higher than wide (calvescens group) or as wide as high, bearing apically 5 - 7 setae. Lower lateral seta on procercus well developed (except in non- ritish cyanea). Supra-anal seta often weakly developed. Body setation frequently well developed particularly in the calvescens- group where the longest seta on each segment may be greater than the length of the abdominal segment bearing the seta. These setae may be terminally branched.

COMMENTS AND SYSTEM TIC STATUS

Eukiefferiella is a well defined genus in all life history stages, although the apomorphic group centred on calvescens may deserve generic status especially if Tvetenia Kieffer (erected for a species from Novaya Zemlya) proves to belong to the calvescens group.

As discussed under Cardiocladius (page 89) the presence of simple SI setae is considered to be apomorphic in the Orthocladiinae, and this is a feature shared in the non-Metriocnemini with Tokunagaia, Cardiocladius and Synorthocladius. The branched SI seta in the calvescens group is not of the same structure as the plumose SI believed to be plesiomorphic within the Orthocladiinae and must be considered to be apomorphic within the genus Eukiefferiella.

The relationships of the genera Cardiocladius, Eukiefferiella and Tokunagaia, which are believed to be a monophyletic unit within the Orthocladiinae, is a matter which has not been resolved. Saether (1977) in placing these three genera as the sister group of all but the most plesiomorph Orthocladiine genera states that there is no unambiguous trend uniting the apomorph sister group, and the single synapomorphy for _Cardiocladius/Eukiefferiella/Tokunagaia_ is unconvincing. The position of _Eukiefferiella_ within the Orthocladiinae is therefore in doubt. The possible relationship with _Synorthocladius_ is discussed on page 312

KEY TO THE KNOWN BRITISH SPECIES OF _EUKIEFFERIELLA_

1 Mentum with four pairs of lateral teeth and a single median mental tooth 2
Mentum with five pairs of lateral teeth and median mental tooth single or double 4

2 Four antennal segments with head capsule pale and mentum brown .... _species A_
Five antennal segments, mentum brown or black and head capsule yellow to dark brown 3

3 Mentum black, head capsule dark brown. _ilklevensis_ (Edwards)
Mentum brown, head capsule pale brown or yellow .... _species B_

4 Setae on body at least half the length of the abdominal segments. Head capsule yellow, procerci at least twice as high as wide. SI seta often lumose 5
Setae on body usually shorter than half the length of an abdominal segment, sometimes absent. Head capsule usually dark and procerci less than 1.5 times as high as wide 8

5 Mentum with a single broad median tooth often with a projecting median hump .... _species C_
Mentum with some signs of a divided median tooth, if apparently single there is no projecting median hump 6

6 Occipita margin pale, inner edge of the mandible with three spines. The first antennal segment of the 4th instar larva is less than 60 um long and the SI seta either apparently simple or weakly branched into at most three fine branches .... calvescens (Edwards)
Occipital margin black, inner margin of mandible smooth. SI plumose. First antennal segment greater than 60 um long 7

7 Antennal spine extends no further than the tip of the third antennal segment .... verralli (Edwards)
Antennal spine extends to the tip of the fifth antennal segment or beyond ...... discolorines Goetghebuer

8 Mentum with a single median tooth 9
Mentum with a pair of median teeth 12

9 Median tooth broad, three to four times the width of the first laterals 10
Median tooth narrow, no more than 2.5 times the width of the first lateral teeth 11

10 Head capsule dark brown, the same colour as the mentum, mandible and occipital margin .... minor (Edwards)
Head capsule pale brown, clearly lighter than the dark brown to black mentum, mandible and occipital margin ..
.... gracei (Edwards)

11 Median mental tooth less than twice the width of the first lateral teeth .... brevicalcar (Kieffer)
Median mental tooth more than twice the width of the first lateral teeth, often with an indication of a double median tooth (see also couplet 12) .... species D

12 Antenna with five segments and poorly divided median mental teeth .... species D

Antenna with four antennal segments, median mental teeth clearly divided 13

13 Median mental teeth narrow, subequal to the first lateral teeth .... clarinennis (Lundbeck)

Median mental teeth broad and bulbous, median teeth each three times the width of the first laterals ....clypeata Kieffer

coerulescens Kieffer is not included in the key since no specimens from Britain have been seen, and there is some confusion over the larval identity in the Thienemann collection.

Eukiefferiella brevicalcar (Kieffer)

Eukiefferiella brevicalcar (Kieffer, 1911:184)

DESCRIPTION OF 4TH INSTAR LARVA (n = 8)

Body length about 3.5 - 4 mm, head capsule 361 (349-371) um, head capsule brown, mentum, mandible, premandible and occipital margin darker brown.

Antenna (Fig. 25a). Five segmented, lengths 53 (48-58); 14 (13-15); 2; 3.8 (3-4); 4 (4-5). Antennal ratio 2.21 (2.0-2.5). Antennal spine 21 (20-22), never extending beyond final antennal segment. Subsidiary spine at apex of second antennal segment about 5 long. Ring organ 9 - 13 from base of first antennal segment.

Mandible (Fig. 25c). 85 (79-89) long with apical tooth shorter than combined width of three inner teeth. eta subdentalis 7 (6-8) long, seta interna with five or six branches, weakly serrate at the apex of the longest pair.

Inner margin of mandible with three or four weak spines.

Labrum. All S setae simple, SI and SII slender. Premandible 43 (39-?52) long, typical for the genus.

Mentum (Fig. 25b). Width of flattened mentum 61 (58-64). Single median tooth 8.1 (6-9) wide, less than twice as wide as a lateral tooth. Ventromental plates absent.

Maxilla (Fig. 25d). One of the sensillae basiconicae of the maxilla is much longer than normal. Antaxial setae fewer and shorter than normal. Few lamellae on galea.

Abdomen. Procerci (Fig. 25e) 26.7 (24-31) high by 23.4 (19-27) wide bearing 6 or 7 apical seta of maximum length 428 (380-455). Lateral seta of procercus 84 (66-102), supra-anal seta of similar dimensions. Posterior parapod 190, anal tubules indistinct. Claws of anterior parapods yellow, a few of the medium sized claws with one or two internal teeth, the smaller claws with many fine teeth (as in Fig. 32d). Claws of posterior parapods brown, simple.

MATERIAL EXAMINED

Site 3 (2 reared larvae); Site 23, a stream at the same elevation as the tarn (2 reared larvae); Site 29 (4 reared larvae); WALES: Powys, nr. Newbridge-on-Wye, River Hirnant, 2.vi.1975, P.S. Cranston (1 reared larva); HAMPSHIRE: Stockley, 40 35-025, 26.iii.1978, P.S. Cranston (4 reared larvae).

COMMENTS

brevicalcar type larvae are very frequent in most samples, but when reared there appear to be more than one type of pupa. The above description is based only on the exuviae of larvae which produce a pupa corresponding to that briefly described by Lehmann (1972:359). I have examined pupae identified by Lehmann as brevicalcar and to his description can be added:

thoracic horn longer than 300 um with the distal part slightly sinuous and distinctly darkened (brown rather than golden). The hook rows on tergites III, IV and V have more than ten hooks in a row which is sometimes only indistinctly divided in the middle. Only larvae which give rise to pupae fitting this description have been described as brevicalcar.

See also further notes on the closely related Eukiefferiella species D.

DISTRIBUTION AND ECOLOGY

Adults identified as brevicalcar are found throughout Europe and records from the British Isles are similarly widespread. Although the larval records cited above are apparently restricted it should be noted that these refer only to those larvae reared to an adult or pupa. There are many further records almost certainly attributable to this species from most running water sites investigated. The larvae are found in the algae covering stones in the fastest to the slowest waters, and there are records from standing water (Botnariuc & Albu 1971:474) although they may have been swept there from flowing waters.

Eukiefferiella calvescens (Edwards)

Eukiefferiella calvescens (Edwards, 1929:353); Fahy, 1972:31-2; ? not Zavrel 1939:4; ? not Pankratova, 1970:156.
Eukiefferiella lobulifera Goetghebuer, 1935;9; Zavrel, 1939:4.
Dactylocladius "Kurzfuhler" Potthast, 1915:295.

DESCRIPTION OF 4TH INSTAR LARVA (n = 13)

Body length 3.6 mm (3.0-4.3), head capsule length 380 (340-470), pale yellow without occipital margin darkened. Mandible and mentum brown to dark brown.

Antenna (Fig. 26a). Segment lengths 52.6 (47-59); 16.3 (15-18); 3.0 (2.5-3.5); 4.7 (4-5.5); 4.3 (4-5). Antennal ratio 1.85 (1.67-2.04). Antennal spine 30.8 (29-37), ring organ 6.7 (5-8) from base of first antennal segment.

Mandible (Fig. 26b). 108 (96-121) long, with apical tooth shorter than inner three teeth combined. Seta subdentalis 9.5 (8-11) long, seta interna of 5 or 6 branches, terminally plumose. Inner margin with three spines.

Labrum. SI seta often divided into two or three fine hairs apically, but sometimes either simple, or indistinctively divided. Other setae simple. Premandible 54 (47-60) long, as normal for the genus.

Mentum (Fig. 26c). Flattened width 78.5 (69-87), paired median teeth 17.8 (16-21) wide. Ventromental plate absent.

Maxilla (Fig. 26d). Antaxial setae strongly serrate. No lamellae on galea. Pecten galearis present. Maxilla very similar to that of discoloripes and verralli.

Abdomen. Procerci 37 (34-44) high by 21.8 (20-26) wide, bearing apically 6 or 7 setae maximum length 589 (466-678). Lower lateral seta 139 (108-163 long. Posterior parapod 169 (148-190) long, anal tubules approximately 80 long by 33 wide. All parapods bearing simple claws. Longest body seta 170 (137-201) long.

MATERIAL EXAMINED

Site 3 (4 exuviae); Site 4 (2 larvae); Site 10a (11 larvae & exuviae); Site 10b (1 larva); Site 11 (1 exuvium); Site 12 (8 larvae & exuviae); Site 10 (1 larva); Site 24 (1 larva); Site 26 (1 larva); Site 27 (8 larvae & exuviae); Site 41 (1 larva); Site 42 (3 larvae).

POWYS: nr Newbridge-on-Wye, R. Hirnant, 2.iv.1976, P.S. Cranston.

COMMENTS

As with all species in the _calvescens/verralli_ group there has been some confusion in the identification of the immature stages, and it is not possible always to determine what an author meant by the species. All records of _calvescens_ determined prior to Lehmann's 1972 paper must be treated with reservations.

DISTRIBUTION AND ECOLOGY

Lehmann (1972:390) states that the adults are only known with certainty from Scandanavia, Austria, Belgium, England, France and West Germany. In Britain the adult is widespread but apparently never very abundant. Fahy records the larva as abundant in a lotic system in the west of Ireland. Larval records, and pupal records (Langton, unpublished) suggest that this is a common species, probably the most widely distributed and abundant species in the genus _Eukiefferiella_.

Eukiefferiella claripennis (Lundbeck)

Eukiefferiella claripennis (Lundbeck, 1898:281)
Eukiefferiella hospita (Edwards, 1929:351); Zavrel, 1939:9
Eukiefferiella stylifer Goetghebuer, 1949:413 sensu Humphries & FitzGerald 1949:414.

DESCRIPTION OF 4TH INSTAR LARVA (n = 16)

Body length 3.5 (3.0-3.9) mm, head capsule 352 um (296-392). Head capsule dark yellow to brown with mandible, occipital margin, mentum and premandible dark brown.

Antenna (Fig. 26g). Four segmented, lengths: 55 (49-60); 15 (13-16); 2 (1-2.5); 5.5 (4-6). Antennal ratio 2.4 (2.1-2.8). Antennal spine 17 14-19) never extending as far as the end of the fourth segment. Ring organ 8.8 (6-11) from base of first antennal segment.

<u>Mandible</u> (Fig. 26e). 88 (84-98) long with apical tooth shorter than inner three combined. Seta subdentalis 9 (8-11) long, seta interna with 5-6 branches, the outer two or three with fine serrations at the apex.

<u>Labrum</u>. All S setae simple, premandible 44 (39-50) long, short and blunt.

<u>Mentum</u> (Fig. 26f). Flattened width 61 (58-68). Paired median teeth subequal to the first laterals. Five pairs of lateral teeth, the outermost bulbous at base.

<u>Abdomen</u>. Procerci darkly pigmented with some traces of a heavily sclerotised area posteriorly. Procerci 26 (22-31) high and 24 (18-26) wide, bearing 6 or 7 setae apically. Posterior parapods longer than usual, 230 (212-243) long (or more in some unmeasurable specimens), anal tubules c 50 long by 40 wide. Anterior parapods with medium and small claws bearing several inner teeth. These claws golden yellow, the posterior claws dark brown. Longest body seta 75 (53-87).

MATERIAL EXAMINED

Site 7 (16 larvae, many reared); Site 8 (1 larva); Site 10b (2 larvae); Site 12 (1 larva); Site 46 (2 reared); POWYS: Nr Newbridge-on-Wye, River Hirnant, .iv.1975 (2 reared larvae); WEST SUSSEX: Rogate, River Rother, .vii.1975 (1 reared larva); (both records P.S. Cranston); KENT: Westwell, 4 kms. N.N.W. Ashford, v.1975, R.W. Crosskey (ex-cocoon <u>Simulium spinosum</u>) (2 larvae); HERTFORDSHIRE: Radwell, vi.1918, F.W. Edwards, determined Zavrel 1939 (3 larvae, 1 pupa).

COMMENTS

Lehmann (1972:349) states that <u>Eukiefferiella stylifer</u> Goetghebuer is a nomen dubium but notes that the description by Humphries and FitzGerald of the pupa resembles that of <u>claripennis</u>. Examination of the larval material of stylifer collected by Humphries at the type locality at the same time as the material described shows that this is indeed *claripennis*. Although most of the description given by Humphries corresponds with the material examined she has drawn a distinctly five segmented antenna for *stylifer* and there is no mention of the number and distribution of mental teeth. It is possible that the antenna has been drawn from another species - all eleven specimens I have examined have only four segments.

Since the adult description is so weak that it could be *claripennis* or many other species, the pupal description is very like *claripennis* and eleven larvae identified as *stylifer* by Humphries (larvae which may in fact have type status) are *claripennis* it is suggested that *stylifer* is a junior synonym of *claripennis*.

DISTRIBUTION AND ECOLOGY

The adult is distributed throughout England and Wales, and is recorded from Greenland to Austria and France. The larvae have been found in Britain in a number of sites, but it was only frequent at site 7. These sites range from the spring source of a chalk stream through fast flowing cold mountain streams to slow flowing lowland chalk streams.

Lehmann (1972:359) states that the larvae are eurythermic but rheobiont, although Brundin (1949:702) records the species from the littoral zone of a lake.

Eukiefferiella clypeata Kieffer.

Eukiefferiella clypeata (Kieffer, 1923:146)

Dactylocladius "Schildgespinst" Potthast, 1915:293.

DESCRIPTION OF 4TH INSTAR LARVA (n = 2)

Body length 4.4 mm, head capsule length 371 - 381 um, yellow-brown to pale brown with occipital margin, mentum and premandible darker brown. Mentum with anterior part brown and a symmetrically darkened posterior area each side of median line of mentum (Fig. 27d).

Antenna (Fig. 27a). egment lengths 50-52; 15-16; 3; 4; antennal ratio 2.2 - 2.3. Other authors (Potthast 1915:293, Zavrel 1939:10) state that there are five antennal segments with the third segment extremely small. On the two specimens examined there are four segments, although there is a larger than normal unsclerotised area between the second and third segments which may have been mistaken for an intermediate segment by earlier workers. The antennal spine is 21 - 24 long, not extending beyond the final antennal segment. Ring organ present in first third of basal segment.

Mandible (Fig. 2/c). 88-92 long with apical tooth only slightly longer than any of the three inner teeth. Seta subdentalis 7 - 9 long, seta interna with 5 or 6 branches, all of which are simple. Inner margin of mandible with three short spines.

Labrum (Fig. 27b). All S setae simple. SI and SII slender. Premandible 48 - 5O long, somewhat broader than normal for the genus. Apically paler than at the base.

Mentum (Fig. 27d). Flattened width 60-63, narrower than usual. Paired bulbous median teeth with five pairs of narrow lateral teeth. Ventromental plates absent. As mentioned above the basal part of the mentum is distinctly darker than the anterior part.

Abdomen. Procerci 18 - 19 high and 18 - 21 wide, weakly sclerotised, be ring 7 apical setae of maximum length 286 - 318. Lower lateral seta 47 - 53 long, less than usual in the genus, as is the 29 long supra-anal seta. Posterior parapods 254 -

286 long, anal tubules indistinct or absent. Claws of posterior parapod simple and brown, those of the anterior parapod simple, finer than posterior and dark yellow-brown. The longest body setae on segments 1 and 2, 80 long. Most of abdominal segments with only short, fine setae at most.

MATERIAL EXAMINED

NORTHUMBERLAND: Upper North Tyne River, 22.ix.1975, A. Brennan (2 larvae associated with reared pupae).

DISTRIBUTION AND ECOLOGY

Eukiefferiella clypeata is a poorly known species with scattered records from throughout Europe as an adult. The species is recorded for the first time from the mainland of Britain with these larvae - the species was added to the British list by Murray (1972:284) from Ireland.

The ecology of the larvae is poorly known. There are records from the River Fulda (Lehmann, 1971:481) for pupal exuviae in the rhithral and potamal, and he cites previous larval records by Zavrel (1939:26) from the banks of the Jihlavka in *Glyceria* growth on the banks in a polluted area. Thienemann (1936:63) found the larvae on stones in fast flowing streams, the larvae either freeliving or in cocoons. The locality for the specimens examined is fast flowing upland small river (Brennan pers.comm.).

Eukiefferiella discoloripes Goetghebuer

Eukiefferiella discoloripes Goetghebuer, 1936:51: ? Zavrel 1939b:4.

Eukiefferiella verralli (Edwards, 1929:346) sensu Lehmann 1972:393 (misidentification of pupa)

DESCRIPTION OF 4TH INSTAR LARVA (n = 6)

Body length up to 6.5 mm, head capsule 494 (455-550), yellow with occipital margin, mentum and mandible dark brown. Premandible golden.

Antenna. (Fig. 28a). Five segmented, lengths 80 (74-85); 20.5 (20-21); 3.7 (2.5-4); 6.2 (5-7.5); 5 (5-5.5). Antennal ratio 2.25 (2.11-2.45). Antennal spine bifid, the long outer branch 42 (36-46) long. Ring organ 8-10 from base of first antennal segment.

Mandible (Fig. 28b). 151 (145-158) long with the apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 13.4 (12-15) long, seta interna with 6 branches, each terminally branched. Inner margin of mandible smooth.

Labrum (as in verralli Fig. 28g). SI divided into 10 or more branches. SII and III simple, fine and long. SIV normal. Premandible 72 (68-79) long, blunt toothed as usual for the genus.

Mentum (Fig. 28c). Flattened width 109 (102-121) with median pair of teeth 26 (24-27) wide. These teeth in worn specimens appear single. Ventromental plates absent.

Maxilla. As in calvescens (Fig. 26d), but pecten galearis more distinctly sclerotised.

Abdomen. Procerci 61 (56-66) high by 31 (26-34) wide, bearing apically 5 (rarely 6) setae of maximum length 826 (212-318). Posterior parapod 233 - 339 long, anal tubules indistinct. Claws of anterior parapods golden, larger claws infrequently with a small tooth within. Claws of posterior parapod golden, simple. Longest body setae 262 (212-307).

MATERIAL EXAMINED

Site 19 (2 reared larvae, 1 larva); Site 21 (3 larvae).

COMMENTS

This species was identified by comparison of the pupal skin of the reared specimens with the pupal skins of the type material of *discoloripes*. This material was reared by Thienemann and the adults sent to Goetghebuer for description. Lehmann examined the pupae and determined it as *verralli* Edwards, probably unaware of the fact that it represented type material of *discoloripes*.

It is apparent that Lehmann did not have any definitely associated pupae and adults before him when he revised these two species of the genus *Eukiefferiella* and the basis of his association between the incorrect pupae and adults is not clear. The adults of the two species are only separated with difficulty by the presence or absence of wing vein r2+3 and the hypopygia are very similar so it is not possible to identify the pharate adult within a pupa as is sometimes the case.

The identification of the larva of *discoloripes* is based upon two larval exuviae which were reared to identifiable pupae and adults. Both of these had long antennal spines and were distinctly larger than the larvae associated with *verralli* pupae and adults. Although the samples are smaller this antennal spine character appears to separate all of these type of larvae into two groups which have no intermediates. Further confirmation is shown by the greater size of all larvae with long antennal spines than those with the short spines. Since the length of the spine is measured relative to the length of the antennal segments, and is not an absolute measurement, this is less likely to be a size related character.

DISTRIBUTION AND ECOLOGY

As shown above larval and pupal records of *discolorines* must be treated with caution due to confusion between this species and *verralli* Edw.. The adult of *discolorines* is recorded only from Germany and Austria. The name is on the British list for a larva recorded by Humphries, but this record may be in doubt. However the material examined here, as well as pupal records from Langton (unpublished) show that the species is present in Britain. Both the sites it is recorded from in this study are fast flowing upland streams with numerous springs in the bed and banks.

Eukiefferiella gracei (Edwards)

Eukiefferiella gracei (Edwards, 1929:346)

Dactylocladius longicalcar sensu Potthast, 1915:290 not Kieffer, 1911, misidentification

Eukiefferiella longicalcar sensu Zavrel, 1939:7 not Kieffer, 1911, misidentification.

Eukiefferiella potthasti Lehmann, 1972.

DESCRIPTION OF 4TH INSTAR LARVA (n = 8)

Body length 5.2 mm (4.3-6.2), head capsule length 450 um (400-510), dark yellow with mandible, mentum and occipital margin dark brown.

Antenna (Fig. 29a). Segment lengths 53.5 (51-55); 14.2 (13-16); 3.6 (3-4.5); 5.7 (5-6.6); 4.5 (4-5). Antennal ratio 1.92 (1.79-2.08). Antennal spine 29 (25-34), subsidiary spine 10 (9-11) long. Ring organ 6.6 (4-9) from base of first antennal segment.

Mandible (Fig. 29b). 142 (132-153) long with apical tooth shorter than inner three teeth. Seta subdentalis 9.2 (6.6-10.5) long, seta interna with 5 or 6 terminally plumose branches.

Labrum. All S setae simple. Premandible 80 (64-87) long, normal for the genus.

Mentum (Fig. 29c). Flattened width 110 (95-120) with broad median tooth 32 (28-36) wide. Ventromental plate absent.

Abdomen. Procerci 26 (21-29) high by 22 (20-26) wide bearing (5) 6 or 7 apical setae, maximum length 470 (390-508). Lower lateral seta 117 (84-137) long. Posterior parapod 275 (230-340) long, anal tubules 84 (63-106) long. Anterior parapods with medium length claws (Fig. 29d) bearing one or two inner teeth. Longest body seta 160 (138-190) long.

MATERIAL EXAMINED

Site 20 (8 larvae, several exuviae), Site 21 (8 larvae, several exuviae); GLOUCESTERSHIRE: Fairford, R. Coln, 30.v.1978, (F.B.A.) (1 larva).

DISTRIBUTION AND ECOLOGY

The adult is distributed through central Europe, and also Britain and Scandinavia. Until reared material was added, adults from Britain were only represented in the B.M. (N.H.) by the two syntypes from Ilkley, N. Yorkshire. Thienemann (1954:347,349,354&360) records the species from moss in streams and Zavrel (1939:27) mentions it from a small stream. In the Fulda Fittkau (cited by Lehmann, 1972:378) found this species on stones and in moss in swift flowing waters.

Eukiefferiella ilkleyensis (Edwards, 1929)

Eukiefferiella ilkleyensis (Edwards)

Eukiefferiella lutethorax Goetghebuer in Goetghebuer, Humphries & Fitzgerald, 1949:411, Pankratova, 1970:158.

Since there is some confusion about the separation of ilkleyensis from devonica: the larvae described here have been reared to *ilklevensis* pupae or have the characteristic dark head capsule exhibited by those specimens which were reared to *ilklevensis*. Specimens with pale head capsules, but otherwise similar, which have not been reared, and whose identity is uncertain are described as *Eukiefferiella* species B.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 7)

Body length 4.2 (4.0-4.4), head capsule length 465 (434-508), dark brown, mentum and mandible black.

Antenna (Fig. 30a). Segment lengths 51 (47-55); 11 (10-12); 4.1 (4-5); 7.0 (6-8); 5.8 (5-7). Antennal ratio 1.87 (1.67-2.06). Antennal spine 29 (26-31). Subsidiary spine 11.4 (10-14) long subapical on second segment, ring organ 4.5 (3-6) from base of first antennal segment.

Mandible (Fig. 30c). 124 (112-137) long with apical tooth shorter than inner three combined. Seta subdentalis 6 (5-7) long, seta interna of 4 or 5 plumose branches. Inner margin of mandible with (? always) 3 long pale spines.

Labrum (Fig. 30b). SI simple about 12 long, SII simple, 15 long, SIII bifid and longer than usual at about 13 long. SIV apparently absent. Premandible 67 (66-68) long, as normal for the genus.

Mentum (Fig. 30d). Flattened width 105 (95-111), median tooth 29 (28-31) wide. Only four pairs of lateral teeth.

Abdomen. Procerci 23 (18-28) high by 21 (20-23) wide, bearing 5 or 6 setae apically, maximum length 363 (330-402). Lower lateral seta 89 (74-97) long. Posterior parapod 193 (159-254) long, anal tubules 24 long (n = 1). Anterior parapods bearing inner teeth on the median length claws. Longest body seta 116 (100-127) long.

MATERIAL EXAMINED

Site 10b (2 larvae, 1 reared); Site 21 (1 larva); Site 41 (1 larva); Site 49 (3 larvae); DORSET: Tadnoll Brook, 30.v.1976, L.C.V. Pinder.

DISTRIBUTION AND ECOLOGY

Adults of the species are only known with certainty from Germany, Austria, Scotland and England. Within Britain the adult is only known from three localities: Ilkley and Malham Tarn (both N. Yorkshire) and the River Endrick (Strathclyde, Scotland).

Humphries and FitzGerald (1949:412) record the species (as _lutethorax_) as a larva from "swiftly flowing water amongst mosses and algae in the lower reaches and, less frequently, in a similar habitat in the upper reaches of the river" (Dodder). The observed distribution of the larvae here recorded shows that all except Site 21 are in the fast flowing middle to lower reaches of rivers. The exception is within 150 m. of the spring source of a stream (Site 21). There were no mosses at any of the sites, the only vegetation being algae on the surface of stones.

Eukiefferiella minor (Edwards)

Eukiefferiella minor (Edwards, 1929:348); Zavrel, 1939:7.
Eukiefferiella flavipes Goetghebuer, 1949:415; Humphries & FitzGerald, 1949:415-6.

DESCRIPTION OF 4TH INSTAR LARVA (n = 10)

Body length 4.1 mm (3.5-4.8), head capsule length 389 um (328-434) dark brown with mandible, mentum and occipital margin scarcely darker.

Antenna (as in _gracei_ Fig. 29a). Segment lengths 51 (47-58); 14.7 (13.5-16); 2.7 (2-3.5); 4.4 (4-5.5). Antennal ratio 1.85 (1.6-2.04). Antennal spine 32 (27-35) long, ring organ 4.6 (3-7) from base of first antennal segment. Subsidiary spine at apex of second antennal segment 9 (8-11) long.

<u>Mandible</u> (Fig. 29e). 112 (102-120) long with apical tooth shorter than inner three teeth. Seta subdentalis 7.5 (6-8) long, seta interna with 6 or 7 branches, several terminally serrate. Inner margin of mandible with (? always) one spine.

<u>Labrum</u>. All S setae simple. Premandible 64 (58-71) long, as normal for the genus.

<u>Mentum</u> (Fig. 29f). Flattened width 90 (79-100) with broad median tooth 25.5 (23-29) wide, Ventromental plates absent.

<u>Abdomen</u>. Procerci 24 (21-29) high by 22 (18-26) wide, bearing 6 or 7 apical setae of maximum length 416 (380-445). Lower lateral seta 130 (124-146) long. Posterior parapod 236 (212-275) long, anal tubules 89 (74-120) long. Anterior parapods with the medium length claws bearing a few inner teeth. Longest body setae 140 (131-150).

MATERIAL EXAMINED

Site 3 (3 larvae); Site 19 (3 larvae); Site 21 (2 larvae); CORNWALL: Polridmouth, 28.ix.1976, J.E. Marshall; POWYS: R. Hirnant, nr Newbridge-on-Wye, 2.iv.1975, P.S. Cranston (1 larva).

DISTRIBUTION AND ECOLOGY

The adult is widely distributed in northern and central Europe and the presence of only five specimens from upland Britain in the B.M. (N.H.) collections is anomalous, perhaps because the first emergence period is early in the ye r and a second one is possibly quite late, times when collectors were less active. The larvae were found in large numbers near the spring source of a stream (Site 24) and also lower down the streams in fast flowing water (Sites 3 and 19). Lehmann (1971:483) records the species from moss covered stones in fast current, and cites Thienemann's (1954:347) records from moss in highland streams. The observations from Britain confirm this with the possible exception of the Cornish record. Here the flow was fast but the altitude low (near the coast).

Eukiefferiella verralli (Edwards)

Eukiefferiella verralli (Edwards, 1929:346); Fahy, 1972:31. Eukiefferiella discoloripes Goetghebuer, 1936 sensu Lehmann, 1972:391 (misidentification of pupa).

DESCRIPTION OF 4TH INSTAR LARVAE (n = 8)

Body length up to 5.5 mm, head capsule 448 (402-498), yellow with occipital margin, mandible and mentum brown to black.

Antenna (Fig. 28d). Five segmented, lengths 71 (66-79); 20 (19-24); 3.3 (3-5); 5.4 (5-7); 4.4 (3-5). Antennal ratio 2.14 (1.97-2.37). Antennal spine 27 (24-31) long extending at most to the fourth antennal segment. Ring organ 8 - 10 from base of first antennal segment.

Mandible (Fig. 28e). 116 (104-122) long with apical tooth shorter than the combined width of the three inner teeth. eta subdentalis 12-13 long, seta interna with 5 or 6 branches, each terminally branched. Inner margin of mandible smooth.

Labrum (Fig. 28g). SI divided into 10 or more branches. SII and III fine and simple, SIV normal. Labral chaetae strongly serrate as in calvescens, discoloripes, ilkleyensis (Fig. 30b etc.) Premandibles 66 (63-71) long, blunt as usual in the genus.

Mentum (Fig. 28c). Flattened width 93 (84-100), double median teeth (single when worn) 19 (16-21) wide. Ventromental plates absent.

Maxilla. As in _calvescens_ and _discoloripes_.

Abdomen. Procerci 55 (46-32) high by 26 (21-31) wide bearing 5 (rarely 6) setae apically, of maximum length 672 (614-795). Lateral seta 168 (131-190), supra-anal seta 271 (243-286). Posterior parapod cir a 250 long, anal tubules small. Claws of anterior parapod golden, usually simple with a few claws with an inner tooth. Posterior parapod claws simple, darker yellow. Longest body seta 257 (180-349).

MATERIAL EXAMINED

Site 14 (2 reared, 7 larvae); Site 29 (1 larva); Site 49 (1 larva); NORTHUMBERLAND: River North Tyne, 1.iv.1975, A. Brennan (2 reared larvae).

COMMENTS

Until it was possible to examine the material upon which Lehmann based his diagnosis of the pupae of this species and _discoloripes_ there was confusion over the identity of the species in this group. The material examined here was reared to an adult identical with the type of _verralli_ (Edwards), but the pupa was of the _discoloripes_ type in the sense of Lehmann (1972:391). As discussed under _discoloripes_ (page 163) examination of the type pupal skins of _discoloripes_ showed that they had been identified by Lehmann as _verralli_ and figured as such in 1972:fig.83. Evidence of the confusion comes in the paper of Fahy (1972) in which pupae without shagreen on abdominal segment 1 is identified as _verralli_ by Lehmann; a correct determination, but in conflict with the diagnosis in his revisionary work of the same year.

Although the figures are poor and spines are shown on the mandible (ab ent in specimens examined for this study) the measurements of the basal antennal segment and mandible suggest that the larva Fahy describes as *verralli* is correctly identified. Unfortunately the mandibular spines cannot be checked since the material is missing (Fahy pers.comm., O'Connor, National Museum of Ireland, pers.comm.).

DISTRIBUTION AND ECOLOGY

Adult *verralli* have been recorded from Austria, France, Scandinavia and West Germany as well as Britain and Ireland. Within Britain the adults have been recorded infrequently since the original specimens of Edwards. Most records are for hilly areas in the north and in Wales. The larval records here are from a range of flowing waters lowland and upland, but the number of specimens is limited and little can be said concerning the ecology.

Eukiefferiella species A

DESCRIPTION OF 4TH INSTAR LARVA (n = 1)

Body length 4.1 mm, head capsule length 381 um, head capsule pale brown with mentum, mandibles and premandibles darker brown.

Antenna (Fig. 30e). Four segmented, lengths 50; 16; 3; 5; antennal ratio 2.08. Lauterborn organs distinct, ring organ 12 from base of first antennal segment. Antennal spine 18 long, subsidiary spine 5 long.

Mandible. 90 long, apical tooth shorter than inner three teeth combined. Seta subdentalis 8 long, seta interna with 4 or 5 branches, all simple. Traces of the stumps of three spines present on inner margin of mandible.

Labrum. All S setae simple. Epipharynx as in *clypeata* (Fig.27 b). Premandible about 34 long, broad and blunt as usual in *Eukiefferiella*.

Mentum. (Fig. 30f). Broad domed median tooth as broad as the combined width of the four lateral teeth. Mentum width 63, ventromental plates absent.

Abdomen. Procerci 21 high, 23 wide, bearing apically 7 setae of maximum length 275. The lower lateral seta is shorter than usual at 45, and the supra-anal seta is similarly reduced. Hind parapod 243, anal tubules 84 long by 40 wide. The claws of the anterior parapod are golden and the medium sized claws bear several internal teeth. The posterior parapod claws are simple and golden brown. The longest body setae are only 15 to 20 long and sparsely distributed.

MATERIAL EXAMINED

DORSET : River Frome, ex-weed, 24.v.1977, L.C.V. Pinder.

COMMENTS

This larva is distinct among *Eukiefferiella* by the combination of only four pairs of lateral mental teeth, a broad domed median mental tooth and the four segmented antenna. No larva fitting this description has been noted previously. An examination of the pupa within the larva indicates that this is a species either new to science, or one in which none of the metamorphic stages have been described.

Since only a single specimen has been seen nothing can be said about the distribution or ecology of the species. The larva does not belong with the *calvescens*-group of species, and the simple SIII suggests that it is not related to the *ilkleyensis*-group. Characters of the pupa suggest a relationship with *claripennis*.

Eukiefferiella species B

DESC IPTION OF 4TH IN TAR LARVA (n = 8)

Body length 3.6 (2.8-4.4), head capsule length 470 (422-508), yellowish brown with dark brown mandible and mentum. Occipital margin only slightly darker than surrounding head capsule.

Antenna. Segment lengths 52 (45-55); 11.8 (10.5-13); 4.4 (4-5); 7.2 (6-3.4); 5.4 (5-6). Antennal ratio 1.81 (1.72-2.04). Antennal spine 29 (27-34) long, subapical spine 13-14 long on second antennal segment. Ring organ 4 (3-6) from base of first antennal segment.

Mandible. 146 (132-158) long with apical tooth shorter than inner three teeth combined. Seta subdentalis 7 - 9 long, seta int rna with 5 branches, terminally plumose.

Labrum. SI and SII simple, SIII bifid and longer than usual, (c. 13). Premandible 62 (58-66) long as normal for the genus.

Mentum. Flattened width 109 (95-121), median tooth 31 (27-34) wide. Only four pairs of lateral teeth.

Abdomen. Procerci 23 (20-26) high by 22.4 (20-26) wide, bearing 6 setae, maximum length 270 - 340. Lower lateral seta 93 (80-105) long. Posterior parapod 197 (170-265) long. Anal tubules not visible in any specimen examined. Median length claws on anterior parapod with inner teeth. Longest b dy seta 109 (100-116) long.

MATERIAL EXAMINED

Site 12 (1 larva); DORSET: Tadnoll Brook, 30.v.1976, L.C.V. Pinder; GLOUCESTERSHIRE: Fairford, R. Colne, 30.v.1978, (F.B.A.).

COMMENTS

This species is separable from ilklevensis Edwards only by the paler head capsule. Whether or not it deserves specific status is uncertain until it can be reared. The presence of a second species in the ilklevensis group, based on adult male and pupal morphology (devonica Edwards), suggests that this may be a different species to ilklevensis. Head capsule colour is apparently an important character in separating the larvae of Eukiefferiella (vide minor and gracei, and calvescens from verralli and discoloripes).

DISTRIBUTION AND ECOLOGY

The three localities at which this larva has been found are all the middle reaches of rivers. All three are on chalk, but with such a limited sample it would be unwise to speculate on the ecology of this species.

Eukiefferiella species C

? Eukiefferiella cfr. similis Zavrel, 1939 sensu Pankratova, 1970:157

DESCRIPTION OF 4TH INSTAR LARVAE (n = 4)

Body length 5.7 (5.4-6.3) mm, head capsule 481 (477-490) um. Head capsule yellow or pale brown, mentum, mandibles and occipital margin darker brown.

Antenna (Fig. 31a). Five segmented, lengths 79 (75-83); 21.5 (20-23); 5 (4-7); 6.6 (6-7); 4.4 (3.5-5). Antennal ratio 2.17 (2.08-2.24). Antennal spine 21 - 26 long, ring organ 9 - 13 from base of first antennal segment. Lauterborn organ single, small.

Mandible (Fig. 31d). 127 (118-148) long, outer tooth shorter than three inner teeth combined. Seta subdentalis 8 - 10 long, seta interna six to seven branched ? all simple.

Inner margin of mandible smooth.

Labrum (Fig. 31b). SI feathered, remaining setae simple. SI 12 - 13 long with circa 12 branches. Premandible 74 (66-79) as normal for the genus.

Mentum (Fig. 31c). 121 (110-129) wide, median tooth 24 - 26 wide bearing a median projection, apparently easily worn away. Ventromental plates absent as usual.

Abdomen. Procerci 58 (53-61) high by 35 (24-40) wide bearing 7 or 8 apical setae of maximum length 742 (689-795). Lateral seta 165 (147-190). Supra-anal seta 405 (371-424). Posterior parapod 254 - 324 long, anal tubules 106 - 1?7 long. Claws of anterior parapod simple, golden, those of the hind parapod simple and dark. Longest body seta 275 (265-296).

MATERIAL EXAMINED

GLOUCESTERSHIRE: Eyreford, River Coln, 42/0320, 25.iv.1978, (3 larvae); DORSET: Tadnoll Brook, no further data (1 larva), (both F.B.A.).

COMMENTS

This species with a feathered SI, long body setae, tall procerci and pale head capsule clearly belongs in the calvescens/verralli group. There are three species in this group which have undescribed or inadequately described larvae. They are bavarica Goetghebuer, scanicus Brundin and saanensis Wulker. Larvae ascribed to the first species are indistinguishable from calvescens as are the pupae. The thoracic horns of one of the pupae visible within the larvae of species C is remarkably long at 600 um, and Wulker (1959: 54) shows a similar thoracic horn for saanensis. The immature stages of scanicus are not known.

DISTRIBUTION AND ECOLOGY

Apart from the two British records the species may be known from the U.S.S.R. (Pankratova, 1970:157)

Eukiefferiella species D

? Eukiefferiella tirolensis Goetgh buer, 1938

DESCRI TION OF 4TH IN TAR LA"VAE (n = 6)

Body length about 4 mm, head capsule 358 (318-381), head capsule brown or pale brown, occipital margin, mentum, mandible and premandible darker brown.

Antenna (Fig. 32a). Five segmented with segment lengths 57.8 (55-61); 14.8 (13-16); 1.8 (1-2); 3.2 (3-3.5); 3.8 (3-4). Antennal ratio 2.40 (2.36-2.59). Ring organ 7.5 (6-10) from base of first antennal segment. Spine 15 (13-17) long, subsidiary spine at apex of second antennal segment 5 long.

Mandible (Fig. 32c). 88 (83-92) long with apical tooth shorter than three inner teeth. Seta subdentalis 7 (6-8) long. eta int rna with five or six branches which are bluntly forked at the apex. Inner margin with three or four spines.

Labrum. As in brevicalcar. Premandible 46 ?40-52) long.

Mentum (Fig. 32b). 59 (52-64) wide when flattened. In unworn specimens the median tooth has a saddle shaped apex which is rapidly worn away giving the impression of a single tooth (as shown in figures above complete mentum). The median tooth is 10.4 (10-11) wide at the base, more than twice the width of a lateral tooth. Ventromental plates absent.

Maxilla. As in brevicalcar (Fig. 25d) with distinctive sensilla basiconica.

Abdomen (n = 1, except for anterior parapod claws). Procerci 25 high by 21 wide, heavily sclerotised and bearing apically 6 setae of maximum length 339. Lateral seta 132, supra-anal seta 63. Claws of posterior parapod yellow-brown, simple. Claws of anterior pa apod (Fig. 32d) yellow; the smallest claws simple, the next size with several fine teeth all longer than the apical tooth. The next largest claws have one or two blunt teeth inside and the largest claws are simple. There appear to be more of the fine toothed claws than in brevicalcar.

MAT_RI L EXAMINED

Site 26b (5 larvae reared to pupae); ite 40 (1 larva reared to a pupa).

COMMENTS

This larva is very similar to brevicalcar particularly when the median tooth of the mentum is worn. However even when worn the median tooth is wider in species D both in absolute t rms and also relative to the lateral teeth. There appears to be some difference in the antenna - the first segment is longer in most specimens of species D, and the spine is somewhat shorter. There also seem to be more of the multiple spined claws in species D. These characters must be treated with caution since there is some overlap and for species D most of the data comes from a single specimen.

The basis for the tentative identification of the species as tirolensis Goetghebuer is the pupal skin, briefly described by Lehmann, 1972:363. The separation of this species in his key is tenuous and difficult to determine. However examination of specimens in Munich Museum determined as tirolensis Goetghebuer by Lehmann showed that there is a better character for separation of the species from brevicalcar. This is the number of hooked spines on each side of the midline on tergites 3, 4 and 5. In brevicalcar this number is at least six but usually seven upwards, and the hook row is sometimes undivided medially. In tirolensis the row is clearly divided and contains less than five hooks, often only two or three, on each side of the midline.

It is the larvae which give rise to the *tirolensis*-type of pupa which have been described here as species D. Were it not for the relatively shorter thoracic horn of *fuldensis* Lehmann this pupa would also resemble the *tirolensis*-type. *fuldensis* is described from a limited amount of material and Lehmann seemed unaware of the potential variability of the length of the thoracic horn. It is possible that *fuldensis* lies within the range of size variability of *tirolensis*. Since there is still some confusion over specific identification in this group it is preferable not to apply the name *tirolensis* to the larva here described as species D until a greater number of specimens in all life history stages can be examined.

DISTRIBUTION AND ECOLOGY

tirolensis has been recorded as an adult from Germany, France, Austria, Spain and Switzerland. It has not been recorded from Britain, and the larva has not been found before so little can be said of the ecology. The two localities in which the larvae were found in Britain were quite similar although geographically far apart. Both were small rivers no more than 20 cms deep with a medium flow rate over a stony bed with a good cover of algae. Both sites were quite open and in both cases there was probably some agricultural pollution.

In Europe the only information about the pupal sites are summarised by ehmann (1972:363) as a mo ntain stream in Germany and a single record from France with no further data. The adult has been taken at 2,400 m.o.d. in central Spain.

xiv. Gymnometriocnemus Goetghebuer

Gymnometriocnemus Goetghebuer, 1932:23, Kruger & Thienemann, 1941:185-195.

Type-species Metriocnemus subnudus Edwards, 1929 by subsequent designation of Goetghebuer, 1940:7.

GENERIC DIAGNOSIS (Based on unreared British material and descriptions of Kruger & Thienemann)

Medium sized to small larvae, up to 6 mm long.

Antenna. Five segmented with variable length segments. Either the fourth segment much longer than third (subnudus Edw.) or third and fourth subequal (Fig.33 a - ? brumalis Edw.). The antennal spine may extend beyond the fifth antennal segment and the ring organ is distinct. Lauterborn organs longer and more distinct than in Bryophaenocladius.

Labrum (Fig.33 b). Very like Bryophaenocladius. SI and SII simple, lanceolate. SIII further anterior than usual. SIV present. Premandible darkened with three teeth.

Mandible. As in Bryophaenocladius (Fig. 8f). Seta interna and subdentalis absent.

Mentum (Fig. 33c). Two broad apical teeth (less broad in subnudus) with four pairs of lateral teeth. Ventromental plates distinct and sclerotised but not extending beyond flattened mentum. Apparently no second pair of ventromental plates.

Abdomen (Figs.33 d and e). Anterior parapods fused, without claws but with fine setae (Fig.33 d). Posterior parapods present, each divided into two parts, the anterior part bearing claws, the posterior part bare. Anal tubules absent, but posterior parapods capable of retraction into preanal segment of abdomen. Parapods and anal segment at right angles to the axis of the body. Procercus absent but at least some anal setae, at most dorso-oral, anal and preanal setae present.

COMMENTS AND SYSTEMATIC STATUS

See Bryophaenocladius (Page 84).

DISTRIBUTION AND ECOLOGY

The species figured is referred to brumalis Edwards since the collector A. Seddon found only this species as an adult in a lengthy ecological survey using emergence traps in ESSEX: Epping Forest. The genus is terrestrial and the basis of the observation of aquatic habit in Fittkau & Reiss in Limnofauna Europea for brumalis is uncertain.

xv. Halocladius Hirvenoja

Halocladius Hirvenoja, 1973:106.

Cricotopus v.d. Wulp, 1874 sensu auctt. (partim).

Type-species Chironomus varians Staeger, 1839:573, by original designation.

GENERIC DIAGNOSIS (modified from Hirvenoja, 1973:109).

Medium sized larvae up to 8 mm long.

Antenna (Fig. 34a). Five segmented with the third and fourth segments subequal, both larger than the fifth. Lauterborn organs indistinct or absent. Antennal spine does not extend beyond the final antennal segment. Subsidiary spine extends to apex of fourth segment. Ring organ low on the first antennal segment.

Labrum. SI bifid in all British species (plumose with about 10 branches in non-British subgenus Psammocladius). Other S setae simple. Pecten epipharyngis of three subequal spines as in Cricotopus s.s. (see Figs.17b & 19b). Chaetulae laterales broad and simple, chaetulae basales teriminally branched. Premandible (Figs. 34b & c) in British species with one or two apical teeth and sometimes with an indistinct premandibular beard.

Mandible (Fig. 34f). Apical tooth shorter than width of three inner teeth combined. Seta subdentalis and seta interna present. Inner margin smooth. Outer margin smooth.

Mentum (Figs. 34d & e). One median tooth and six pairs of laterals. Ventromental plates absent, no setae beneath.

Abdomen. Parapods present. Procerci as high as wide and bearing apically six o seven setae. Anal tubules absent. Only fine, simple setae present on body segments.

COMMENTS AND SYSTEMATIC STATUS

Halocladius was separated from *Cricotopus* by Hirvenoja (1973) and all the included species are halobionts. The three British species have been found around the coast of Britain, but being marine are only included in this survey for completeness of the generic survey.

The descriptions and figures of the larvae by Hirvenoja are excellent and permit recognition of the three British species. The key to the three British species below is modified from Hirvenoja (1973:115) after examination of the British material available, and the only figures given are those required for the key.

Hirvenoja (loc.cit.) states that this genus is the sister group of *Cricotopus* as he redefines the genus. No evidence is presented to dispute this thesis.

KEY TO TH. BRITI H SPECIES (modified from Hirvenoja)

1 Second lateral mental teeth reduced and partially fused with the first laterals (.ig. 34d). Premandible with two distinct apical teeth as well as inner teeth (Fig. 34b) .... _fucicola_ (Edwards)
All lateral mental teeth subequal, the second not fused to the first (Fig. 34e). Premandible with one strong apical tooth as well as the inner teeth (Fig. 34c) 2

2 On the anterior parapod the smallest claw bearing more than one inner tooth has the apical tooth longer than any of the inner teeth (see Fig. 34g) ..... _varians_ .taeger
On the anterior parapod the smallest claw bearing more than one inner tooth has the apical tooth shorter than the next inner tooth (see Fig. 34h) .... _variabilis_ Staeger

DISTRIBUTION AND ECOLOGY

Hirvenoja (loc.cit.) discussed the ecology of these three marine species and no additional information is presented in this survey.

xvi. _Heleniella_ Gowin

Heleniella Gowin, 1943:116

Type-species _Heleniella thienemanni_ Gowin, 1943 (= _ornaticolis_ Edwards) by monotypy.

GENERIC DIAGNOSIS (based on the larvae of the British species, the only one described).

Larva small, up to 4.5 mm long, head capsule 250 um.. Head capsule yellow with some darkening of mandibles and mentum.

Antenna. Five segmented, second segment shorter than first, fourth longer than third. Second antennal segment with a weakly sclerotised portion at the extreme of proximal third. Lauterborn organs present, as long as third antennal segment. Antennal spine long, extending beyond final antennal segment by the same distance as segments two to five. Ring organ present between $\frac{1}{2}$ and $\frac{2}{3}$ of the length of the first antennal segment.

Labrum. SI branched (4-7 from descriptions), SII simple and broad, SIII simple and narrow, SIV apparently in two, one short spine, one peg-like. Pecten epipharyngis of three broad spines, chaetae laterales 5 or 6 pairs of broad spines (almost lamellar in shape). Premandible present with three or four teeth.

Mandible, with an apparently short apical tooth and three inner teeth. Seta interna of many fine branches, seta subdentalis very small.

Mentum with a pair of broad central teeth, divided by a broad notch. Five pairs of lateral mental teeth, the first taller than the median teeth, the fourth pair smaller than the third or the fifth. Ventromental plates apparently absent, no setae beneath.

Abdomen. Parapods well developed with anterior claws terminally bluntly serrate, the posterior claws smooth. Procerci well developed with a long basal lateral seta. No setae on body.

COMMENTS AND SYSTEMATIC STATUS

Heleniella is a distinctive genus in all life history stages, and clearly belongs in the Metriocnemini. Within this tribe the genus has several plesiomorphic characters including the presence of procerci and separate parapods. Saether (1977) places Heleniella as the sister group of Parakiefferiella, Zpoicocladius and Krenosmittia combined and the larvae show a number of similarities which separate them from the more plesiomorphic Metriocnemini. These include the reduced plume of the SI seta, the absence of labral lamellae and setae under the ventromental plates and the reduced ventromental plates. Ringe (1976:264) examined the internal structure of the hypopygium of the adult male and concluded that this showed a relationship with Parakiefferiella and Krenosmittia although he did not examine all possible hypopygia.

Heleniella ornaticollis (Edwards, 1929)
Spaniotoma (Smittia) ornaticollis Edwards, 1929:359
Heleniella thienemanni Gowin, 1943. Synonymy by Brundin, 1956.
DESCRIPTION OF 4TH INSTAR LARVA (n = 2, one with pupa visible within, one larval exuvium)

As generic description, with body length 4.2 mm and head capsule 250 - 265 long.

Antenna (Fig. 35a) with segments 35-39; 19-20; 2; 3; 2 long. Antennal ratio 1.35 - 1.48. Antennal spine 42 - 49 long, subsidiary spine 6 um long. Ring organ situated 22 - 23 from base of first antennal segment, large and clearly visible.

Labrum (Fig. 35b). SI 12 - 14 long with four apical teeth. SII 17 - 18 um long, broad and simple, SIII 7.5 um long, thin. SIV both 5 um long. Premandible 51 - 52 long with four teeth, the inner two poorly defined.

Mandible (Fig. 35d). 68 (worn) - 86 long. Outer tooth shorter than combined width of the three inner teeth. Contrary to the observations of Gowin the last mandibular tooth is not twice the size of the third tooth. Seta interna with six or seven branches; the outer three finely branched. Seta subdentalis only 5 - 6 um long.

Mentum (Fig. 35c). Flattened width 83 um. Outer mental teeth characteristically arranged: the fourth lateral teeth smaller than either the third or the fifth. The median mental teeth separated by a U-shaped notch.

Maxilla with anterior chaeta and antaxial setae terminally serrate.

Abdomen. Hind parapods 132 um long, claws simple. Fore parapods with ends of the claws bluntly serrate. Procerci 11 um wide by 12 um long, bearing 5 procercal setae of subequal length. Lower procercal seta long: 75 um. Supra-anal seta 106 um long.

MATERIAL EXAMINED

Site 50, River Duhonw (1 larva reared to pupa); CORNWALL: Brocton, R. Camel, 20/015 685 (F.B.A.) (1 larva with pupa visible within).

DISTRIBUTION AND ECOLOGY

Fittkau and Reiss (1978:418) record *Heleniella ornaticollis* from Scandinavia, the Pyrenees, the Alps and central European mountains, Spain, the Balkans and Ireland, but omit Edwards (1929:359) records from Britain (Durham and Lancashire). No further adult records have been made since Edwards, and the species is undoubtedly uncommon throughout much of its range.

Ringe (1974:241) found the adults, emerging from May to October, peaking in July and August in the brooks he studied near Schlitz (West Germany). The species occurred most frequently in the Breitenbach, less commonly in the Rohrwiesenbach.

All larval records are from running waters, usually from cold, fast flowing streams. Lehmann (1971) records specimens taken by Fittkau from a helocrene and from stones in a limnokrene. He also cites Thienemann (1954:350) who found the larvae in the mud of a mountain stream. Brundin (1956:144) stated that the larvae were rheophilic, which is confirmed by all studies since.

xvii. Heterotanytarsus Sparck

Heterotanytarsus Sparck, 1922:88

Type-species: Metriocnemus apicalis Kieffer, 1921, by monotypy.

GENERIC DIAGNOSIS

Small larvae, up to 3.5 mm long, head capsule up to 320 um long.

Antenna. Four segmented, the second longer than the first and the whole antenna subequal in length to the head. Lauterborn organs long and alternate on the second segment. Antennal spine fine and extends to near the end of the second segment. Ring organ between one third and the middle of the first segment.

Labrum and palatum. SI plumose, SII and SIII simple, SIV not visible. Pecten epipharyngis of fine spines, 5 chaetae laterales and 2 or 3 chaetae basales. Labral chaetulae plumose apically. Premandible with four teeth.

Mandible. Apical tooth slightly shorter than inner three teeth. Seta interna and seta subdentalis present.

Mentum. Distinctive with two pairs of median teeth recessed and five pairs of laterals. Ventromental plates extend beyond outer mental teeth without setae beneath.

Abdomen. Anterior parapods with two groups of claws, an additional pre pical group pr sent (Fig. 36e). Posterior parapods normally developed. Procercus at least twice as high as wide bearing 6 - 8 apical setae. Lower lateral seta of procercus often long, but not heavily sclerotised. nal tubules pr sent, shorter than posterior parapods.

COMMENTS AND SYSTEMATIC STATUS

Heterotanytarsus is a very distinctive larva, resembling, as the name implies, the larva of the Tanytarsiinae, particularly in the antennal structure. Brundin (1956:81) placed the genus, on the adult characters in his tribe Orthocladiini, but aether (1976:36) showed that this tribe is polyphyletic. Saether (loc.cit.) argues that Heterotanytarsus is the sister group of all the Metriocnemini plus all the more apomorphic genera of "Orthocladiini" and strictly warrants tribal status. This is unnecessarily cumbersome but r flects the position as a plesiomorphic non-Metriocnemine genus.

Heterotanytarsus apicalis (Kieffer, 1921)

Heterotanytarsus apicalis (Kieffer), Sparck, 1922:88-92, Thienemann 1941:fig. 29.

DESCRIPTION OF 4TH INSTAR LARVA (n = 6)

Body length 2.6 mm (2.1-3.1); head capsule length 294um (275-318) brown, with mentum and mandible darker. Prementum slightly darker than surrounding area.

Antenna (Fig. 36a). Segment lengths: 107 (104-108); 142 (138-145); 19.6 (18-21); 7.1 (5-8). Antennal ratio 0.64 (0.62-0.66). Antennal spine 105 (100-112) long, Ring organ 38 (34-44) from base of first antennal segment. Basal Lauterborn organ 22 (18-26) and distal Lauterborn organ 58 (55-60) from base of second antennal segment.

Mandible (Fig. 36b). 117 (110-121) long with apical tooth slightly shorter than three inner teeth. eta interna of 6 - 8 simple branches. Seta subdentalis 12 (9-15) long, simple.

Labrum and palatum (Fig. 36c). SI plumose, 26 (25-29) long, SII 40 (38-42) long, broad and simple, rising from a pedestal, SIII fine, 10 (10-11) long, SIV ?absent. Premandible 60 (58-61) long with four apical teeth, the outer one pointed, the inner three more blunt.

Mentum (Fig. 36d). Only slightly darker than surrounding head capsule, the median area usually paler. Width of flattened mentum 92 (87-97), ventromental plates extending beyond outer mental tooth by 17.5 (16-21) and 30 (24-34) long, no setae beneath.

Abdomen. Procerci 91 (89-95) high by 38 (31-4) ide, bearing 6 to 8 apical setae maximum length 839 (657-911). Lower lateral seta apparently of v riable length 218 (105-290) and, as with the 240 - 260 long supra-anal seta, tapering to a thin hair. Posterior parapod 135 (100-159) long, anal tubules 95 (84-116) long by 32 (30-33) wide.

MATERIAL EXAMINED

NORTHUMBERLAND: tributary of R. North Tyne, .xi.1977, A. Walentowicz (5 larvae); HAMPSHIRE: New Forest, Stockley, 40/35.025, 26.iii.1978, P.. Cranston (1 larva).

DISTRIBUTION AND ECOLOGY

Sparck (1922:91) records the larva from pools in woodland in Germany, and Thienemann (1944:589) mentions both moorland pools and moss in lake shores. Brundin (1949:703) summarises the distribution as northern: an oligotrophic species tolerant of humic material found in Swedish lakes where it is bivoltine. The only previous records of the species in running waters are those of Lehmann (1971:483) who found the larvae in the slowly flowing headwaters of the River Fulda, and Lindegaard-Petersen (1972:430) at several sites in Kolding Å, Denmark.

Based on records of the adult the species appears to be distributed through northern, western and central Europe. Saether (1975:260) has described a species *Heterotanytarsus perennis* from CANADA: British Columbia, which cannot be separated as a larva from *apicalis*. Within Britain *apicalis* is only known from three localities in Cumbria, all relatively oligotrophic bodies of water. Although the finding of the larvae in running waters suggests another species may be involved, rearing of the larvae by A. Walentowicz shows that the adults obtained are inseparable from *apicalis*.

xviii. *Heterotrissocladius* Sparck

Heterotrissocladius Sparck, 1922:92; Saether, 1975:1-67.

Type-species *Metriocnemus cubitalis* Kieffer, 1911:200 (?= *marcidus* Walker, 1856) by designation of Goetghebuer, 1940:6.

GENERIC DIAGNOSIS

Medium to large larvae, up to 9 mm long. Head capsule up to 500 um.

Antenna. Seven segmented, the third segment much shorter than the fourth and the seventh segment vestigial. Lauterborn organs absent, ring organ low, in the first quarter of the first antennal segment. Antennal spine not extending beyond terminal antennal segment.

Labrum and palatum. SI plumose, other S setae simple. Pecten epipharyngis of three weakly sclerotised serrate scales. Chaetulae laterales simple, chaetulae basales apically serrate. Premandible bifid.

Mandible. Apical tooth shorter than combined width of the three inner teeth. Seta subdentalis present, seta interna present.

Mentum. Median mental teeth paired, five pairs of lateral teeth. Ventromental plates distinct, extending beyond flattened mentum, without setae beneath.

Abdomen. Parapods, procerci and anal tubules all well developed.

COMMENTS AND SYSTEMATIC STATUS

The generic description above is based upon examination of one British species (*marcidus*) and the published description of another (*grimshawi*) which has not been taken in this study.

Heterotrissocladius and *Paratrissocladius* are very similar in the larval stage particularly in the structure of the antenna, mentum and labrum. The two genera are only separated on the structure of the spines of the pecten epipharyngis. The seven segmented antenna possessed uniquely in the Orthocladiinae by these genera shows that these are sister groups, and the fourth segment longer than the third indicates that they are both in the Metriocnemini.

The presence of normal procerci and parapods as well as the distinctly developed ventromental plates and plumose SI suggest that these two genera are amongst the more plesiomorphic genera of Metriocnemini. Saether (1975) suggests that the sister group of *Heterotrissocladius* and *Paratrissocladius* combined is *Parametriocnemus* and *Paraphaenocladius* combined and there is no evidence presented in this study to contradict this interpretation.

KEY TO THE BRITISH SPECIES OF HETEROTRISSOCLADIUS*

1 Postmentum dark brown to black. First antennal segment over 75 um long .... *marcidus* (Walker)
Postmentum pale, the same colour as the surrounding area of head capsule. First antennal segment less than 75 um long .... *grimshawi* (Edwards)

* This key is based upon the description of *grimshawi* Edw. by Saether (1975:74).

Heterotrissocladius marcidus (Walker)

Heterotrissocladius marcidus (Walker, 1856:177); Zavrel, 1934:8; Saether, 1975:32.

DESCRIPTION OF 4TH INSTAR LARVA (n = 10)

Body length 6.3 (5.1-7.4) mm, head capsule 404 (365-440)um. Head capsule yellow; mentum, submentum, mandible and premandible dark brown.

Antenna (Fig. 37a). Seven segmented, lengths 83 (78-89); 30.4 (27-36); 4.8 (4-6); 15.5 (14-18); 5.5 (5-6); 4.3 (4-5); 2.9 (2-4). Antennal ratio 1.31 (1.14-1.48). Spine 58 (48-66) long, subsidiary spine at apex of second antennal segment 7 - 8 long. Ring organ 9.8 (6-11) from base of first antennal segment.

Labrum and palatum (Fig. 37b). SI seta 24 - 27 long, apically plumose. SII 32 - 42 long, simple. Six or seven chaetulae laterales, two chaetulae basales. Premandible 78 (72-82) long, two apical teeth, one broad, blunt inner tooth.

Mandible (Fig. 37c). 154 (135-164) long, apical tooth shorter than combined width of three inner teeth. Seta interna present, six or seven branched, each teriminally serrate. Seta subdentalis 18 (14-21) long.

Mentum (Fig. 37d). Flattened mentum 126 (114-137) wide. Ventromental plates extend beyond flattened mentum by up to 30 um.

Maxilla (Fig. 37e). Antaxial setae broad and bluntly serrate. Pecten galearis present.

Abdomen. Procerci 42 (37-47) high by 32 (26-37) wide bearing six or seven apical setae of maximum length 713 (585-773). Both lateral setae of similar length - 71 (60-92). Supra-anal setae 148 (127-190) long. Posterior parapod 171 (158-190) long, anal tubules 131 (118-150) long by 39 (35-42) wide.

Claws of posterior parapods yellow-brown, simple. Claws of anterior parapods golden, finely serrate apically. Anterior to the base of the anterior parapods is a band of fine, straight 10 - 15 um long tr nslucent spines. This band extends for about a quarter of the circumference of the irst segment, and is dist'nctly separated from the claws of the parapod.

MATERIAL EXAMINED

Site 9 (12 larvae, 3 reared); Site 10a (1 reared); Site 3 (1 larva); Site 35 (1 larva); Site 40 (1 reared); Site 43 (1 reared); ite 47 (1 reared); Site 50 (1 reared); WALES: POWYS, nr Newbridge-on-Wye, R. Hirnant, .iv.1075, "in drift", P.S. ranston.

DISTRIBUTION AND ECOLOGY

Adults of this species have been recorded relatively infrequently from the British Isles considering the frequency of larval records, although the records which do exist are widely distributed throughout the country. In Europe the species is widespread from Scandinavia to the Pyrenees and it is also known from Canada and the U.S.A. (Florida).

Saether (1975:32) states that although the larvae are found in most water bodies (e.g. Brundin 1949, Thienemann 1954) they seem to prefer the littoral zones of lakes. In Britain, however, the species is most frequently found in cold running water, and is the dominant species in many of the acid, iron-rich streams in the Ashdown Forest. The paucity of adult capture may be due to the time of emergence - the first emergence in May and the second in September and October (Ringe, 1974:236) in Germany.

Heterotrissocladius grimshawi (Edwards)

Heterotrissocladius grimshawi (Edwards, 1929:313); Saether, 1975:53.

No larvae of this species have been found in the present survey, but for the purposes of identification the description of Saether (loc.cit.) should separate this species from *marcidus*, although the separation from the non-British *scutellatus* is not possible in the larval stage.

Beside the characters noted in the key, Saether notes that the antennal ratio in *grimshawi* is less than 1.12; it is greater than 1.14 in *marcidus* in Britain.

This species is a typical lake inhabitant, with maximum abundance in the profundal and sublittoral zones of lakes. Brundin (1949:704) says that this is a northern species, present in polyhumic and moderately eutrophic lakes, but most abundant in oligotrophic lakes. This information, as well as the British distribution of the adults, suggests that the larvae may be found in northern meso- or oligotrophic lakes, particularly those in Scotland.

xix. _Krenosmittia_ Thienemann & Kruger

Krenosmittia Thienemann & Kruger, 1939:253.

Type-species _Smittia gynocera_ Edwards, 1937 sensu Thienemann & Kruger, 1939 (misidentification, = _camptophleps_ (Edwards, 1929:353) by monotypy.

GENERIC DIAGNOSIS (Based on Thienemann material and description).

Small species up to 3.5 mm.

Antenna (Fig. 38a). Thienemann & Kruger (loc.cit.) state that the antenna is five segmented with the fifth longer than the fourth and the third longer than the fourth. Examination of material determined by Thienemann shows a four segmented antenna however with the terminal segment longer than the third. It is not possible to determine whether there is a fifth segment present; the material has suffered from the lengthy storage in alcohol. The Lauterborn organs appear to be small and the outer branch of the strongly bifid antennal spine extends no further than the terminal antennal segment. The ring organ is weak about half way up the first antennal segment.

Labrum (Fig. 38b). SI described as terminally serrate (difficult to confirm from material examined as with most labral characters). Pecten epipharynx of three fine spines, chaetulae laterales and basales present. Premandible described as short with some four very short blunt teeth. Specimens examined have two subequal apical teeth with a distinct but shorter, blunt inner tooth.

Mandible (Fig. 38c). Long, narrow, pointed apical tooth longer than combined width of the three inner teeth. Seta subdentalis long and narrow, seta interna present with some pectinate branches. The whole mandible is strongly curved inwards.

Mentum (Fig. 38e). Single median tooth with projecting nipple. Six pairs of needle-like lateral teeth. Ventromental plates small, not extending beyond outer teeth of flattened mentum, without setae beneath.

Maxilla (Fig. 38d). The length of the palpiger is unique amongst described orthocladiine larvae, coming to resemble the palpiger of the Tanypodinae. Basally there is a long seta, and the apical part has elongate bisensillae. Terminally there are distinct sensillae and a long apical seta. The structure of the galea cannot be determined from the material available.

Abdomen (Fig. 38f). The procerci resemble Pseudorthocladius in bearing one elongate seta (in this case it reaches up to half the body length) amongst the sparse apical setae. Anterior and posterior parapods both separate with claws. Anal tubules shorter than posterior parapods without constrictions.

COMMENTS AND SYSTEMATIC STATUS

There are several disparities between the description by Thienemann and Kruger (loc. cit.) and the material examined (which may be that described). They are undoubtedly congeneric and it is possible that the species is just poorly described. The material is in poor condition and may have been in the same state when described. It is noticeable that there is no figure of the antenna, labrum or palatum contrary to the normal practice, which suggests these structures may have been difficult to see when described.

In the absence of these characters which are of phylogenetic importance it is difficult to discuss the position of the genus. The pupae and adult however are very close to Parakiefferiella not to Pseudorthocladius. There are larval characters which suggest that although the elongate procercal bristle is present in both the genera this has arisen in parallel, and the two genera are not close relatives. These characters include the structure of the anterior parapods (separate in *Krenosmittia*, fused in *Pseudorthocladius*), the number of mental teeth (six regular laterals in *Krenosmittia* , four irregular laterals in *Pseudorthocladius*) and premandibular structure (two pointed teeth in *Krenosmittia*, one blunt tooth in *Pseudorthocladius*).

Saether (1977:86) placed *Krenosmittia* with *Parakiefferiella*, *Epoicocladius* and *Lapposmittia*, basing this upon features of the adult and particularly the pupa. The larva is clearly very strongly modified - the elongate apical tooth to the mandible and the needle like mental teeth suggest a predatory diet unusual in the Metriocnemini. To ascertain the relationships based upon the larva it is necessary to examine the character states not affected by this postulated way of life, and it is these very characters of the labrum and antenna which are inadequately described in the genus.

DISTRIBUTION AND ECOLOGY (of the genus *Krenosmittia*)

The genus *Krenosmittia* is apparently poor in species, and is known from three Palaearctic species, one Afrotropical species and several larval records in the Nearctic. The ecology of *Krenosmittia camptophleps* is summarised by Thienemann (1949) as hygrobiontic-terrestrial and krenophilic species. The species was recorded from the River Fulda (Lehmann, 1971).

Krenosmittia camptophleps (Edwards)

Krenosmittia camptophleps (Edwards, 1929:353)

Krenosmittia gynocera Thienemann & Kruger, 1939:253. (misidentification).

The present survey has not revealed any larvae which can be ascribed to this species. As noted above the generic diagnosis is based upon published descriptions and examination of Thienemann's material which is in poor condition. In view of this no species description is possible.

xx. Limnophyes Eaton

Limnophyes Eaton, 1875:12

Type-species Limnophyes pusillus Eaton, 1875, by monotypy.

GENERIC DIAGNOSIS (Based on published descriptions and two species described here)

Medium sized larvae, up to 6 mm long.

Antenna. Five segmented, the third usually shorter than the fourth, at most subequal. Lauterborn organs present or absent. Ring organ present, up to half way on first antennal segment. Antennal spine as long as or longer than flagellum (much longer in Limnophyes karelicus Chernovski, if this species is correctly placed). Subsidiary spine present. Antenna scarcely longer than half the mandible length, sometimes shorter.

Labrum. Most of the adequately described species have a plumose SI with a reduced number of branches. Sometimes these branches may be very reduced and the SI is virtually simple. Other S setae normal. Labral chaetae simple. Pecten epipharynx and chaetulae laterales not always separable, all simple scales. Premandible with two or three teeth, no beard.

Mandible. Apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis present, seta interna with (? all) branches plumose.

Mentum. Usually, perhaps always, two median teeth as high or higher than the first pair of lateral teeth. Five pairs of lateral teeth. Ventromental plates small or absent, no setae beneath. Base of mentum with rounded tooth.

Maxilla. Palpiger normally developed. Galear lamellae absent. Pecten galearis absent. Maxillary setae (? always) simple.

Abdomen. Anterior and posterior parapods separate. Procerci usually higher than wide, bearing apically six or seven setae. Anal tubules of variable length but usually shorter than the posterior parapods.

Variably developed body setae, usually simple, but sometimes plumose.

COMMENTS AND SYSTEMATIC STATUS

The genus *Limnophyes* is world-wide and contains many species, the boreal region being particularly rich. Despite the abundance of some species of the genus the larvae of few are known, and even fewer are adequately described. Thus the preceding generic diagnosis must be treated with caution. Some species described from larvae and placed in the genus *Limnophyes* by Pankratova (1970), if correctly assigned, would entail redefinition of the larval generic diagnosis.

Saether (1977:86) places *Limnophyes* with *Paralimnophyes*, *Pseudorthocladius* and *Parachaetocladius* as the sister group of all the Orthocladiinae with reduced abdominal characters. As discussed under *Paralimnophyes* this genus is obviously closely related to *Limnophyes* and may not warrant separate generic status. Both these genera resemble *Pseudorthocladius* in several characters including the shape of the mentum, labrum and the SI seta. These characters are undeubtedly apomorphic, but there are several characters which clearly separate *Pseudorthocladius* from *Limnophyes*. These are characters which relate *Pseudorthocladius* to the orthoclads with reduced abdominal characters including the fusion of the anterior parapods and the reduced procerci. It is therefore possible that the relationship suggested by Saether based upon adult and pupal characters is correct, and that *Paralimnophyes* and *Limnophyes* are related to *Pseudorthocladius* with the latter genus possessing more plesiomorphic characters than the former.

The discovery of the immature stages of *Parachaetocladius*, *Kiefferophyes* and *Psilometriocnemus* which Saether tentatively places with the above mentioned genera should help to elucidate the relationships within this group of genera.

Limnophyes globifer (Lundstrom)

Limnophyes globifer (Lundstrom, 1915:16); Cranston, 1979 (in press).

DESCRIPTION OF 4TH INSTAR LARVA (n = 1 exuvium)

Body length unmeasurable, head capsule c. 250 um, yellow with occipital margin, mentum and all of mandible dark brown to black. Submentum and frontal apotome darker than remaining area of head.

Antenna (Fig. 39a). Five segmented, lengths 40; 9; 2; 4.5; 3.5. Antennal ratio 2.08 (reciprocal cited in Cranston, 1979). Antennal blade 28 long extending to tip of final antennal segment. Subsidiary spine 4 long inserted subapically on second antennal segment, Lauterborn organs indistinct. Ring organ 13 from base of first antennal segment.

Labrum and palatum (Fig. 39b). SI seta 15 - 16 long with two or three fine branches on the outer edge of the seta. SII 20 long, SIII 10 long, SIV 3 - 4 long, all simple. Labral setae simple. Pecten epipharynx of three subequal setae, three simple chaetulae laterales. Chaetulae basales, if present, not visible. Premandible (Fig. 39c) 62 long with two apical teeth and a distinct inner tooth, no beard.

Manlible (Fig. 39e). 110 long, apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 15 long, seta interna of five or six branches, each finely serrate.

Mentum (Fig. 39d). Flattened width 80. Paired median teeth less distinctly separated than the five pairs of lateral teeth. There is a distinct projection or tooth at the base of the mentum which may be a generic characteristic. Ventromental plates very small, no setae beneath.

Maxilla (Fig. 39f). No lamellae on either palpiger or galea. Sensillae on palpiger and galea distinct but small. Maxillary setae simple, one almost triangular in shape and more strongly darkened than the others. Appendix not visible.

Abdomen. (Fig. 39g). Procercus 42 high by 35 wide bearing apically six bristles, the longest of which is 44 long. Dorso-lateral or supra-anal seta strongly developed, 260 long, darkly pigmented and divided into a number of branches. Posterior parapods 90 long, anal tubules not measurable in this exuvium. Longest seta on any abdominal segment 80 long but several of at least 50 long on each segment.

MATERIAL EXAMINED

Site 17, (1 reared larva).

DISTRIBUTION AND ECOLOGY

Cranston (1979) in reviewing the distribution of the adult Limnophyes globifer from Siberia, North-Eastern Canada, Spitzbergen and East Greenland as well as several western European countries suggests that the species has a circum-polar distribution. The most southerly records are from Lake Bodensee in southern Germany and Lake Winnipeg in Canada.

The specimen reared in this survey is the basis for the record of *Limnophyes cfr globifer* in Pinder (1978:Fig. 128b). Subsequent studies showed that this was conspecific with Lundstrom's species *globifer*, and that further adult material was known from two Scottish localities, Lochs Rannoch and Lomond.

Reiss (1968:244) recorded *Limnophyes globifer* from the encrusted stones of the surf spray zone of Lake Bodensee, but the single larva and pupa of *globifer* taken in this survey was from 1.5 metres in a benthic sample from Malham Tarn. *Limnophyes globifer* larvae were not found in the spray zone of Malham Tarn.

The three water bodies from which the adults are known in Britain are rather different. Malham Tarn is a marl lake with high calcium levels, the northern end of Loch Lomond is oligotrophic and Loch Rannoch shows a tendency towards dystrophy.

Limnophyes species A

DESCRIPTION OF 4TH INSTAR LARVA (n = 1 exuvium)

Body length unmeasurable, head capsule 291 um, pale brown with dark brown mentum and mandible.

Antenna (Fig. 40a). Five segmented, lengths 34; 11; 2; 6; 4. Antennal ratio 1.48. Antennal spine 32 long, subsidiary spine 6 long. Lauterborn organs not visible. Ring organ 214 from base of first antennal segment.

Labrum and palatum. SI setae and pecten epipharyngis not visible on preparation. SII long and broad, SIII thin and short. SIV normally developed. Premandible (Fig. 40b) 61 long, with two apical teeth and two inner teeth. No beard present.

Mandible (Fig. 40d). 103 long with the apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 6 long, seta interna of four or five simple (?) branches.

Mentum (Fig. 40c). Flattened width 85, median paired teeth not as strongly divided from each other as the five pairs of laterals. Distinct tooth or projection at the base of the mentum. Ventromental plates very small, no setae beneath.

Maxilla (Fig. 40e). Two simple lamellae on galea. Distinct sensillae on both palpiger and galea. Maxillary setae simple, only three in number and the innermost strongly triangular in shape, although not darkened (unlike *globifer*).

Abdomen. Procercus 32 high by 24 wide, bearing apically five dark setae of maximum length 413. The lateral procercal setae are very fine and short but the supra-anal seta is dark and simple and 259 long. The parapods and anal tubules are not measurable and the claws on both the anterior and posterior parapods are yellow. The anterior claws have fine inner teeth and those on the posterior parapod are simple. The longe.t of the numerous distinct darkened body setae are 143 long.

MATERIAL EXAMINED

STAFFORDSHIRE: Rede House Pond, near Keele University, 8.iii.1979, leg. T. Mountain. (Specimen in collectors collection).

COMMENTS

The adult *Limnophyes* reared from this larva appears to be unknown from Britain and there is no satisfactory key to the many species known in this genus from outside Britain. The adult is distinct in possessing only a single lanceolate humeral and prescutellar bristle on each side of the abdomen. The hypopygium is quite distinct with the spine of the gonostylus inserted at right angles to the gonostylus, and the inner lobe of the gonocoxite somewhat resembling *Limnophyes habilis* with the numerous setae on the lobe.

Since only a single larva and adult is known it is not possible to give any details of the distribution and ecology beyond noting that the collecting site was a small pond.

xxi. *Mesosmittia* Brundin

Mesosmittia Brundin, 1956:16.

"*Limnophyes*" *flexuella* Edwards, 1929; description of larva by Strenzke, 1950:105.

Type-species *Pseudorthocladius flexuella* Edwards, 1929 by original designation. (However there is some confusion over the genera *Mesosmittia*, *Pseudorthocladius* and *Pseudokiefferiella* and a case for the validation of these genera as currently recognised is made in Cranston, 1974:88)

GENERIC DIAGNOSIS (Based on Strenzke, 1950)

Antenna. Five segmented, the first and second of similar lengths, the third segment shorter than the fourth. Antennal spine slightly longer than the flagellum, small subsidiary spine present on second antennal segment. Lauterborn organs absent. Ring organ high on first antennal segment.

Labrum and palatum. All S setae simple, labral chaetae fine and ? simple. Pecten epipharyngis of three spines with two similarly blunt spines and a complex spine forming the chaetulae laterales. Two small chaetulae basales present on the ungula. Premandible with two apical teeth and two inner teeth. On the inner margin there is a single spine, in the same position as the premandibular beard when it is present (e.g. *Metriocnemus*).

Mandible. Apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis and seta interna absent.

Mentum. One domed median tooth and four pairs of laterals, the outermost only a bulge on the outside of the third laterals.

Ventromental plates very small without setae beneath.

Abdomen. Procerci absent. Anterior parapods fused with scattered fine simple claws. Posterior parapods short but separate, bearing a few simple claws.

COMMENTS AND SYSTEMATIC STATUS

Strenzke's (1950:101) description of the immature stages and male and female of "*Limnophyes*" *flexuella* Edwards do not belong to the same species. The adult male is not the same as the holotype of Edwards' *flexuella* as pointed out in a letter from Laurence to Strenzke. Laurence stated that the female did belong to *flexuella*, and Strenzke surmised that the metamorphosis was correctly ascribed. Examination of the females of *flexuella* Edwards in the B.M.(N.H.) collections shows that these are conspecific with the female Strenzke described. An important feature confirming this identification are the distinctive heavily sclerotised seminal vesicles. Although there may still be doubts about the association of the immature stages with the adult *flexuella* it seems likely that the association is correct.

If correctly ascribed the larvae clearly belong to the more apomorphic Metriocnemini, with reduction in the procerci and parapods and the fourth antennal segment longer than the third. Saether (1977:86) proposed that Mesosmittia was related to *Pseudosmittia* and *Camptocladius* based on a postulated apomorphic feature of the antenna - the relative length compared with the mandible. This is a tenuous character but Saether's view of the relationships concurs with that of Strenzke (1950:110) who suggested that it was near *Smittia* (as *Euphaenocladius*) and *Pseudosmittia*.

The genus is frequently cited as terrestrial but at Site 3 in this survey adult males were collected in a fully submerged emergence trap in the middle of a fast mountain stream. There were no terrestrial adults in the trap or evidence of possible aerial contamination, so the ecology of this infrequently found monospecific genus must remain in doubt.

xxii. Metriocnemus v.d.Wulp

Metriocnemus v.d.Wulp, 1874:36; Potthast, 1915:336; Thienemann, 1937:179.

Type-species Chironomus albolineatus Meigen, 1818, by designation of Coquillett (1910:569)

GENERIC DIAGNOSIS (Based on published descriptions and two species described here)

Medium sized larvae, head capsule of variable colouration, body frequently striped.

Antenna. Five segmented, quite variable in structure. Often with third segment shorter than fourth segment when antenna normally developed but in some species the antenna is strongly reduced. Antennal blade often longer than flagellum. Subsidiary blade present, Lauterborn organs variable, sometimes absent, often well developed and distinctly longer than the third segment. Ring organ distinct in basal third of first antennal segment.

Labrum and palatum. SI plumose, remaining S setae normally developed, Labral lamellae present (? always) between bases of SI setae, these lamellae often serrate and closely appressed to each other. Labral chaetae simple and serrate, pecten epipharyngis of three spines, chaetulae laterales reduced and no larger than the scales of the pecten epipharynx. Premandible with two or more apical teeth and a distinct beard.

Mandible. Apical tooth shorter than combined width of the four inner teeth. Seta subdentalis present, seta interna of six or seven branches which may be broad and serrate.

Mentum. Median tooth either single or paired, when paired these may be lower than the first laterals. Five (? rarely six) pairs of lateral teeth. Ventromental plates weak without setae beneath.

Maxilla. Sensillae on galea and palpiger distinct. Few lamellae on galea, numerous maxillary setae, either simple or serrate, frequently with a group of shorter, finer setae external to the long maxillary setae. There may also be a group of fine short setae on the end of the galea adjacent to the palpiger. No pecten galearis present in the species examined. Apparently only one long seta on the base of the maxilla instead of the usual two.

Abdomen. Procerci well developed bearing relatively short apical setae. Procercus may bear a posterior spur or uneven sclerotisation. Anterior and posterior parapods present, divided, anal tubules variably developed. Any body setae short.

COMMENTS AND SYSTEMATIC STATUS

The range of variation in the larval characters in *Metriocnemus* is high, and based upon published description separation from *Thienemannia* and *Chaetocladius* is difficult. The characters used in the generic key work for all material examined, but problems may be encountered with some species. The premandibular beard and four inner teeth on the mandible should separate *Metriocnemus* from other Metriocnemini. Unfortunately the larvae of *Chaetocladius* and *Metriocnemus* were infrequently discovered in this survey - it appears that many may be semi-terrestrial or even terrestrial.

Saether (1977:86) placed *Metriocnemus* and *Thienemannia* together as the sister group of the remainder of the tribe

Metriocnemini combined. Metriocnemus possesses a number of plesiomorphic features including the strong beard on the premandible, broad serrate seta interna, labral lamellae and plumose SI.

Limited material available means that a key to the larvae of Metriocnemus cannot be constructed.

Metriocnemus ? hygropetricus Kieffer

Metriocnemus ? hygropetricus Kieffer, 1911:181.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 1 exuvium)

Body length not measurable, head capsule 445 um, brown with occipital margin dark brown, mandible brown, mentum scarcely darker than head capsule.

Antenna.(Fig.41a). Five segmented, lengths 48; 10.5; 2.5; 4; 3. Antennal ratio 2.40, antennal spine 27 long, extending beyond final antennal segment. Subsidiary spine 7 long, Lauterborn organs small or absent. Ring organ 21 from base of first segment, just short of midway on segment.

Labrum (Fig. 41b). SI setae plumose, remainder simple. Labral lamellae lying between bases of SI setae, closely appressed at base and plumose. Labral chaetae both simple and terminally serrate. Palatum not clearly visible but apparently with three subequal scales and similar chaetulae laterales. Premandible (Fig.41c) 60 long with a distinct beard originating about the midpoint of the premandible. A single apical tooth with a broad inner tooth visible in this view although there are apparently two indistinctly separated apical teeth.

Mandible (Fig.41e). 138 long with apical tooth shorter than the combined width of the four inner teeth. Seta subdentalis short, 5 long. Seta interna of six broad, serrate branches although there may be a seventh fine seta lying beneath one of the broad setae.

Mentum (Fig. 41e). 116 wide with median tooth 20 wide. Five pairs of lateral teeth, the median slightly lower than the first laterals. Ventromental plates absent, no setae beneath.

Maxilla (Fig. 41f). Two rounded triangular lamellae on base of palpiger, none on galea. ensillae on palpiger small, those on galea normally developed. No pecten galearis present. Maxillary setae numerous, some simple, some weakly serrate. ~everal fine, simple setae in a group exterior to the long maxillary setae. Also present is a group of similarly fine setae on the edge of the galea adjacent to the palpiger base. Only one setae on the base of the maxilla.

Abdomen. Procercus 63 high by 32 wide bearing apically 5 setae of maximum length 185. Lateral seta of procercus weakly developed and supra-anal seta absent. Parapods not measurable but anal tubules 212 long tapering to a point. Claws on posterior parapods yellow-brown, those on anterior parapods dark brown, both sets of claws simple.

MATERIAL EXAMINED

HERTFORDSHIRE: Rye Meads ~ewage Works lagoon 2, 2.vi.1975, leg. B. Kemplay (B.M.(N.H.) coll.).

DISTRIBUTION AND ECOLOGY

If this species is correctly ascribed to Metriocnemus hygropetricus (specimen reared to a female adult) the species is widely distributed throughout Britain and Europe, unrecorded only from the far north. British specimens in the B.M.(N.H.) are from many localities from the Grampian mountains of North Scotland to the lowlands of South East England.

Lehmann (1971:494) in recording the species from springs to the middle salmonid zone of the River Fulda, quotes Thienemann (1950:417) terming *M. hygropetricus* as a "basic part of the chironomid spring fauna throughout Europe". There are however many records of the species from organically polluted waters similar to the habitat of the specimen putatively ascribed to *hygropetricus* in this work.

Metriocnemus cavicola Kieffer

Metriocnemus cavicola Kieffer, 1921:85

Metriocnemus martinii Thienemann, 1921:816; Sparck, 1922:84.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 2)

Body length 4.7 - 4.8 mm, head capsule 339 - 402 um, pale brown with occipital margin only slightly darker and mentum and mandible dark brown. Premandible pale brown or yellow.

Antenna (Fig. 42a). Five segmented with segment lengths 51 - 55; 11 - 13; 1.5 - 2; 3 - 4; 3. Antennal ratio 2.62 - 2.76. Antennal spine 24 - 26, subsidiary spine 3 - 4 long. Ring organ 8 - 11 from base of first antennal segment. Lauterborn organs distinct, extending to tip of fourth antennal segment.

Labrum and palatum (Fig. 42b). SI setae plumose, remainder simple. Labral lamellae strongly developed, virtually contiguous, plumose and their bases lying posterior to the bases of the SI, closer to the bases of the SIII. One pair of labral chaetae serrate the remainder simple. Three subequal scales form the pecten epipharyngis, two further scales, scarcely larger than those of the pecten epipharyngis form the chaetulae laterales. Ungula and chaetulae basales not visible. Premandible (Fig. 42c) 58 long with two apical teeth and two broad inner teeth. The premandibular beard is distinct.

Mandible (Fig.42d). 112 - 114 long with the apical tooth longer than the combined width of the four inner teeth. Seta subdentalis 4 long, seta interna with six branches all but the innermost finely serrate, the innermost simple. Inner and outer margins smooth.

Mentum (Fig. 42e). 91 - 98 wide. Paired median teeth distin tly smaller than the first of five pairs of lateral teeth. Ventromental plates absent, no setae beneath.

Maxilla. Very similar to ?hygropetricus (Fig. 41f) but detail of maxillary setae not easily visible in preparations.

Abdomen (Fig. 42f). Procercus 40 - 42 high by 32 - 39 wide bearing apically six setae of maximum length 275 - 279. Lateral setae weak, supra-anal seta apparently absent. Hind parapod 220 - 249 long, anal tubules simple, tapering to a point and 60 - 63 long. Claws on posterior parapods yellow and simple, claws on anterior parapods yellow-brown, very fine and without inner teeth.

MATERIAL EXAMINED

N.YORKSHIRE: N.E. Tarn House, ex - water filled tree hole in beech tree, 19.iv.1973, leg. R.H.L. Disney (1 larva); same locality 29.viii.1972, tree hole in sycamore, leg. Disney (1 larva).

DISTRIBUTION AND ECOLOGY

Metriocnemus cavicola is infrequently recorded, Fittkau & Reiss (1978:419) noting only Britain, the Alps, Germany. (A Swedish record is omitted). British specimens are from a number of localities in southern England, and there is one male from central Wales and another from lowland Scotland. Many of these specimens are reared from rot holes in trees, few were caught on the wing.

Kitching (1971) investigated water filled rot holes in beech trees in Oxfordshire and found _Metriocnemus cavicola_ (as _martinii_) to be one of the commonest species. In this finding he agreed with Rohnert (1954), who termed the species "a dendrolimnobiont" - a species specifically associated with tree holes and seldom found elsewhere. Records from other aquatic habitats including Elbourn (1965) and Bryce (1963:82) are probably based on larval identification and should be treated with caution because most larvae in the genus _Metriocnemus_ are inadequately described.

xxiii. _Nanocladius_ Kieffer

Nanocladius Kieffer, 1913:31; Saether, 1977:2

Microcricotopus Thienemann & Harnisch, 1932:137 (Synonymy by Freeman, 1956:338, Sublette 1973:310, 1970:67 and Saether 1977:2, here accepted).

Type-species _Cricotopus albicornis_ Goetghebuer (= _Nanocladius bicolor_ (Zett.)) by Goetghebuer, 1944.

GENERIC DIAGNOSIS (based on British species)

Larvae small, no longer than 4.5 mm., head capsule no longer than 350 um. Body yellow, head capsule pale yellow with some darkening of occipital margin, mandibular teeth, mentum and premandible.

Antenna. Five segmented, segments consecutively smaller with fifth segment thin and hair like. Antennal ratio 1.2 - 2.1. Spine not extending beyond tip of antenna. Lauterborn organs as long as third antennal segment. Ring organ low on first antennal segment.

Labrum and Palatum. All S setae very weak and difficult to see, simple. Labral chaetae and setae absent. Epipharyngeal pecten of three equal length spines, terminally pointed.

6 - 7 pairs of chaetae laterales, all simple. Premandible 40 - 50 um long with trace of second outer tooth.

Mandible with one long outer tooth, much longer than combined width of three inner teeth. eta interna of three setae.

Mentum with one partially divided paler central tooth and five pairs of more sclerotised lateral teeth. Ventromental plates long with no setae beneath.

Abdomen. Parapods well developed with anterior claws eithe smooth or strongly serrated. Procerci well developed, sclerotised posteriorly and bearing 3 - 5 anal setae. Two pairs of anal tubules.

COMMENTS AND SYSTEMATIC STATUS

Nanocladius, with its elongate, broad ventromental plates lacking setae beneath, and with weakly developed S setae, is a distinctive genus in the larval stage. The pupae and adults are similarly distinctive even with the inclusion of the Nearctic symphoretic Plecopteracoluthus as a subgenus of Nanocladius (Saether, 1977b:12).

Saether (1977:86) places Nanocladius with Rheocricotopus, Psectrocladius, Paracricotopus and Mesocricotopus, and suggests this group is the sister gro p of all the "Cricotopus + Orthocladius group". This suggestion is discussed under Psectrocladius (page 274) and Rheocricotopus (page 300) but no evidence is available from this study to further elucidate the relationships of Nanocladius within this group of genera.

KEY TO BRITISH SPECIES

1 Claws of anterior parapods simple. Antennal ratio 1.8 or more ....bicolor (Zetterstedt)

Claws of anterior parapods with numerous serrati ns. Antennal ratio less than 1.7 .... rectinervis (Kieffer)

Nanocladius rectinervis (Kieffer, 1911)

Microcricotopus rectinervis (Kieffer, 1911). Larva described by Lindegaard-Petersen 1972:485-488.

DESC. IPTION OF 4TH INSTAR LARVAE (n = 7)

Body length 3.8 mm (3.2-4.3), head capsule length 295 um, (280-310). Head capsule pale with light brown occipital margin and apex of mandible, mentum relatively pale.

Antenna (Fig. 43a). Five segmented, third and fourth indistinctly separated, segment lengths 48 (45-56); 22.5 (19-24); 7.5 (6-9); 4 (2-5); 2 (1-3). Antennal ratio 1.38 (1.22-1.64). Two antennal blades both 28 long (2'-31). Ring organ 25 (24-26) from base of first antennal segment.

Labrum and palatum (Fig. 43b). All S bristles fine and difficult to distinguish. Pecten epipharyngis of three weakly sclerotised spines; 6 - 7 chaetulae laterales, simple. Premandible 42.5 (39-45) with trace of outer tooth.

Mandible (Fig. 43d). 93 (85-100) long with outer tooth clearly longer than combined length of three inner teeth. Seta subdentalis 12 (8-14) long extending to base of inner tooth. Seta interna divided into three simple branches.

Mentum (Fig. 43c). Two broad median teeth paler than five pairs of lateral teeth. Ventromental plates 73 (67-76) long and 16 (13-18) wide. Mentum 69 (66-71) wide between outer margins of most lateral teeth.

Abdomen. Procerci 19 (18-25) high by 15 (13-18) wide bearing very weak lateral setae. Three strong apical setae with up to two weaker setae, maximum length of long setae 250 (215-290). Hind parapods 176 (158-201) long, anal tubules 127 (105-137) long by 21 - 34 wide without constrictions. Claws of anterior parapod (Fig. 43e) serrate, of posterior parapod simple.

MAT RI L EX MIN D

Sites 9a (1 larva) and 26b (1 larva). Also HER FORDSHIRE: Evesbatch, R. eadon, 32/688 481, 31.v.1978 (2 larvae); LOTHIAN: Or iston, R. Tyne, 36/413 689, 29.v.1978 (1 larva); Easter Pencartland, R. Tyne, 36/ 459 690 (1 larva); SOMERSET: Broom, R. xe, 31/ 326 025, 11.v.1978 (1 larva) all F.B.A.

DIS RIBUTION ND ECOLOGY

Nanocladius rectinervis is fairly widespread in Europe and North merica. It is a lotic species in urope but Saether (1977:36) records the species from lentic habitats in North America. In Europe the species has been confused with *bicolor* and was only added to the British list by Cranston (1974:90). Lehmann (1971:484) notes that the species reaches its highest abundance in the River Fulda in the potamal zone, where it replaced *N. parvulus* (Kieffer), a more cold stenothermic species in the rhithral zone. *N. parvulus* is not yet recorded from Britain and several of the British records of *N. rectinervis* are from the rhithral zone.

Nanocladius bicolor (Zetterstedt, 1838)

Larvae described by Chernovskii (1949:198) as *Eukiefferiella bicolor* and by Lindegaard-Petersen (1972:488) as *Microcricotopus bicolor*

DESCRIPTION OF 4TH INSTAR LARVAE (n = 2)

Body length 3.9 - 4.6 mm, head capsule length 296 - 328 um. Head capsule pale yellow with occipital margin, apical tooth of mandible and all mental teeth brown.

Antenna (Fig. 43f). Five segmented, lengths 58 - 66; 17 - 21; 7 - 8; 4; 3 - 4. Antennal ratio 1.81 - 1.83. Two spines each 24 - 26 long. Ring organ 24 - 28 from base of first antennal segment, second smaller ring organ at 53 - 55 from base.

Mandible. Outer tooth clearly longer than combined length of inner three teeth. Length 95 - 105 with seta subdentalis 12 - 13 long.

Labrum. As in N. rectinervis, premandible 42 - 50 long, terminally bifid.

Mentum. Two median teeth dark, as outer teeth. Ventromental plates 63 - 64 long by 15 - 16 wide. Flattened mentum width 76 - 79 from outer edge of most lateral teeth.

Abdomen. Procerci 26 high by 21 - 24 wide, bearing apically 3 setae, maximum length 349 - 360. Hind parapods 158 - 169 long, anal tubules 118 long by 37 wide. Claws on anterior and posterior parapods simple.

MATERIAL EXAMINED

OXFORDSHIRE: River Thames between Days' Lock and Clifton Lock, 5.ix.1977, 1m depth on Nuphar (2 larvae) (F.B.A. collection)

DISTRIBUTION AND ECOLOGY

bicolor is widely distributed in Europe and Saether (1977: 31) records a possible bicolor from Arctic Canada. The immatures have been found in both lotic (Brundin 1949:396, Reiss, 1968:241) and lentic (Berg 1948:178, Lindegaard-Petersen, 1972:488, Lehmann, 1971:484) habitats.

Fittkau and Lehmann (1970:396) say that it avoids the upper reaches of water courses and Lehmann (1971:484) says that the larvae reach their highest numbers in the potamal zone of the River Fulda.

The absence of this species in smaller streams and rivers, and its presence in the Thames suggests that these observations apply also in ritain.

xxiv. Orthocladius v.d. ulp

Orthocladius v.d.Wulp, 1874:132; Soponis, 1977:13.

Type-species Chironomus oblidens Walker, 1856:180 designated by Edwards, 1929:335. (validation by I.C.Z.N. required).

GENERIC DIAGNOSIS

Medium to large larvae, up to 12 mm long. Head capsule up to 550 um long, of varying colour which may be of subgeneric value.

Antenna. Usually five segmented (four in s.g. Pogonocladius), segments consecutively smaller or third and fourth subequal. Lauterborn organs present, sometimes weak usually stronger. Antennal spine may extend beyond terminal antennal segment. Ring organ present in basal third of first antennal segment.

Labrum. SI always bifid, SII, SIII and SIV simple. Pecten epipharyngis of three simples spines never fused, as in Cricotopus (Isocladius). Chaetulae laterales simple subequal, never broad as in some Cricotopus (Fig. 23b), chaetulae basales terminally branched. Premandibles simple or bifid without a beard.

Mandible. Apical tooth usually shorter than combined width of three inner teeth (exception: O. (Euorthocladius) rivulorum). Seta subdentalis present, seta interna usually present (apparently absent in at least one species of Orthocladius s.s.). Outer margin with or without crenulations. Inner margin without spines.

Maxilla. Sensillae on galea and palpiger usually well developed. Lamellae on palpiger base and galea very variably developed, complex lamellae infrequent. Pecten galearis only strongly developed in O. (P.) consobrinus (Holm). Maxillary setae well developed, appendix present or absent.

Mentum. One median tooth, usually six pairs of lateral teeth (eight or nine pairs in O. (Euorthocladius) rivulorum). No British species with less than six pairs of laterals. Ventromental plates absent, no setae beneath.

Abdomen. Procerci usually as high as wide, bearing apically six or seven setae. Parapods normal, anal tubules shorter than posterior parapods sometimes with the dorsal pair longer than the ventral pair. All body setae fine and simple.

COMMENT AND SYSTEMATIC STATUS

Hirvenoja (1973) and Soponis (1977) were unable to find any character to separate all Orthocladius from all Cricotopus larvae, and the pupae are similarly difficult to separate. Those species of Cricotopus with the l_4 seta developed into a setal brush are readily separated from Orthocladius but the separation of the remaining species must be made on specific or species-group characters.

At the moment a large proportion of the Palaearctic larvae of Cricotopus are known because of the work of Hirvenoja. Although Soponis has reviewed the Nearctic species of Orthocladius (s.s.), which includes some Holarctic species, there is a great need for a revision of all the life history stages of the genus. In Orthocladius (s.s.) particularly there are many more larval and pupal forms than adults. Langton (manuscript key, 1978) gives eleven pupal species, Pinder (1978) gives 5 adult species. It has not proved possible to find specific names to go with these pupal forms, and this has also been found with the larval forms. Only those larvae with reared adult males have been included in this work because a full generic revision is outside the scope of this study.

Despite the problems in separating the larvae and pupae of *Orthocladius* from *Cricotopus*, Hirvenoja (loc.cit) excludes *Orthocladius* from the monophyletic group *Acricotopus*, *Paratrichocladius*, *Paracladius*, *Halocladius* and *Cricotopus*. This group is established on the basis of characters of the female genitalia, and Hirvenoja's findings are accepted by Saether (1977:86). Saether goes further than Hirvenoja in placing *Synorthocladius* and *Orthocladius* combined as the sister group of the *Cricotopus* group of genera. Neither of these authors is able to find any larval or pupal characters to reinforce their views on the phylogeny of these genera, and as noted above the evidence of the larvae is perhaps contradictory.

KEY TO THE SUBGENERA OF LARVAL ORTHOCLADIINAE (from Soponis, 1977:15)

1 Mentum with eight or nine pairs of lateral teeth .... *Euorthocladius* (part)
Mentum with six pairs of lateral teeth 2

2 Antenna four segmented, Lauterborn organs very small .... *Pogonocladius*
Antenna five segmented, Lauterborn organs usually stronger 3

3 Head capsule yellow or yellow-brown, seta interna present .... *Orthocladius*
Head capsule light to dark brown, if paler then seta interna absent 4

4 Head capsule light brown .... *Euorthocladius* (part)
Head cpasule dark brown ....*Eudactylocladius*

subgenus *Eudactylocladius* Thienemann

Eudactylocladius Thienemann, 1935:206.

Type-species *Orthocladius fuscimanus* Kieffer, by original designation.

SUBGENERIC DIAGNOSIS

As generic diagnosis except: head capsule dark brown, occipital margin, mentum and mandible only slightly darker. Outer margin of mandible smooth, (?) never crenulate. Lauterborn organs absent to strong.

KEY TO THE KNOWN LARVA OF BRITISH *EUDACTYLOCLADIUS*

1 Lauterborn organs distinct, extending at least to the apex of the third antennal segment .... *species B*
  Lauterborn organs weak or absent, never as long as the third antennal segment 2

2 Seta interna of mandible absent. Ratio of median mental tooth to width of whole mentum less than 0.20 .... *species A*
  Seta interna of mandible present. Ratio of median mental tooth to width of whole mentum greater than 0.30 .... *mixtus* (Holmgren)

Orthocladius (*Eudactylocladius*) *mixtus* (Holmgren)

Orthocladius mixtus (Holmgren, 1869:45)

DESCRIPTION OF 4TH INSTAR LARVA (n = 1 exuvium).

Body length not measurable, head capsule 487, dark brown with occipital margin, mentum and mandible almost black. Antenna and premandible dark yellow.

Antenna (Fig. 44a). Five segmented, lengths 48; 13; 5; 5; 3. Antennal ratio 1.85. Antennal spine 28 long, subsidiary spine 5 long. Lauterborn organs absent. Ring organ 21 from base of first antennal segment.

Labrum and palatum (Fig. 44b). SI seta bifid, the inner branch a little horter than the outer one. Other S seta normal, simple. Labral chaetae simple. Pecten epipharyngis of three subequal scales, chaetulae laterales of two scales, the anterior resembling the scales of the pecten epipharyngis. Premandible 95 long with a broad apical tooth and a broad inner tooth.

Mandible (Fig. 44d). 154 long with apical tooth shorter than the combined width of the three inner teeth. eta subdentalis small, seta interna with five simple branches. Outer margin of mandible smooth.

Mentum (Fig. 44c). Flattened width 61, width of median tooth 23. R tio of width of median tooth to width of mentum 0.38. Six pairs of lateral teeth, the first pair somewhat broader than the others which are subequal in height.

Maxilla. Distinct triangular lamellae on palpiger base, a few simple lamellae on galea, some pointed. Sensillae on palpiger and galea distinct, no pecten galearis. Appendix terminally branched.

Abdomen. Procercus 16 high by 20 wide, brown, bearing apically six setae of maximum length 286. Lateral seta of procercus 32 long. Anal tubules and parapods not measurable in the exuvium. Claws of hind parapod brown and simple, those on anterior parapod golden with inner teeth. The apical tooth on the smallest claw with more than one tooth is longer than any of the inner teeth.

MATERIAL EXAMINED

Site 17 (1 larva reared to adult male).

DISTRIPJTIO A D ECJLOJY

Orthocladius mixtus (Holmgren) is a circumpolar species occurring in candinavia, Greenland, ear Island, Spitzbergen and North We t erritory of anada. In urope it has been recorded from the Alps and entral uropean mountains. Although Fittkau and Reiss record the species from Britain (1978:420) the specimen cited above, together with an adult reared from a pupa from the same locality and an unpublished record of Langton (1978) are the first specimens of this species recorded from ritain.

The only record of the larva of *mixtus* is that of Thienemann, 1941:225 who found larvae in a rock pool near the Abisko Tourist Hotel (Lappland). There is no description beyond stating that they belong to *udactylocladius*. It seems that *mixtus*, unusually for the subgenus, lives in standing waters.

Orthocladius (*udactylocladius*) species A

DESCRIPTI N OF 4TH IN TAR LARVA (n = 1)

Body length not measurable, head capsule 424 um long, brown, with occipital margin,mentum and mandible dark brown to black.

Antenna (Fig. 45a). Five segmented, lengths 59; 13; 9; 8; 4. Antennal ratio 1.51. Antennal spine 25 long, subsidiary spine 7 long. auterborn organs present but small. Ring organ 4 from base of first antennal segment.

Labrum and palatum. As in *Orthocladius* (*Eudactylocladius*) *mixtus* (Fig. 44b), except there are three pairs of cha tulae laterales, all elongate scales and the two terminally branched chaetulae basales are more distinct. Premandible 55 long, with a broad apical and inner tooth.

Mandible (Fig. 45b). 145 long, apical tooth narrower than normal but still shorter than the combined width of the three inner teeth. Seta subdentalis present, terminally bifid. Seta interna apparently absent. Inner margin of mandible with an inwardly directed hook, different from the spines of Eukiefferiella and Cricotopus bicinctus (q.v.). Outer margin smooth.

Mentum (Fig. 45c). Flattened width 106, width of median tooth 18. Ratio of width of median tooth to width of whole mentum 0.17. Median tooth rounded, six pairs of laterals. The second laterals reduced in size relative to the first and third. Ventromental plates absent.

Maxilla (Fig. 45d). A few triangular, pointed lamellae on palpiger base, some similar lamellae as well as three complex lamellae on the galea. Sensillae on palpiger and galea smaller than usual, but distinct. Maxillary setae simple, appendix simple.

Abdomen. Procercus small, weakly sclerotised, 8 high by 11 wide, bearing apically six setae of maximum length 370. Lateral seta weak. Anal tubules and parapods not measurable. Claws on posterior parapod brown, simple; those on anterior parapod yellow-brown, also apparently simple.

MATERIAL EXAMINED

Site 34 (1 unreared larva)

COMMENTS

This single larva from a fast river in S.W. England apparently belongs to the subgenus Eudactylocladius but could not be reared for confirmation. There are three further species in the subgenus which have been recorded from Britain - gelidus Kieffer, obtexens Brundin and species a of Pinder, 1978:63. None of these species is common, and, like most of the genus *Orthocladius*, this subgenus needs revision of all stages.

Orthocladius (*Eudactylocladius*) species B

DESCRIPTION OF 4TH INSTAR LARVA (n = 7)

Body length 4.6 (4.3-4.9)mm, head capsule 383 (365-413) um, dark brown with mentum and mandible no darker but occipital margin black except ventrally where it is the same colour as the head capsule.

Antenna (Fig. 46b). Five segmented, lengths 42 (37-45); 10.9 (10-12); 5.4 (5-6); 4.7 (4-5); 3.8 (3-4). Antennal ratio 1.70 (1.48-1.83). Antennal spine 24 - 26 long, subsidiary spine 8 - 9. Ring organ 8 (6-10) from base of first antennal segment. Lauterborn organs very distinct and broad, extending beyond the third antennal segment.

Labrum and palatum (Fig. 46a). SI bifid, branches subequal. SII, SIII and SIV normally developed. Numerous simple labral chaetae. Pecten epipharyngis of three subequal scales. Four chaetulae laterales, two terminally bifid chaetulae basales. Premandible 75 (69-80) long, with a single apical tooth and a broad inner tooth.

Mandible (Fig. 46d). 113 (111-114) long, apical tooth no longer than the first of three inner teeth. Seta subdentalis short, simple. Seta interna with six or seven fine simple branches. Outer margin of mandible smooth.

Mentum (Fig. 46c). Width of flattened mentum 83 (80-87), width of median tooth 13.8 (13-15). Ratio of width of median tooth to width of whole mentum 0.17 (0.15-0.18). First pair of lateral teeth somewhat wider than the other five pairs which are subequal in size. Ventromental plates small without setae beneath.

Maxilla. Similar to O.(E.) mixtus (Fig. 44e). Maxillary setae simple, appendix also simple. Few simple lamellae on galea, none pointed. Sensillae on palpiger and galea well developed.

Abdomen. Procerci 26 - 30 high by 18 - 20 wide (n = 3), procercus pale, unsclerotised and bearing apically four to six setae of maximum length 352 (333-371). Lateral seta of procercus weak, supra-anal seta ? absent. Posterior parapods 256 - 282 long, anal tubules simple 130 - 143 long (n = 3). Claws of posterior parapod dark brown, simple; those of anterior parapod yellow with inner teeth as long as the apical teeth.

MATERIAL EXAMINED

DERBYSHIRE: High Stock Bridge, River Derwent, 10.v.1978; GWYNEDD, Bangor, River Teife, 10.iv.1978 (both River Classification Survey collection, F.B.A.).

COMMENTS

This species, clearly belonging to the subgenus *Eudactylocladius* is only known from the larva and cannot be identified with any certainty. See under *species A* for comments on the possible identity.

subgenus *Euorthocladius* Thienemann

Euorthocladius Thienemann, 1935:201

Type-species *Orthocladius thienemanni* Kieffer, 1906:43, by original designation.

SUBGENERIC DIAGNOSIS

As generic diagnosis except: head capsule light brown except *thienemanni* which is yellow-brown. Mentum, mandible and occipital margin darkened. Mentum of British species with either six pairs of lateral teeth or eight or nine pairs (*rivulorum*). Soponis (1977; Fig. 122b) shows an unnamed species with seven pairs of lateral teeth. Outer margin of mandible without crenulations. eta interna may be absent (*fri.idus*).

COMMENTS

This is a very heterogeneous sub_enus, and, as pointed out by Soponis (loc.cit.), there are also three kinds of larvae. It is possible that *rivulorum* does not belong in the subgenus, but as with all of the Palaearctic *Orthocladius* these problems await a full revision of the genus.

KEY TO THE KNOWN SPECIES OF *ORTHOCLADIUS EUORTHOCLADIUS*

1 Eight or nine pairs of lateral mental teeth .... *rivulorum* Kieffer

Six pairs of lateral mental teeth 2

2 Lauterborn organs very distinct, seta interna of mandible present .... *thienemanni* Kieffer

Lauterborn organs weak, seta interna of mandible absent .... *frigidus* (etterstedt)

Orthocladius (*Euorthocladius*) *frigidus* (Zetterstedt)

Orthocladius frigidus (Zetterstedt, 1838:811); Zavrel, 1938:9.

DESCRIPTION OF 4TH INSTAR LARVA (n = 8)

Body length 5.4 (4.2-6.7) mm (n = 3), head capsule 577 (530-614) um, yellow to light brown, with occipital margin broadly darkened, nearly black. Mentum brown, premandible yellow-brown, all mandible dark brown to black.

Antenna (Fig. 47a). Five segmented, lengths 62.5 (56-69); 14.9 (14-16); 6.3 (5.5-7); 5.9 (5.5-7); 3.3 (3-4). Antennal ratio 2.07 (1.75-2.36). Antennal spine 31.5 (21-40), subsidiary spine 8 long. ing organ 8.3 (5-11) from base of first antennal segment. Lauterborn organs weak, scarcely the length of the third antennal segment.

L.brum and palatum (Fig. 47b). SI seta bifid, the branches subequal or the inner somewhat shorter. SII, SIII and IV simple. Labral chaetae all simple. ecten epipharyngis of three scales, the median longer. haetulae laterales of three scales, two chaetulae basales, both terminally bifid. Premandible 103 (85-111) long with a single apical tooth.

Mandible (.ig. 47c). 196 (180-220) long, apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis short, 4 - 11 long. eta interna absent. Outer mar-in of mandible weakly crenulate on the basal part.

Mentum (ig. 47d). Flattened width of mentum 163 (154-190), median tooth 27 (24-31) wide. Ratio of median tooth to mentum width 0.17 (0.15-0.19). Six pairs of lateral teeth and a strong basal projection. Ventromental plates weak without setae beneath.

Maxilla (Fig. 47e). Two weak lamellae on palpiger base, a few pointed lamellae on the galea, no complex setae. Sensillae on palpiger weakly developed, those on galea strongly developed. No pecten galearis. Maxillary setae strong and simple. No appendix.

Abdomen. Procercus 35 (32-42) high by 35.5 (30-39) wide, bearing apically six setae of maximum length 609 (551-657). Lateral seta of procercus c. 36 long, weakly developed. Posterior parapod 307 - 371, anal tubule 135 - 159, narrow (both n = 3). Claws of posterior parapod brown and simple, those of anterior parapod yellow, mostly with apical tooth longer than inner teeth. Longest and shortest claws simple.

MATERIAL EXAMINED

Site 19 (numerous larvae, reared and unreared); Site 21 (2 larvae); WALES: County ?, Afon Nadnedd, 15.vii.1977, leg. P. . ʟangton (3 larvae) (B.M.(N.H.) Coll.).

DISTRI UTIO ʟCOʟO Y

Fittkau and eiss (1978:421) summ rise the distribution of the species as idespread in ʟurope as far east as Eastern Siberia and outh to North Africa. *Orthocladius frigidus* has not been recorded from the alkans and Italy, but it is likely that the species occurs here too. Within Britain there are adult records from most parts of the country, particularly from upland areas.

Zavrel (1933:9) notes that the larva may live in houses built from al ae but also were found free living in flowing water . ʟittmar (1955:482) termed *frigidus* a rheobiont and a hemistenotherm, although this last finding is somewhat surprising in view of the southern extent of the range of the species. Lehmann (1971:437) found the species on moss in the middle reaches of the River Fulda (West Germany) nd also in the limnokrene. The principal site in which the larvae were found in this survey as a torrential stream running over large boulders. The larvae were living freely on the surf ce of these stones and boulders. All three sites are upland with cold water, confirming Dittmar's suggestions on the ecology of the species (loc.cit.).

Orthocladius (*Euorthocladius*) *rivulorum* Kieffer

Orthocladius rivulorum Kieffer, 1909:48; Thienemann, 1935:204.

DE CRIPTI N OF 4TH INʟT R LA VA (n = 4)

Body length 3.1 - 4.1 mm (n = 2), head capsule length 485 (439-508), pale brown with occipital margin black; mentum, apical third of mandible and premandible brown.

Antenna (Fig. 48a). Five segmented, lengths 58 (56-60); 10.1 (9-11); 4.8 (4-5); 3; 3.9 (3-4.5). Antennal ratio 2.70

(2.48-2.95). Antennal spine 32 - 39 long, extending beyond fifth antennal segment. Subsidiary spire 8 long. Lauterborn organs present, slightly shorter than third antennal segment. Ring organ 9.8 (8-13) from base of first antennal segment.

Labrum and palatum (Fig. 48b). Inner branch of bifid SI shorter than outer part, remaining 5 setae simple. Labral chaetae simple. Pecten epipharyngis of three scales, the middle one longer than the two outer ones. Chaetulae laterales of about six scales forming a "moustache", drooping each side of the pecten epipharyngis. Two ter inally branched chaetulae basales. Premandible 90 (87-95) long with a single apical tooth.

Mandible (Fig. 48d). 171 (160-180) long, apical tooth subequal to the length of the three inner teeth combined. Seta subdentalis 11 - 13 long, seta interna of six simple branches.

Mentum (Fig. 48c). Flattened width 143 (132-159), median tooth 33 (3 -36) wide, ratio of median tooth to width of whole mentum 0.23 (0.21-0.24). Eight pairs of lateral teeth, rarely a trace of a ninth tooth. Ventromental plates absent, no setae beneath.

Maxilla (Fig. 48e). ensillae on palpiger and galea small, no lamellae on base of palpiger, few simple lamellae on galea. No pecten galearis. Maxillary seta of variable lengths, all sim le. No a pendix.

Abdomen. Procerci 20 - 23 high by 18 - 23 wide, scarcely darkened, bearing apically four or five setae of maximum length 438 (466-492). Lateral procercal setae weak, supra-anal seta absent. Lengths of parapods not measurable, anal tubule in the single specimen measured 185 long. Claws of posterior parapods brown and simple, those of anterior parapods yellow, the lon est and shorte-t cla s simple, the remainder with inner teeth as long as the apical tooth.

4T IL& I D

Site 26b (4 unreared 4th in-tar larvae, numerous 3rd instars).

COMM NT

Orthocladius rivulorum is a distinctive larva, the only Briti h Orthocladiinae nown to the author with eight or more pairs of lateral teeth. The elongate apical tooth to the mandible is also distinctive in the genus Orthocladius.

DI-TRI UTION D COLOGY

Fittkau and Reiss record O. rivulorum from the Pyrenees, Alps, central uropean mountains, North frica, the Caucasus and Lake aikal area. Humphries and rost (1937:179) record larvae from moss in the River Liffey (Ireland) while Thienemann found the species on stones in streams and refers to it as characteristic of the rhithral zone.

There are several unpublished records of the larvae in Britain mainly from the collections of the F. . . and angton. The-e inclu e the iver erwent (Derbyshire) and River Frome and Ta lnoll rook Dorset).

Orthocladius (Euorthocladius) thienemanni Kieffer

Orthocladius (E.) thienemanni Kieffer, 1906:143; Thienemann, 1935:201

DESCRIPTI N of 4TH IN T-R LARVA (n = 7)

Body length 4.2 (3.9-4.4) mm (n = 3), head capsule 444 (413-498) um, yellow-brown, occipital margin black, apical half of mandible and mentum brown, basal half of mandible pale brown.

Antenna (Fig. 49a). Five segmented, lengths 51.3 (43-55); 10.3 (9-11); 3.1 (3-3.5); 3.1 (3-3.5); 4 (3-5). Antennal ratio 2.52 (2.33-2.74). Antennal spine 24 - 27 long, with a short inner branch. Subsidiary spine 4 long, ring organ 6 - 7 from base of first antennal segment. Lauterborn organs distinct and broad, longer than third antennal segment.

Labrum and palatum (Fig. 49b). SI seta bifid with both branches subequal. SII, III and SIV normally developed. Numerous simple labral chaetae. Four chaetulae laterales, two terminally bifid chaetulae basales. Premandibles 74 (68-80) long, with a single apical tooth and a broad inner tooth.

Mandible (Fig. 49d). 127 (119-137) long with the apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis short, seta interna of six fine branches. Outer margin smooth except for an incision about a third of the way along from the base.

Mentum (Fig. 49c). Flattened width 104 (95-109), median tooth 16 (15-17) wide. Ratio of median tooth to width of flattened mentum 0.15 (0.15-0.16). Six pairs of lateral teeth.

Maxilla (Fig. 49e). Sensillae on palpiger smaller than usual, those on galea well developed. Few lamellae on base of palpiger, only a small group of spines on the galea. Maxillary setae simple. Appendix ? a single spine.

Abdomen. Procerci 17.8 (13-21) high and 28.5 (23-32) wide, unsclerotised and bearing apically six setae of maximum length 418 (381-434). Lateral seta very weak, supra-anal seta apparently absent. Posterior parapods 275 - 296 (n = 2), anal tubules 90 - 106 (n = 4). Claws on posterior parapods brown and simple; those on anterior parapods yellow with the apical tooth longer than any inner teeth.

MATERIAL EXAMINED

Site 37 (1 larva); DORSET: River Frome, 1 .v.1978; S.Winterbourne, River Stour, 27.2.1974, both leg. & det. L.C.V. Pinder, F.B.A. Coll. (1 reared male from each site); WILTSHIRE: Savernake, ex-Schoenoplectus, 24.vii.1975, leg. C.M. Drake (F.B.A. Coll.) (5 larvae).

DISTRIBUTION AND ECOLOGY

Fittkau and Reiss (1978:421) record O.(E.) thienemanni from the Alps, Pyrenees, Balkans, central Europe, Britain and Siberia but it is not recorded from Finland and Scandinavia. Adult males in B.M.(N.H.) are all from central and southern England, but not from either Wales or Scotland.

Lehmann (1971) citing records from the potamal of the River Fulda (W. Germany) and those of Thienemann (1954), describes the species as typical of the algal growth on stones in rivers of the central German hills and lowlands. This is confirmed by the restricted lowland distribution of adults and larvae within Britain.

subgenus Orthocladius v.d.Wulp

Orthocladius v.d. Wulp, 1874:132; Soponis, 1977:18.

Rheorthocladius Thienemann, 1935:205

Type-species Chironomus oblidens Walker, 1856:180, designated by Edwards, 1929:335.

SUBGENERIC DIAGNOSIS

As generic diagnosis except: Mentum always with six pairs of lateral teeth and a single median tooth. Antenna with five segments and Lauterborn organs varying in size, but rarely as large as in Orthocladius (Euorthocladius) thienemanni Kieffer (Fig. 49a). Seta interna of mandible always present, outer margin of mandible either smooth or weakly crenulate. Pecten galearis may be weakly indicated on the maxilla.

KEY TO THE KNOWN LARVAE OF BRITISH ORTHOCLADIUS (S.S.)

Note: The descriptions upon which this key is based are of limited numbers of specimens, and the key therefore is highly tentative.

1 Antennal ratio greater than 2.0. First antennal segment greater than 50 um long 2
Antennal ratio less than 2.0. First antennal segment less than 50 um long 3

2 Ratio of median tooth to width of whole mentum greater than 0.20. Claws on anterior parapod which bear more than one inner tooth have the apical tooth shorter than the inner teeth (Fig. 52e). ..... *wetterensis* Brundin
Ratio of median tooth of mentum to width of whole mentum less than 0.20. Claws on anterior parapod which bear more than one inner tooth have the apical tooth subequal to the inner teeth (Fig. 52e) .... *rhyacobius* Kieffer

3 Numerous (10 or more) complex lamellae on the galea of the maxilla. Apical tooth of the mandible longer than the first inner tooth of the mandible ..... *species A*
Less than five complex lamellae on galea of maxilla. Apical tooth of the mandible no longer than the first inner tooth 4

4 Complex setae of maxilla lying in the middle of the galea, No trace of pecten galearis ... *rubicundus* (Meigen)
Complex setae of maxilla lying on galea towards the palpiger and may be obscured by palpiger. Weak pecten galearis present .... ? *oblidens* (Walker)

Orthocladius (*Orthocladius*) *rhyacobius* Kieffer

Orthocladius rhyacobius Kieffer, 1911:181

DESCRIPTION OF 4TH INSTAR LARVAE (n = 4)

Body length not measured, head capsule length 593 - 610 um (n = 2), pale yellow with occipital margin black and apical third of mandible and all mentum brown.

Antenna (Fig. 50a). Five segmented, lengths 55 (53-58); 11.7 (11-13); 4.5 (4-5); 4.2 (4-5);/3. Antennal ratio 2.35 (2.12-2.55). Antennal spine 29 (28-32), subsidiary spine 9 (8-10), ring organ 7 (5-8) from base of second antennal segment. Lauterborn organs distinct, nearly as long as third antennal segment.

Labrum (Fig. 50b). SI bifid, branches subequal. SII long, simple, SIII and SIV normal. Labral chaeta simple, chaetulae laterales of six scales on each side of the three subequal scales of the pecten epipharyngis. Two terminally bifid chaetulae basales. Premandible 104 (100-106) long, with a single apical tooth.

Mandible (Fig. 50d). 185 (181-188) long, apical tooth no longer than the first of three inner teeth. Seta subdentalis 16 long, simple. Seta interna with seven branches, each finely serrate. Outer margin of mandible very weakly crenulate, inner margin smooth.

Mentum (Fig. 50c). Width of flattened mentum 159 (150-169), Median tooth 29 (28-31) wide. Ratio of median tooth to width of mentum 0.18 (0.17-0.19). Six pairs of lateral teeth subequal, the first with a rounded base like *Paratrichocladius*. Ventromental plates weak without setae beneath.

Maxilla. Like *species A* (Fig. 53d) except the pecten galearis is very weak and there is no appendix and all maxillary setae are simple.

Abdomen. Procercus 20 - 21 high by 20 - 26 wide, bearing apically six setae of maximum length 483 - 561 (n = 2). Lateral setae of procercus weak, maximum length 28. Claws of posterior parapod yellow-brown, simple; those of anterior parapod yellow with apical claw no longer than the inner claws (Fig. 49e).

MATERIAL EXAMINED

Site 37 (2 reared, 2 larvae).

DISTRIBUTION AND ECOLOGY

Fittkau and Reiss (1978) record Orthocladius rhyacobius Kieffer from the Pyrenees, central European mountains, north Germany as well as Britain and Ireland. There are few records of the adult from Britain, but these include three Scottish localities and two from North Yorkshire. Fittkau and Reiss summarise the ecology as rhithral but the single British larval locality from this survey is from the upper reaches of a tributary of the River Medway.

Orthocladius (Orthocladius) rubicundus (Meigen)

Orthocladius rubicundus (Meigen, 1818:35); Thienemann & Kruger, 1937:17.

DESCRIPTION OF 4TH INSTAR LARVA (n = 6)

Body length 5.4 (4.1-6.3) mm (n = 3), head capsule 430 (397-466) um, pale yellow-brown. Occipital margin brownish black, mentum and apical half of mandible brown.

Antenna (Fig. 51a). Five segmented, lengths 41.6 (38-45); 11.0 (10-12); 5.0 (4.5-5.5); 4.2 (4-5); 2.9 (2-3). Antennal ratio 1.81 (1.68-2.05). Antennal spine 26 (24-28) long, subsidiary spine 7 (5-8) long placed subapically on the apex of the second segment. Ring organ 5 - 8 from base of first antennal segment. Lauterborn organs present, not as long as the third segment.

Labrum and palatum (Fig. 51b). Inner branch of bifid SI shorter than the outer branch, other S setae simple. Few simple labral chaetae. Pecten epipharyngis of three subequal scales. Five chaetulae laterales, each scale subequal and lying like a moustache each side of the pecten epipharyngis. Two terminally bifid chaetulae basales. Premandible 80 (75-87) long with a single apical tooth and a weak inner tooth.

Mandible (Fig. 51c). 136 (127-143) long, apical tooth only slightly longer than the first of three inner teeth. Seta subdentalis 11 - 14 long, simple. Seta interna with six simple branches. Outer margin of mandible smooth.

Mentum (Fig. 51d). Flattened width 117 (111-127), median tooth 25.7 (23-31) wide. Ratio of median tooth width to that of whole mentum 0.22 (0.20-0.27). Six pairs of lateral teeth, ventromental plates small without setae beneath.

Maxilla. (Fig. 51e). Sensillae on palpiger and galea distinct. Few simple and complex lamellae on galea, ? no lamellae on base of palpiger. No pecten galearis. Five or six simple maxillary setae, simple appendix.

Abdomen. Procercus 18 (16-20) high by 22 (16-29) wide, bearing apically five or six setae of maximum length 457 (413-480). The procercus is unevenly sclerotised and one of the lateral setae 39 - 42 long, is stronger than usual in the genus. Supra-anal seta 84 (n = 1) long. Hind parapods 212 - 243 (n = 2) long, anal tubules 80 - 100 (n = 2) simple. Claws on posterior parapods yellow-brown, simple, those on anterior parapods yellow with very fine inner teeth even on the longest claws.

MATERIAL EXAMINED

CORNWALL: Polridmouth near Par, 28.ix.1976, small stream outflow from lake, leg. J.E. Marshall (B.M.(N.H.) coll.). (6 larvae, some exuviae attached to pupae with pharate male within)

DISTRIBUTION AND ECOLOGY

Adults ascribed to Orthocladius rubicundus (Meigen) have been recorded in Fittkau & Reiss (1978) from many localities including central Europe, the Alps and Pyrenees, Scandinavia and East Siberia as well as Britain. Within the B.M.(N.H.) collections there are adults identified as rubicundus from throughout England, Scotland and Wales, although few have been slide prepared for the necessary close examination.

The larvae are apparently restricted to running waters but previous larval records must be treated with caution in this genus unless reared. Thienemann & Kruger (1937:265) state that the species is found in rapidly running water including streams and rivers on stones and in algae.

Orthocladius (Orthocladius) wetterensis Brundin

Orthocladius wetterensis Brundin, 1956:104.

DESCRIPTION OF 4TH INSTAR LARVA (n = 1)

Body length not measurable, head capsule 572 um, yellow-brown with occipital margin dark brown and mentum and mandible pale brown.

Antenna (Fig. 52a). Five segmented, lengths 53; 11; 5; 4; 3. Antennal ratio 2.30. Antennal spine 14, subsidiary 6 long, subapical on second segment. Ring organ 8 from base of first antennal segment. Lauterborn organs present but weak, not as long as third segment.

Labrum and palatum (Fig. 52b). (Specimen poorly prepared). SI bifid inner branch shorter than outer. Remainder simple.

Labral chaetae numerous, simple. Premandible 58 long with a simple apical tooth and a well developed, blunt inner tooth. Palatum otherwise not visible.

Mandible (Fig. 52d). 185 long, apical tooth longer than the first of three inner teeth but shorter than the combined width of the inner teeth. Seta subdentalis 14 long, simple, seta interna of seven or eight fine, simple branches.

Mentum (Fig. 52c). Flattened width 175, median tooth 37 wide. Ratio of width of median tooth to width of mentum 0.21. Six pairs of lateral teeth, ventromental plates small without setae beneath.

Maxilla. Well developed sensillae on galea and palpiger. No pecten galearis. Few simple and complex lamellae on galea. Maxillary setae simple, appendix absent (not visible).

Abdomen. Missing. Anterior parapod with yellow claws with fine inner teeth on all but the longest and shortest claws (Fig. 52e).

MATERIAL EXAMINED

Site 21 (1 larva reared to pupa, associated with 1 pupa reared to an adult male. Identity confirmed by P.H. Langton).

DISTRIBUTION AND ECOLOGY

Brundin (1956:105) described wetterensis from a swarm in April over the shores of a south Swedish lake. The only other published record of the species is Lehmann (1971:488) who found adults and pupae in the middle salmonid region of the River Fulda (West Germany). Langton (unpublished manuscript, 1978) found the pupal exuvium in Britain and this appears to be the first larval description.

<u>Orthocladius</u> (<u>Orthocladius</u>) species A of Pinder

<u>Orthocladius</u> species A Pinder, 1978:72

DESCRIPTION OF 4TH INSTAR LARVA (n = 1)

Body length not measurable, head capsule 540 um, yellow with apical third of mandible, mentum and occipital margin black.

<u>Antenna</u> (Fig. 53a). Five segmented, lengths 47; 13; 6.5; 6; 4. Antennal ratio 1.59. Antennal spine 34, subsidiary spine 9. Ring organ 4 from base f first antennal segment. Lauterborn organs distinct, as long as third antennal segment.

<u>Labrum and palatum</u>. SI bifid with the branches subequal, remainder simple. Numerous simple labral chaetae. Pecten epipharyngis of three subequal scales. Five or six chaetulae laterales and two terminally bifid chaetulae basales. Premandible 85 long, simple and pale.

<u>Mandible</u> (Fig. 53c). 159 long, apical tooth longer than first inner tooth but shorter than combined width of the three inner teeth. Seta subdentalis 16 long, with an apical hook. Seta interna of seven simple or very finely serrate branches. Outer margin crenulate.

<u>Mentum</u> (Fig. 53b). Flattened width 130, median tooth 32 wide. Ratio of width of median tooth to whole mentum 0.25. Second of six pairs of lateral teeth smaller than the others. Ventromental plates weak without setae beneath.

<u>Maxilla</u>. (Fig. 53d). Sensillae on palpiger and galea distinct. Numerous lamellae on base of palpiger, similarly numerous simple and complex lamellae on galea. Maxillary setae long and weakly serrate. Appendix of three or four weak setae. Trace of a weak pecten galearis.

Abdomen. Procercus 21 high by 24 wide bearing apically six setae of maximum length 604. Lateral seta and supra-anal seta weak. Posterior parapod c. 180 long, anal tubules not measurable. Claws of posterior parapods yellow-brown, those of anterior parapods yellow with inner teeth shorter than apical tooth on all claws. Only longest and shortest claws simple.

MATERIAL EXAMINED

Site 48 (1 larva reared to male)

COMMENTS

This larval type of Orthocladius is the most frequently encountered but since only one specimen has been reared to a male which can be unambiguously referred to the species A (near oblidens Walker) described by Pinder, the description is based upon that single specimen.

DISTRIBUTION AND ECOLOGY

It is not clear how many of the records of Orthocladius oblidens refer to this species and how many to the true oblidens (see Pinder, 1978 for separation). Based on British records it is clear that species A is much the commoner species, being spread throughout the British Isles and there are few specimens clearly ascribed to oblidens.

If most records of oblidens are in fact species A the larvae are found in running waters in both lowland and mountain areas.

Orthocladius (Orthocladius)?oblidens (Walker)

DESCRIPTION OF 4th INSTAR LARVA (n = 1 exuvium)

Body length not measurable, head capsule 466 um, yellow brown with occipital margin, apical half of mandible and mentum darker brown.

Antenna (Fig. 54a). Five segmented, lengths 37; 11; 4; 4; 3. Antennal ratio 1.68. Antennal spine 23 long, subsidiary spine well developed, 10 long. Ring organ 7 from base of first antennal segment, Lauterborn organs very weak.

Labrum and palatum. As in rubicundus (Fig. 51b) except branches of bifid SI subequal. Premandible 79 long, with a single apical tooth and a broad inner tooth.

Mandible (Fig. 54c). 148 long with apical tooth no longer than the first of three inner teeth. Seta subdentalis 10 long, seta interna of six or seven fine, simple branches. Outer margin of mandible smooth.

Mentum (Fig. 54b). Width of flattened mentum 111, width of median tooth 25. Ratio of median tooth to width of flattened mentum 0.23. First pair of lateral teeth rounded, the remaining five pairs triangular and subequal in size. Ventromental plates small, without setae beneath.

Maxilla (Fig. 54d). Sensillae on palpiger and galea distinct. Lamellae on base of palpiger distinct, those on galea both simple and complex. The complex lamellae are on the palpiger edge of the galea, hidden behind the palpiger in Fig. 54d. Maxillary setae weakly serrate. Appendix apparently absent. Pecten epipharyngis of weak spinules present.

Abdomen. Procercus 21 high by 24 wide, posteriorly darkened and bearing apically six setae of maximum length 508. Lateral seta of procercus more distinct than usual, 48 long. Supra-anal seta 106 long. Claws of posterior parapod yellow with inner teeth shorter than the apical teeth. Posterior parapod 275 long, anal tubules apparently very short.

MATERIAL EXAMINED

Site 10a (reared to male)

COMMENTS

See page 239 under species A.

Subgenus *Pogonocladius* Brundin

Pogonocladius Brundin, 1956:99.

Type-species *Chironomus consobrinus* Holmgren, 1869:44, by original designation.

SUBGENERIC DIAGNOSIS

As generic diagnosis except: head capsule yellow (Soponis, 1977 - brown; Goetghebuer, Humphries and Fitzgerald, 1949 - yellow). Antenna four segmented with very small Lauterborn organs. Outer margin of mandible strongly crenulate. Pecten galearis present on maxilla.

COMMENTS

This subgenus was erected by Brundin for a single species, *consobrinus* based principally on the distinctive pupal stage which is similar to *Acricotopus*. The adult was distinguished from the other *Orthocladius* by characters shared by the species *glabripennis*, which Brundin synonymised with *consobrinus*. Pinder and Cranston (1976) showed that *glabripennis* was a valid species which probably belonged to the subgenus *Orthocladius*, and therefore that the adult characters Brundin used to separate *Pogonocladius* were invalid.

Soponis (1977:18) therefore questions the validity of the erection of subgenera based upon the unusual features of a single life stage, and rightly suggested that this could not be evaluated until there is better taxonomic knowledge. It is felt that there are not only unique features of the pupa of *consobrinus* but that larval characters including the four segmented antenna, shape of the mentum and presence of a pecten galearis on the maxilla suggests that this species warrants at least subgeneric status.

Orthocladius (*Pogonocladius*) *consobrinus* (Holmgren)
O. (*P.*) *consobrinus* (Holmgren, 1869:44); Soponis, 1977:18. *Orthocladius crassicornis* Goetghebuer, 1937:508 (larval description Goetghebuer, Humphries and Fitzgerald, 1949:417).

DESCRIPTION OF 4TH INSTAR LARVA (n = 8)

Body length 7.2 (6.9-7.7) mm (n = 4), head capsule 682 (636-752) um, yellow, with occipital margin, apical third of mandible, apical third of premandible and anterior part of mentum black.

Antenna (Fig. 55a). Four segmented, lengths 81.7 (75-88); 17.1 (16-19); 7.7 (7-9); 3.6 (3-5). Antennal ratio 2.89 (2.50-3.27). Antennal spine 19 (16-21) long, subsidiary 7 (6-9) long. Ring organ 13 (11-16) from base of first antennal segment. Lauterborn organs small.

Labrum and palatum (Fig. 55b). SI seta bifid with inner branch shorter and weaker than the outer branch. Other S setae simple, the SII lying more posterior than usual. Labral chaetae simple. Strong spine on each side of the palatum on the labral margin. Pecten epipharyngis of three subequal spines, three or four scales form the chaetulae laterales. Premandible 119 (111-132) long with two apical teeth and a broad inner tooth.

Mandible (Fig. 55d). 219 (201-238) long, apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis 20 - 22 long with an apical hook. Seta interna with seven or eight finely serrate branches. Outer margin of mandible strongly crenulate.

Mentum (Fig. 55c). Flattened width 161 (153-177). Median tooth lower than first laterals, second laterals lower than the third laterals. Six pairs of lateral teeth. Ventromental plates weak, no setae beneath.

Maxilla (Fig. 55e). Sensillae on palpiger and galea distinct. Simple lamellae on both base of palpiger and on galea, those on the galea quite numerous. Pecten galearis present. Maxillary seta stout, some terminally serrate. No appendix visible.

Abdomen. Procerci 51 (43-58) high by 49 (42-53) wide, strongly sclerotised posteriorly, and bearing apically five or six setae of maximum length 741 (551-1038). Lateral seta of procercus weak, supra-anal seta ? absent. Hind parapod 265 - 370 long (n = 2), anal tubules small. Claws on posterior parapod yellow, simple; those on anterior parapod yellow with very fine inner teeth on all but the smallest claws.

MATERIAL EXAMINED

Site 17 (2 m deep) (1 larva); Site 24 (3 reared); RUTLAND: Rutland Water, 2.vi.1976, Leg. and det. A. Brown (B.M.(N.H.) coll.), (many unreared larvae).

DISTRIBUTION AND ECOLOGY

Adults of Orthocladius consobrinus (Holmgren) have been recorded from Britain, Ireland, Iceland, Germany (northern lakes and Bodensee), Scandinavia and several Arctic localities including Spitzbergen, Bear Island, Greenland and North Western Territories of Canada. Within Britain the species is now known to be widespread, the previous paucity of records, being apparently due to the early emergence of the adults.

Reiss (1968:233) noting that the species was scarce in Bodensee cited the observations of others including Meuche (1939) who found the larvae in the littoral of the north German lakes, and also in the emergent stone zone. Brundin (1949) found O. consobrinus in sediments down to 15m in the southern Swedish lakes. Humphries and Fitzgerald (in Goetghebuer, Humphries and Fitzgerald, 1949) found the larvae in modest numbers in the littoral zone of the upper reservoir on the River Dodder (Ireland). In this survey the larvae were found in the benthos of Malham Tarn and more frequently in the stream draining the Tarn. The species is one of the most abundant in winter in Rutland Water, a recently impounded reservoir (Brown, pers. comm).

xxv. Paracladius Hirvenoja

Paracladius Hirvenoja, 1973:91.

Paratrichocladius Thienemann, 1942:314, preoccupied by Paratrichocladius Santos Abreu, 1918:48.

Type-species Chironomus insernens Walker, 1856 (= conversus Walker 1856) by original designation.

GENERIC DIAGNOSIS

Medium sized, up to 9 mm long, head capsule up to 500 um long.

Antenna. Five segmented with last three segments subequal or diminishing in length. Lauterborn organs present, ring organ present low on first antennal segment. Antennal spine not extending beyond terminal antennal segment.

Labrum. SI bifid, remainder of S setae simple. Pecten epipharyngis of three spines, chaetulae laterales long and simple. Premandible bifid.

Mandible. Apical tooth subequal to the combined length of the three inner teeth. Seta interna and seta subdentalis present.

Mentum. Six pairs of lateral teeth. Median tooth broad and pale. Ventromental plates do not extend beyond mentum on flattened mentum. Sparse beard present (not always very distinct).

Abdomen. Parapods present bearing simple claws on the posterior pair and finely toothed claws on the anterior. Procercus bearing 6 - 7 terminal setae.

COMMENTS AND SYSTEMATIC STATUS

Paracladius is a distinctive genus in the larva, sharing the presence of a beard beneath the ventromental plates with _Acricotopus_ within the _Cricotopus_ series of genera. The presence of this beard is probably a plesiomorphic character in the Orthocladiinae and cannot be used to indicate affinities within the _Cricotopus_ group.

Based on characters found in the adult both Hirvenoja (1973:66) and Saether (1977:86) believe _Paracladius_ to be the sister group of _Halocladius_ and _Cricotopus_ combined. The shape of the mentum is quite distinctive in _Paracladius_ with an unusually broad median tooth for the _Cricotopus_ group. It shows similarities to the mentum of the non-British _Halocladius_ (_Psammocladius_) _braunsi_, but there are many differing features in the labrum and mandible.

There do not appear as yet to be any larval characters found which are synapomorphic for the genera suggested by Hirvenoja and Saether.

Paracladius conversus (Walker)

Paracladius conversus (Walker, 1856:175); Hirvenoja, 1973:94.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 3)

Body length 5.2 - 7.1 mm, head capsule 448 - 477 um. Head capsule pale yellow, occipital margin golden, mandible golden with three inner teeth brown, premandible and mentum (except for median tooth) brown. Median tooth of mentum very pale almost translucent.

Antenna (Fig. 56a). Five segmented, lengths 68 - 74; 10 - 13; 5 - 6; 3 - 3.5; 3 - 3.5. Antennal ratio 2.6 - 3.0. Lauterborn organs distinct, ring organ 8 - 13 from base of first antennal segment. Spine 16 - 21, not extending beyond final antennal segment.

Labrum (Fig. 56b). SII bifid 24 - 28 long, remaining S setae as normal, simple. Pecten epipharyngis of three spines, six or seven chaetulae laterales, ?2 chaetulae basales. Premandibles 118 - 121, bifid, the outer tooth a long and slender spine.

Mandible (Fig. 56c). 184 - 192 long with outer tooth subequal to or slightly longer than combined width of three inner teeth. The outer tooth is less sharply pointed than in many other species with elongate outer teeth to the mandible. Seta subdentalis present 13 - 16, seta interna present with 6 simple branches.

Mentum (Fig. 56d). 219 - 227 wide with the pale median tooth 60 - 68 wide. Six pairs of lateral teeth. Ventromental plates large but not extending beyond the outer tooth of the flattened mentum. Five to seven fine hairs making up the beard under the mentum.

Maxilla (Fig. 56e). Distinct beard of three setae present, as is the appendix. The antaxial seta is present but pointing posteriorly in Fig. 56e. Chaetae of lacinia simple. Paraxial surface of the galea bearing only three scales.

Abdomen. Procerci unusual in *Cricotopus* group bearing a posterior area which is more heavily sclerotised resembling a scale or blunt spur (Fig. 56f). Procerci 24 - 32 high by 12 - 16 wide and bearing apically 6 setae of maximum length 318 - 402. Lateral seta of procercus well developed 130 - 150 long. Supra-anal seta 69 - 95 long. Posterior parapod 328 (n = 1), anal tubule 75 (n = 1).

Claws on anterior parapod golden, finely tapering to a finely toothed apex. Claws of posterior parapod dark brown, blunt and simple.

MATERIAL EXAMINED

RUTLAND: Rutland Water, orth Arm of lake, 2.vi.1976, A. Brown (3 unreared larvae).

DISTRIBUTION AND ECOLOGY

Hirvenoja surveying previous records (1973:98) states that the species is widespread in Europe from Iceland to Italy and eastwards to Siberia. In Britain the species has apparently not been recorded from further north than Derbyshire, but it is widely distributed further south.

Thienemann (1942:309, 1950:127) and Reiss (1968:237) record the larvae from lakes particularly on algal covered stones but also from the mud of Lunzer Mittersee and from the splash zone. The larva is also noted from slowly flowing waters and there is a record by Lehmann (cited in Hirvenoja, 1973:98 but not in Lehmann, 1971) from the River Fulda.

xxvi. Parakiefferiella Thienemann

Parakiefferiella Thienemann, 1936b:195

Type-species Spaniotoma (Eukiefferiella) coronata Edwards, 1929:354, by original designation.

GENERIC DIAGNOSIS (Excludes tentatively identified material mentioned by Saether, 1969:142)

Small larvae, up to 4 mm long, head capsule up to 400 um.

Antenna. Five or six segmented; the sixth when present is vestigial. There are two antennal types in the genus, one has the basal segment longer than the remainder (A.R. more than 1), and the other with a short basal segment (A.R. less than 1). Lauterborn organs absent, although there is a strong subterminal spine on the second antennal segment. Spine may extend beyond apex of antennal flagellum. Ring organ present on basal part of first antennal segment.

Labrum. SI (? always) divided into a variable number of spikes. SII long, SIII and SIV normal. Pecten epipharyngis of three scales; chaetulae laterales simple, 6 - 7 in number. Premandible simple.

Mentum. Usually one median tooth and six pairs of laterals, the first pair of laterals are closely appressed to the median tooth which is usually broad. Wulker (1957:417) figures the larva of the non-British gracillima Kieffer which has a mentum with five pairs of lateral teeth and a double median tooth. It is not clear whether there is a small sixth tooth fused with the median teeth. Ventromental plates strongly developed, but not extending beyond outer teeth of flattened mentum.

Mandible. Outer tooth usually subequal in length to the combined width of the three inner teeth (not two in coronata as suggested by Thienemann, 1944:647). Apical tooth longer than three inner teeth in coronata. Seta subdentalis present, seta interna of six or seven simple branches. Inner margin of mandible smooth.

Maxilla. Antaxial setae simple, no pecten galearis present. The lamellae on the galea are distinct and broad.

Abdomen. Procerci about as high as wide without scales, bearing apically six or seven setae. Lateral setae of procercus weakly developed. Parapods normal, bearing simple claws. Anal tubules distinctive, conical, shorter than anal parapods. Simple body setae present in bathophila.

COMMENTS AND SYSTEMATIC STATUS

Saether (1969:142) in describing Parakiefferiella torulata stated that the species was atypical, based on the published descriptions of the larvae. However re-examination of these larvae shows that the previous descriptions are poor, and in fact torulata closely resembles bathophila. In his paper Saether notes that larvae ascribed to Parakiefferiella by Hamilton (unpublished Ph.D.) are extremely divergent from torulata and, if these larvae are correctly placed, the genus would need redefinition.

Parakiefferiella larvae have the characteristic shorter third antennal segment than the fourth indicating that it belongs in the tribe Metriocnemini. Within this tribe Parakiefferiella has normally developed procerci and parapods and thus belongs with the more plesiomorphic genera within the tribe. Based on the adults and pupae Parakiefferiella shows relationships with Heleniella and particularly with Krenosmittia although this is less apparent in the larvae.

KEY TO THE BRITISH SPECIES OF PARAKIEFFERIELLA

1 Antennal ratio greater than 1.2. Median tooth has a double hump in the centre .... bathophila (Kieffer)
  Antennal ratio less than 1. Median tooth broad and domed ....coronata (Edwards)*

* Keyed from a single unreared larva in Thienemann collection.

Parakiefferiella bathophila (Kieffer)

Parakiefferiella bathophila (Kieffer, 1912:88)

DESCRIPTION OF 4TH INSTAR LARVAE (n = 3)

Body length 3.4 - 3.6 mm (n = 2, exuviae), head capsule 327 (310 - 343), pale yellow, occipital margin, labral margin and premandible brown. Mentum brown, median teeth paler. Inner three teeth of mandible brown, apical tooth and remainder of mandible golden.

Antenna (Fig. 57a). Six segmented, the sixth vestigial, lengths 32.8 (30-35); 12.3 (12-13); 1.7 (1.5-2); 2.7 (2-3); 3.2 (3-3.5); 2.2 (2-2.5). Antennal ratio 1.49 (1.40-1.56). Antennal spine apparently shorter than the flagellum but difficult to see. ubsidiary spine placed subapically on the second antennal segment 7.5 (6.5-9) long. Lauterborn organs absent, ring organ placed 7 - 9 from the base of the first antennal segment.

Mandible (Fig. 57c). 86 (84-90) long. Apical tooth subequal to the combined width of the three inner teeth. Seta subdentalis 8 long, seta interna of six or seven almost simple branches. There is a trace of plumose ending on some of the branches.

Labrum and palatum (Fig. 57b). SI seta divided into about 8 - 10 pointed branches presumably derived from the plumose condition. SII long and simple, SII and SIV as normal. Pecten epipharyngis of three blunt scales, six chaetulae laterales, chaetulae basales not visible. Premandible simple 57 (50-61) long.

Mentum (Fig. 57d). Flattened width 86 (84-90), one median tooth with a pair of humps and six pairs of laterals. The first pair of laterals partially fused to the median tooth and this central area paler than the rest of the mentum.

Ventromental plates distinct but not extending beyond the outer mental teeth on the flattened mentum. No setae beneath the plates.

Maxilla (Fig. 57e). As generic diagnosis.

Abdomen (n = 2). Procerci 25 - 26 high by 20 - 26 wide bearing apically 6 - 7 setae of maximum length 318 - 392. Lateral setae fine 15 - 20 long, anal tubules conical 52 long, 47 wide at the base. Some body setae 50 um long.

MATERIAL AMINED

Site 17 (2 reared); Site 26 (1 reared).

DISTRIBUTION AND COLOGY

The species is distributed throu h northern and central Europe but as with many Orthocladiinae there are few adult records from Britain. umphries and rost (1937:179) found the larvae in the iver Liffey (Ireland) living in the moss, and Site 26 in this survey is a wee'y stream, but most records of the immature stages are from standing waters. ulker (1957:412) summarises the sites from which pupae have been found including the north German lakes and northern Finnish lakes.

Altho gh many species of Orthocladiinae are found in both running and standing water in Europe, most of these species appear to be more restricted in their ecology in Britain. This is one of the few species which have been found in both lotic and lenitic habitats in the course of this study.

<u>Parakiefferiella coronata</u> (Edwards)

<u>Parakiefferiella coronata</u> (Edwards, 1929:359)

BRIEF DESCRIPTION OF 4TH INSTAR LARVA (n = 1)*

* Specimen slide mounted and identified by Thienemann. Too poorly prepared for figuring, and only limited measurements can be taken.

<u>Antenna</u>. ? Five segmented, vestigial sixth, if present, not visible. Lengths 17; 8; 2; 5; 3. Antennal ratio 0.95. Spine extends beyond the final antennal segment.

<u>Mandible</u>. About 70 long. The apical tooth slightly longer than the combined width of the three inner teeth.

<u>Labrum</u>. SI seta divided into a number of points. Otherwise as in generic diagnosis. Premandible simple.

<u>Mentum</u>. Not fully flattened but about 58 wide. The median tooth is 20 wide and there appear to be lateral notches on the side of the broad, domed median tooth which may represent a sixth pair of lateral teeth. Median area pale.

<u>Abdomen</u>. Anal tubules conical. Procerci as in <u>bathophila</u>. Body setae apparently absent.

MATERIAL EXAMINED

1 poorly mounted, unreared larva with no data except Thienemann's determination as "<u>Parakiefferiella coronata</u>".

DISTRIBUTION AND ECOLOGY

This species is distributed through Northern Europe and two localities in Germany (Titisee, ulker (1957:415); Bodensee, Reiss (1968:244). In Britain the species is known from Scotland and Wales, and it seems likely that this is a boreoalpine species as suggested by Reiss (1968:244).

In contrast to <u>bathophila</u>, <u>coronata</u> has only been found in standing waters, mostly in the littoral zone of lakes among the plants at the edge. It is likely that the larvae of <u>coronata</u> will be found in this littoral zone of the higher Scottish and Welsh lakes, which were not examined in this study.

xxvii. <u>Paralimnophyes</u> Brundin

<u>Paralimnophyes</u> Brundin, 1956:129

Type-species <u>Camptocladius hydrophilus</u> Goetghebuer, 1921: 169, by original designation.

GENERIC DIAGNOSIS (Based on unreared Munich Museum material and descriptions of Thienemann)

Medium or small larvae.

<u>Antenna</u>. Five segmented with the fourth segment longer than the third. Lauterborn organs distinct, antennal spine extends beyond fifth antennal segment.

<u>Labrum and palatum</u>. SI seta apparently simple as are the other S seta. Labral chaetae terminally serrate. Pecten epipharyngis of three subequal scales with two or three chaetulae laterales each side. Premandible with more than one apical tooth.

<u>Mandible</u>. Apical tooth shorter than the four inner teeth. Seta subdentalis and seta interna present.

<u>Mentum</u>. Paired median teeth taller than the rest of the five pairs of lateral teeth. Ventromental plates present, weakly developed. A projection at the base of the outer lateral teeth.

<u>Maxilla</u>. Sensillae on palpiger and galea present, distinct. Only simple lamellae on base of palpiger and galea. Short simple setae as well as normal simple maxillary setae. No pecten galearis.

<u>Abdomen</u>. Procerci well developed bearing apical setae.

Anterior and posterior parapods present, separate, bearing claws. Anal tubules distinct.

COMMENTS AND SYSTEMATIC STATUS

Brundin (1956:129) separated the species _hydrophilus_ from _Limnophyes_ on the basis of the more distinct anal point in the adult male. Quoting Thienemann's observations on the immature stages he mentioned also the long setae on the abdomen of the larva and the pupa, the violet colour of the larva and the long prothoracic horn setae of the pupa and stated that these warranted generic status for the "_longiseta_" type of _Limnophyes_. Examination of the pupa and larva of _longiseta_ Kieffer (= _hydrophilus_ Goetghebuer) and comparison of this material with the known immature stages of _Limnophyes_ suggests that generic status for _Paralimnophyes_ is not warranted and that the species _hydrophilus_ and _arcticus_ Brundin are no more than a subgenus or species-group of _Limnophyes_ at most. See under _Limnophyes_ (page 190) for comments on the systematic status of this generic grouping.

'_Paralimnophyes_' _hydrophilus_ (Goetghebuer)

Paralimnophyes hydrophilus (Goetghebuer, 1921:169).

Paralimnophyes longiseta (Kieffer); (Thienemann, 1921:816)

DESCRIPTION OF 4TH INSTAR LARVA (n = 3, unreared, preserved in spirit for 61 years, determined by Thienemann)

Body length 3.9 (3.8-4.0) mm, head capsule 343 (339-344) um, pale yellow-brown, occipital margin scarcely darkened, mentum and mandible pale brown.

Antenna (Fig. 58a). Five segmented, lengths 43 (40-45); 12.3 (12-13); 3.3 (3-4); 9.7 (9-10); 3.7 (3-4). Antennal ratio 1.45 (1.38-1.50). Antennal spine 38 (35-41) long, extending beyond fifth antennal segment. Subsidiary spine small, no more than 5 long. Ring organ 10 - 12 from base of first antennal segment. Lauterborn organs distinct, longer than third antennal segment.

Labrum and palatum. See generic diagnosis, visible only with difficulty in this material which has been in alcohol for a number of years. Premandible c. 60 long with two apical teeth and two broad smaller inner teeth.

Mandible (Fig. 58d). 99 (94-103) long, apical tooth shorter than combined width of the four inner teeth, which are more triangular than usual. Fourth (innermost) tooth clearly delimited from the rest of the mandible. Seta subdentalis short and pointed. Seta interna of six or seven fine branches.

Mentum (Fig. 58b). Width of flattened mentum 71 (69-74). Paired median teeth larger than lateral teeth. Five pairs of laterals, the first larger than the remainder. Ventromental plates small without setae beneath.

Maxilla (Fig. 58c). Sensillae on palpiger and galea distinct, no pecten galearis. Few simple lamellae on either palpiger base or galea. Both long and short maxillary setae.

Abdomen. (Fig. 58e). Procerci 31 - 34 high and 21 - 26 wide bearing apically six setae of maximum length 508 - 525. Lateral seta weak, procercus scarcely sclerotised. Supra-anal seta 370 - 395 long, mounted on a distinct pedestal. Posterior parapods 159 - 185 long, anal tubules 111 - 114 long, tapering to a point. Claws on posterior parapods pale yellow and simple, those on anterior parapods scarcely pigmented and simple.

MATERIAL EXAMINED

? GERMANY: "nordliche von Dicksee, Quelle, 15.iii.1918, *Camptocladius longiseta*" (3 larvae mounted in Berlese from

60 year old alcohol material, Munich Museum coll.).

DISTRIBUTION AND ECOLOGY

Fittkau and Reiss (1978:423) record adult *hydrophilus* from lowland western Europe, Norway and the Caucusus as well as Britain. Within Britain adults are recorded from several lowland southern English localities as well as a single specimen from the River Endrick (lowland Scotland, leg. Maitland), and a further single specimen from Stickle Tarn, Westmoreland. Most adult records are for only a few specimens at most and larval records are even more infrequent. No larvae have been recorded from Britain and the description is based upon specimens of Thienemann. Thienemann (1921:820) records the larvae from pools and ditches in meadow land.

xxviii. *Parametriocnemus* Goetghebuer

Parametriocnemus Goetghebuer, 1932:22; Zavrel, 1941:18.

Type-species *Metriocnemus stylatus* Kieffer, 1924:97 by monotypy.

GENERIC DIAGNOSIS

Medium to large larvae, up to 9 mm long.

Antenna. Five segmented, the fourth segment may be longer than, subequal to, or shorter than the third segment. Lauterborn organs distinctly longer than the third antennal segment. Ring organ present in the basal half of the first segment. Spine extends no further than the terminal antennal segment.

Labrum. SI setae plumose but with fewer branches than the SI of *Brillia*, *Heterotrissocladius* etc. SII, SIII and SIV normal. Weakly sclerotised labral lamella present between SI. Labral chaetae serrate, as may be some of the chaetulae laterales. 2 simple chaetulae basales. Pecten epipharyngis of three small, simple spines. Premandible with two to six teeth (two in British species). No beard on premandible.

Mandible. Apical t oth shorter than the combined width of the three inner teeth. eta subdentalis and seta interna present.

Mentum. One pair of median teeth each rounded basally but terminating in a point. Five pairs of lateral teeth, the fourth tooth sometimes higher than the third tooth. Ventromental plates distinct, extending beyond the outer mental teeth on the flattened mentum. No setae beneath.

Maxilla. (Based on the single sp cies *stylatus*). Palpiger small, lamellae on outer margin of galea terminally branched, lamellae on outer surface of galea normal. Maxillary setae simple. No pecten galearis. Bisensillae short.

Abdomen. Procercus taller than wide but relatively small, bearing apically six or seven setae. Parapods present and divided. Anal tubules present usually shorter than the posterior parapods, but may be longer (*boreoalpinus*). No body setae.

COMMENTS AND SYSTEMATIC STATUS

Saether (1977:86) proposed that *Parametriocnemus* was the sister group of *Paraphaenocladius*, based on the adults and pupae. In the larvae the genera are very similar particularly in possessing large Lauterborn organs, plumose SI setae, similar mental structure (including the well developed ventromental plates) and structure of the palatum. All these are believed to be plesiomorphic character states within the tribe Metriocnemini to which these two genera belong. Saether (1975:58-62) was unable to find any larval synapomorphies for

Paraphaenocladius and *Parametriocnemus* combined, and unless the absence of a pecten galearis is an apomorphic character no synapomorphy has been found in this study either. As Saether (1975:57) pointed out the key to understanding the relationships with other genera in this area rests, to a large extent, with the imagines. The observations made in this study are not in conflict with the relationships thus derived.

Parametriocnemus stylatus (Kieffer)

Parametriocnemus stylatus (Kieffer, 1924:97); Zavrel, 1941, 13; Kownacka & Kownacki, 1967:190).

DESCRIPTION OF 4TH INSTAR LARVA (n = 1, but 3 3rd instars also examined)

Body length 5.2 mm, head capsule 318 um long, pale yellow, with an occipital margin pale brown and the mentum, mandibles and premandible darker brown.

Antenna (Fig. 59a). Five segmented, lengths 49; 18; 4; 5.5; 4. Antennal ratio 1.56. Antennal spine 30, extending to the terminal antennal segment. A subsidiary spine of 6 long is placed subapically on the second antennal segment. Ring organ large, 6 from base of first antennal segment.

Labrum (Fig. 59b). SI plumose, SII long and simple, SIII a simple seta and SIV as normal. Labral chaetae serrate on the inner surface, numerous simple labral spines above the labral margin. Pecten epipharyngis not visible on the 4th instar larva examined, but in the 3rd instar larvae they are three small simple spines. The four or five chaetulae laterales are simple, and there are two chaetulae basales, also simple. The premandible is 69 long and is terminally bifid with a broad inner tooth.

Mandible (Fig. 59c). 108 long, apical tooth slightly shorter than the three inner teeth combined. Seta interna of six or seven serrate branches, seta subdentalis present.

Mentum (Fig. 59d). A pair of median teeth, each broader than two of the five pairs of laterals. The fourth pair of lateral teeth is higher than the third pair. Ventromental plates large, but not extending beyond the outer teeth of the flattened mentum (unlike figure of Kownacka and Kownacki, 1967). No setae beneath plates.

Maxilla (Fig. 59e). Palpiger relatively short. Lamellae on outer margin of galea divided into fine branches apically, although the outer lamellae are simple, as usual. Bisensillae on galea normal, no pecten galearis present. Maxillary setae simple including antaxial and paraxial setae.

Abdomen. Procerci weakly sclerotised 27 high by 18 wide, bearing apically 6 setae of maximum length 230. The lateral setae are weak, up to 64 long. The supra-anal seta is 74 long.

The posterior parapod is 223 long, the anal tubules present, tapering to a point, but not measurable in the 4th instar. The claws of the anterior parapod are pale yellow and all but the smallest have a number of inner teeth. The posterior parapod claws are golden and simple.

MATERIAL EXAMINED

Site 4 (1 larva reared to pupa); EAST SUSSEX: Ashdown Forest, .ix.1976, leg. J. Francis (3 3rd instar larvae).

DISTRIBUTION AND ECOLOGY

Parametriocnemus stylatus (Kieffer) is a species widely distributed in western and northern Europe. In Britain, as with so many Orthocladiinae, there are few adult records, mostly from high ground in Wales and northern England. Thienemann (1954:328) states that the species is a typical spring dwelling chironomid, and several other observations suggest that this is the case (Dittmar, 1955:469; Ringe, 1974: 241). Lehmann (1971:494) suggests that the species is found further down the water course in the middle Salmonid region of the River Fulda.

Site 4 in this survey is similar to that studied by Ringe (loc.cit.) - a narrow, relatively fast, high stream, not far from the source at a spring. Emergence traps showed that Parametriocnemus was an important genus at this site, but only a single larva was taken.

xxix. Paraphaenocladius Sparck & Thienemann

Paraphaenocladius Sparck & Thienemann, 1924:223; Strenzke, 1950:322.

Type-species Metriocnemus ampullaceus Kieffer (= impensus Walker) by original designation.

GENERIC DIAGNOSIS (Based on published descripti ns and Thienemann material

Small to medium sized larvae, up to 6 mm long.

Antenna. Five segmented, the third segment usually shorter, sometimes much shorter than the fourth. Lauterborn organs large, longer than the third antennal segment. Antennal blade as long as or longer than the ant nnal flagellum. Ring organ lar e. Antennal ratio usually less than 1.

Labrum. SI plumose, SII and SIII simple, SIV better developed than usual. Weak, poorly sclerotised labral lamellae present between bases of SI seta. Labral chaetae simple or serrate. Pecten epipharynx of three simple short spines. Chaetulae late ales (? always) simple, chaetulae basales branched. Premandible apparently always with three teeth and no beard.

Mandible. Outer tooth shorter than the combined width of three inner teeth. Seta subdentalis present. Seta interna present with simple and serrate branches.

Mentum. One or two median teeth. Perhaps more species have paired median teeth than is inferred in the descriptions since there is a great deal of wear of the median part of the mentum in these terrestrial species. Five pairs of lateral teeth, often of unequal sizes. The ventromental plates are quite variable in this genus; frequently there are a second pair of plates lying inside the often large main plates. There are no setae present.

Maxilla. Palpiger small. Lamellae of palpiger present but small. Lamellae of galea present, simple and small. No pecten alearis. Bisensillae on galea small. Maxillary setae usually simple, but in one species (figured) these setae are very broad.

Abdomen. The anterior parapods are fully divided and bear simple claws. The 9th abdominal segment (preanal) is curved over the remaining segments so that the procerci and procercal setae are directed backwards and the posterior parapods directed ventrally. The procerci are usually higher than wide but are variable in size and sclerotisation. There are usually no more than four procercal setae and they are relatively short. Usually four anal tubules which may be segmented and can be as long as the posterior parapods.

COMMENTS AND SYSTEMATIC STATUS

The larvae of Paraphaenocladius show many of the plesiomorphic characters typical of the more plesiomorphic genera of the tribe Metriocnemini including the well developed ventromental plates, plumose SI, palatal structure and antennal form. As mentioned under Parametriocnemus (page 257) there are a number of genera in the Metriocnemini with these character states, and on the adult and pupa Saether suggests that *Paraphaenocladius* is the sister group of *Parametriocnemus*. No evidence has been found to contradict this, but no larval synapomorphy has been found to confirm it either.

Paraphaenocladius species A

DESCRIPTION OF ?4TH INSTAR LARVAE (n = 3)

Body length 3.05 (2.8-3.4), head capsule 294 (275-310), yellow. Occipital margin not darkened, mentum and mandibles dark brown.

Antenna (Fig. 60a). Five segmented, lengths 14.7 (13-16); 7.7 (7-8); 2.2 (2-3); 7.7 (7-8); 4. Antennal ratio 0.68 (0.65-0.71). Antennal spine 23 (21-25), extending to or beyond fifth antennal segment. Subsidiary spine on 2nd antennal segment 4 long. Ring organ 4 - 6 from base of first antennal segment, distinct.

Labrum (Figs. 60b & c). SI seta plumose, remaining S setae as normal although SIV larger than usual. Pecten epipharyngis of three small simple spines. Labral chaetae serrate. Chaetulae laterales simple, 4 or 5. 2 Chaetulae basales both branched apically. Premandible 40 - 43 long with three teeth.

Mandible (Fig. 60e). 78 (74-80) long. Apical tooth shorter than combined width of the three inner teeth. Seta subdentalis present, seta interna of five branches each terminally strongly serrate.

Mentum (Fig. 60d). Width of flattened mentum 59 (58 - 62). Ventromental plates weak compared to other members of the genus and the outer plates not evident. No setae outside the lateral teeth. Fourth lateral teeth nearly as high as the third.

Maxilla (Fig. 60f). Palpiger small, less than 20 um high. The maxillary setae are modified and are broader than normal. The longest maxillary seta is 22 um high. Only one bisensillum present on the galea.

Abdomen (Fig. 60g). Procerci 12 (10-13) high by 10 (8-11) wide, weakly sclerotised and bearing apically 4 setae of maximum length 78 (68-84). Lateral setae of the procercus weak no more than 20 um long. Supra-anal seta weak (? sometimes absent) 25 long. Hind parapods about 66 long, anal tubules 31 - 40 long by 15 - 18 maximum width, ? only one pair. Claws of anterior parapod pale yellow with a few small teeth on the inner margin of all but the shortest claws. Posterior parapod claws golden, simple. Both parapods well developed and fully separated.

MATERIAL EXAMINED

ESSEX: Epping Forest, Coronation Woods, 10.ii.1977, leg. A. Seddon, ex. leaf litter. (3 larvae).

COMMENTS

These larvae have not been reared and their position in Paraphaenocladius may be open to question. The distinctive preanal segment is indicative of this genus though the reduction in the ventromental plates and the development of the maxillary setae are more apomorphic characters than have been noted previously in the genus. Of the British species only impensus (Walker) has been described while cuneatus (Edwards), irritus (Walker) and penerasus (Edwards) remain undescribed. This species can be distinguished from impensus (Walker) as described by Thienemann & Strenzke (1941:141) by the three inner teeth on the mandible (four in impensus), the simple anal tubules (three contractions in impensus) and the broad maxillary setae (narrow in *impensus*). Examination of larvae identified as *impensus* by Thienemann (from alcohol) shows that (besides the *Cricotopus*, *Orthocladius* and *Paratrichocladius* present in the sample), larvae which belong to *Paraphaenocladius* have only three inner mandibular teeth. However the other characters cited should serve to separate the species.

DISTRIBUTION AND ECOLOGY

Little can be said about species A, so these are general comments on the genus *Paraphaenocladius*. This genus really lies outside the scope of the current study since it seems that all the larvae are terrestrial or semiterrestrial. No *Paraphaenocladius* have been seen in this survey from aquatic habitats. The genus is found in most regions of the world and is probably larger than currently recognised.

Strenzke (1950:211) believed that all the species he described inhabit damp soil by springs, in meadows and alder carr. The sole locality for this species is somewhat drier than this.

xxx. *Paratrichocladius* Santos Abreu

Paratrichocladius Santos Abreu, 1918:204; Hirvenoja, 1973:88.
Syncricotopus Brundin 1956:106.

Type-species *Orthocladius tenuipes* Becker 1908:75 (= *rufiventris* Meigen, 1830) by subsequent designation of Hirvenoja 1973:88.

GENERIC DIAGNOSIS

Medium sized larvae with head capsule up to 600 um long.

Antenna. Five segmented with segments consecutively smaller and antennal spine not extending beyond fifth segment. Lauterborn organ present. Ring organ present near base of first antennal segment.

Labrum. SI completely bifid, other S setae simple. Pecten epipharyngis of three slender spines with four to five chaetulae laterales and two apically toothed chaetulae basales. Premandible with one apical tooth in British species (two in nivalis Goetghebuer, see Fittkau 1954:20-26).

Mandible with apical tooth scarcely longer than second tooth and clearly shorter than combined width of three inner teeth. Seta subdentalis present as is the seta interna (contrary to Hirvenoja 1973:89). Outer edge of mandible with, at most, a few weak crenulations on the basal part.

Mentum with six pairs of lateral teeth, the first laterals characteristically shaped being broader in the middle than at the base. The median tooth appears to be simple in British species but is slightly divided in nivalis. Ventromental plates extend slightly beyond mentum giving an appearance of a rounded shoulder posterior to the outer lateral tooth. This shoulder is never squared off as in some Orthocladius species which are otherwise very similar.

Abdomen. Procercus broader than high bearing six or seven apical setae. Claws of fore parapod serrate, claws of hind parapod large and simple. Anal tubules present.

COMMENTS AND SYSTEMATIC STATUS

Paratrichocladius larvae are only separable with difficulty from Orthocladius and Cricotopus. The character used previously by Hirvenoja (and cited by others), the absence of the seta interna on the mandible, is shown here to be incorrect. The author has examined the original larval material of nivalis Goetghebuer, collected by Fittkau, upon which the larval definition of Paratrichocladius was based, and confirms that a seta interna is present. However the proposed synonymy of *nivalis* Goetghebuer with *skirwithensis* Edwards, based on the redescription of the adult by Fittkau (1954), was shown to be incorrect after examination of the immature stages of both species.

Hirvenoja (1973:65-73) in his discussion on the phylogeny of the *Cricotopus* group of genera, to which *Paratrichocladius* belongs, places this genus as the sister group of *Acricotopus*. This placement is based upon a synapomorphy in the adults and the absence of the seta interna in the larvae of these two genera (also a synapomorphy). Although it is here shown that the seta interna is present in *Paratrichocladius* and is therefore not a synapomorphy for the two genera it is still possible that the genus *Paratrichocladius* is the sister group of *Acricotopus* based on the single adult synapomorphy. No characters to refute or confirm this have been found in the larvae in this study.

KEY TO THE BRITISH SPECIES OF *PARATRICHOCLADIUS*

1 Seta at base of mentum level with base of ventromental plate (Fig. 61b). Posterior parapod claws dark brown. Occipital margin, mentum and mandible dark brown to black .... *skirwithensis* (Edwards)

Seta at base of mentum retracted posterior to ventromental plate (Fig. 61g). Posterior parapod claws yellow. Occipital margin, mentum and mandible light to medium brown, never black ... *rufiventris* (Meigen)

Paratrichocladius rufiventris (Meigen)

Paratrichocladius rufiventris (Meigen, 1830:249)

DESCRIPTION OF 4TH INSTAR LARVAE (n = 2)

Body length not measured, head capsule length 470 um. Head capsule colour pale yellow with apical half of mandible, mentum and occipital margin pale to medium brown. Premandible pale brown.

Antenna (Fig. 61a). Five segmented, lengths 42 - 45; 11 - 12; 6 - 7; 5 - 6; 4. Antennal ratio 1.55 - 1.62. Antennal spine 20 - 23, subapical spine 8 - 9. Ring organ 6 - 7 from base of first antennal segment.

Labrum. Not figured (preparation inadequate). Premandible 89 - 91 with a single tooth. Otherwise as in generic diagnosis.

Mandible (Fig. 61c). 145 - 150 long with three inner teeth longer than apical tooth. Seta subdentalis 18 long, seta interna with 6 - 7 branches, the apical two branches finely serrate apically.

Mentum (Fig. 61b). 124 - 126 wide with a simple median tooth and six pairs of laterals. Posterior to the outermost tooth is a projection associated with the ventromental plates. In this species this shoulder is darker pigmented and rounded. Seta at base of mentum is withdrawn posteriorly.

Abdomen. Procerci 29 broad by 13 high bearing 6 to 8 apical setae of maximum length 300. Other setae of posterior end impossible to see on exuviae. Claws of anterior proleg yellow and finely toothed, those of the posterior proleg are simple and yellow. All setae on the body are simple including the l_4.

MATERIAL EXAMINED

Site 12 (2 larval exuviae)

DISTRIBUTION AND ECOLOGY

This species is widely distributed throughout Britain and Europe and as far east as Afghanistan. Brundin (1949) states that it is a typical lake dweller, and Reiss (1968) found that the larvae were typical dwellers in the exposed shore zone of Bodensee. There are several records of this species from flowing water notably Thienemann (1950:126) from springs and small streams, and Lehmann (1971:490) from the River Fulda.

Lehmann describes the species as relatively eurythermic but rheophilic or rheobiontic. The River Lea site where the two British specimens were collected was relatively fast flowing for a lowland river. Previous larval records of this species should be treated with caution since the larva has not been described and may have been confused with Orthocladius spp. particularly frigidus which closely resembles Hirvenoja's (loc.cit.) generic description of Paratrichocladius.

Paratrichocladius skirwithensis Edwards

Paratrichocladius skirwithensis Edwards 1929:329.
nec Trichocladius nivalis Goetghebuer 1938:61 sensu Fittkau 1954:20.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 6)

Body length not measured, head capsule 503 (460-530). Head capsule colour brownish with the occipital margin, mandible, mentum and premandible dark brown to black especially the occipital margin.

Antenna (Fig. 61f). Five segmented, lengths 57 (53-67); 13 (11-15); 8 (7-8); 5.6 (5-6); 4.2 (3.5-5.5). Antennal ratio 1.87 (1.8-2.0). Antennal spine c 21 long, subsidiary spine c 8 - 9 long. Ring organ 3 - 4 from base of first antennal segment.

Labrum. Not figured. Premandible 89 (87-91). Distribution of setae on dorsal surface of clypeus as in Fig. 61e. Otherwise labrum as in generic diagnosis.

Mandible (Fig. 61d). 154 (150-158) long, apical tooth shorter than inner three teeth. Seta interna with 7 or 8 branches with two apical branches apica ly serrate; seta subdentalis 7 - 8 long.

Mentum (Fig. 61g). Six pairs of lateral teeth, mentum width 130 (124-142). Shoulder at base of mentum rounded. Seta at base of mentum is anterior to the line connecting the bases of the ventromental plates on each side of the mentum.

Abdomen. Procercus 25 broad by 10 high bearing apically 7 or 8 setae maximum length 477. Claws of anterior proleg golden and all are serrate. Claws of hind parapods are dark brown and simple. All body setae simple.

MATERIAL EXAMINED

Site 34 (4 reared, 2 larvae)

DISTRIBUTION AND ECOLOGY

All records of this species must be treated with caution since there is confusion between this species and *nivalis* Goetghebuer. The adult definitely ascribed to *skirwithensis* Edwards is scarce in Britain recorded from five localities on high ground in England and Scotland. From the available evidence both *skirwithensis* and *nivalis* are rheophilic and probably cold stenothermic with *nivalis* more stenothermic than *skirwithensis* which was taken from the upper/middle reaches of a river in S.W. England.

xxxi. *Paratrissocladius* Zavrel

Paratrissocladius Zavrel, 1937:10, Saether, 1976:253-265.

Parachaetocladius Freeman, 1964:150 not Wulker, 1959 (Junior homonym).

Type-species: *Trissocladius fluviatilis* Goetghebuer, 1937 (= *Chironomus excerptus* Walker, 1856), by original designation.

GENERIC DIAGNOSIS

Medium sized larvae up to 6.6 mm long, head capsule up to 500 um long.

Antenna. Appears distinctly six segmented, but a fine seventh just visible. The fourth antennal segment is clearly longer than the third. Antennal ratio 1 - 1.3. Antennal spine at least as long as segments 2 - 7 combined. Lauterborn organs apparently absent. Ring organ near middle of first antennal segment.

Labrum and palatum. SI apically split into fine branches continuing in the direction of the stem. SII strong and simple, SIII fine and simple, SIV peglike. Simple labral lamellae between SI and pecten epipharyngis. Pecten epipharyngis of three broad, sclerotised spines. All labral chaetae simple. Premandible with one apical tooth and trace of inner tooth.

Mandible. Apical tooth shorter than combined length of inner three teeth. Seta interna and seta subdentalis present.

Mentum. Two pairs of median mental teeth, four pairs of laterals (Saether, 1976 quotes five pairs exceptionally). Ventromentum extends beyond dorsomentum, without setae beneath.

Abdomen. Parapods well developed, claws simple. Procercus with distinct subapical, posterior tooth, six or seven apical setae. Supra-anal seta well developed, about a third the length of procercal seta. Anal tubules well developed but shorter than posterior parapod.

COMMENTS AND SYSTEMATIC STATUS

The genus *Paratrissocladius* is clearly closely related to *Heterotrissocladius*. The antennal structure, with seven segments and the absence of Lauterborn organs is unique to these two genera. The reduction in length of the third antennal segment relative to the elongate fourth places these two genera within the Metriocnemini. The presence of procerci and parapods places the genera in the first half of this tribe, with Parametriocnemus, Paraphaenocladius, and the genera around Metriocnemus.

Paratrissocladius excerptus (Walker, 1856)

DESCRIPTION OF 4TH INSTAR LARVA (n = 9)

Body length 6.0 (5.4-6.6) mm, head capsule 412 (325-504) um, dark brown to black.

Antenna (Fig. 62a). Indistinctly seven segmented: 73 (66-76); 26 (21-33); 4 (4-6.5); 17 (16-19); 5 (4-6); 5 (4-6); ?1 - 2. Seventh scarcely distinguished from sixth. Antennal ratio 1.22 (1.14-1.31). Ring organ 34 (27-37) from base of first antennal segment. Spine 67 (62-79) long, subapical spine of second antennal segment 8 (7-9) long.

Labrum (Fig. 62c). SI finely divided apically, 31 (26-36) long. SII 41 (39-45) long, SIII 18 (16-21) long, SIV 12 (11-14) long on pedestal. Premandible 86 (68-92) long, strongly sclerotised with apical sharp tooth, and trace of broad inner tooth.

Mandible (Fig. 62b). 182 (168-195) long, with apical tooth shorter than combined width of three inner teeth. Seta interna of 6 or 7 branches, the median three, four or five with fine serrations at the end. Seta subdentalis 21 (18-23) extending beyond third tooth and either simple or forked at the tip.

Mentum (Fig. 62d). Completely dark with two large median teeth and four pairs of laterals, the third of these no higher than the fourth. Width of flattened mentum 156 (140-179). Ventromentum extending beyond fourth lateral tooth by 10 (6-13), no setae beneath.

<u>Abdomen</u> (n = 4). Procerci 49 (42-53) high by 31 (29-34) wide, with clear subapical, posterior tooth, and 6 - 7 apical procercal setae, maximum length 613 (590-640). Lateral setae of procercus weak, maximum length 85. Supra-anal setae simple, 203 (159-265) long.

Hind parapod 155 (137-169) long. Anal tubules 125 (121-127) long. Claws on posterior parapod yellow-brown, simple. Claws on anterior parapods both simple and terminally serrate. Posterior to the parapods on the first body segment is a row of fine translucent spines no more than 10 um long, extending no more than a third of the circumference of the segment.

MATERIAL EXAMINED

WALES: POWYS: nr. Builth Wells, R. Duhonw, 32/020 474, 6.x.1978 (2 reared); STAFFORDSHIRE: Cannock Chase, R. Sherbrook, 33/988 187, 30.v.1976 (1 larva); DEVON: Bovey Woods, R. Bovey, 30/780 800, 1.vi.1978 (4 larvae); STAFFORDSHIRE/DERBYSHIRE: Milldale, R. Dove, 43/139 547, 28.viii.1978 (2 larvae).

DISTRIBUTION AND ECOLOGY

In Europe the species is recorded from rivers and streams in Austria, Belgium, Germany, Sweden and the U.S.S.R. In Britain the adults are poorly recorded, only from Cumbria, Derbyshire, Devon and Dorset.

There are no British larval records other than those mentioned above. All the sites are cool and tree shaded. The Rivers Duhonw and Bovey are deeply shaded, fast flowing, boulder strewn, nutrient rich rivers while the River Dove flows through limestone, the bed is stony with some sand in the substrate. The River Sherbrook is a smaller, alder-lined stream with a sandy bed, flowing over Bunter Sandstone. The emergence period of the adults (cited from Saether, 1976) appears to be an early (May/June) and a late (September/October) peak, but either may be missing. The collection of 4th instars in May, June and October suggests this emergence pattern is possible.

xxxii. Psectrocladius Kieffer

Psectrocladius Kieffer, 1906a:26.

Type-species Orthocladius sordidellus Zetterstedt, 1838:814 by designation of Kieffer, 1906c:356.

GENERIC DIAGNOSIS

Medium to large larvae, up to 11 mm, head capsule usually pale, up to 600 um long.

Antenna. Five segmented, each segment consecutively smaller, blade not extending beyond the final antennal segment. Lauterborn organ either small, not as long as the third antennal segment or absent. Ring organ present low on the first antennal segment.

Labrum. SI distinctive (? unique), palmate with from three to ten lobes. These lobes are either subequal in size or the outer lobes may be smaller. SII elongate, SIII shorter and fine and SIV small or absent. Pecten epipharynx of three usually subequal spines. Four or five chaetulae laterales present (? always) simple. Two chaetulae basales, normally well developed and terminally branched. Premandible with one apical tooth and no beard.

Mandible. Apical tooth subequal to or longer than the combined width of the three inner teeth. Seta subdentalis present with a distinct apical hook. Seta interna present (absent in obvius), the five or six branches either weakly serrate or simple.

Mentum. One or two median teeth each often bearing a nipple-like median projection. Five pairs of lateral teeth.

Ventromental plates broad, extending beyond the outer teeth of the flattened mentum and with a variable number of distinct setae beneath.

Maxilla. A variable number of lamellae present on the palpiger, these lamellae triangular or rounded, always simple. The palpiger is moderately well developed with two strong sensillae on the basal part and sometimes an elongate apical seta. The galea bears two kinds of lamella, a medial row of simple lamellae and a more ventral area of lamellae resembling fused spines. A pecten galearis of fine teeth present in most (? all) species. Distinct sensillae present on galea. Five or six maxillary setae present which may include some setae at the lateral end of the row which are broader than the others. An a pendix may be present, but it should not be taken to be absent in those species in which the appendix is not figured.

Abdomen. Parapods present bearing simple claws. Procerci large bearing one or more spurs and/or tubercles on the apico-posterior margin and apically either five strong and two weak, or seven subequal setae. Anal tubules present, shorter than posterior parapods.

COMMENTS AND SYSTEMATIC STATUS

Psectrocladius, from the species studied here as well as published descriptions, is a homogeneous genus, quite distinctive in the larval stage. The palmate SI is quite distinctive and may be derived from the plesiomorphic plumose SI seta. Saether (1977:84) unites *Psectrocladius* with *Rheocricotopus*, *Paracricotopus*, *Nanocladius* and *Mesocricotopus* on the basis of characters of the female genitalia and the presence of the apicoposterior spurs on the procerci. The larvae of *Mesocricotopus* are as yet undescribed and the spurs may be secondarily lost in some species in the genera Saether cited. There are several symplesiomorphic characters in these genera particularly the large ventromental plates and strong setae beneath but the relationships between two of these genera appear to be confirmed by apomorphic characters. In both *Psectrocladius* and *Rheocricotopus* the spurs are always present and the seta subdentalis is characteristically apically hooked. This seta subdentalis state is considered here to be synapomorphic for the two genera and indicates a close relationship.

If this interpretation is correct it appears that the bifid SI of *Rheocricotopus* has arisen independently in this genus, in the *Cricotopus* series of genera and perhaps also in some genera of Metriocnemini.

KEY TO THE KNOWN BRITISH SPECIES OF *PSECTROCLADIUS*

1 Antennal ratio higher than 3.5. First antennal segment longer than 200 um. Seta interna absent. Apical mandibular tooth 2.5 times the combined width of the three inner teeth .... (*Allopsectrocladius*) *obvius* Walker[1]

Antennal ratio less than 3.5. First antennal segment less than 150 um long. Seta interna present. Apical mandibular tooth less than twice as long as the combined width of the three inner teeth 2

2 Mentum with a single broad median tooth with a pair of median nipple shaped projections. Only the three inner teeth of mandible darkened .... (*s.s.*) *psilopterus* Kieffer

Mentum with paired median teeth, sometimes indistinctly separated. All of apical third of mandible darkened 3

3 Paired median mental tooth distinctly lower than first laterals ....(*s.s.*) *barbimanus* (Edwards)
Median mental teeth higher than first laterals 4

4 Apical tooth of mandible shorter than combined width of three inner teeth. Occipital margin scarcely darker than the remainder of head capsule ....(*s.s.*) *sordidellus* (Zetterstedt)
Apical tooth subequal to or longer than combined width of the three inner teeth. Occipital margin distinctly darker than remaining region of head capsule 5

5 Five long, two short procercal setae. Apical seta on palpiger elongate, up to 18 um long .... (*s.s.*) *octomaculatus* Wulker
Seven subequal procercal setae. Apical seta on palpiger very short ....(*s.s.*) *limbatellus* (Holmgren)
(*s.s.*) *edwardsi* Brundin[2]

[1] *platypus* (Edwards) may key here

[2] For possible separation of these two species see *edwardsi* (page 282).

Species not keyed: (*Allopsectrocladius*) *platypus* (Edwards); (*Monopsectrocladius*) *calcaratus* (Edwards); *ventricosus* Kieffer; and *turfaceus* (Edwards). Doubt has been cast upon the generic placement of the latter species but examination of the adult confirms its identity as a *Psectrocladius*.

<u>Psectrocladius</u> (<u>Allopsectrocladius</u>) <u>obvius</u> Walker

<u>Psectrocladius obvius</u> (Walker, 1856:174); Dorier, 1933:138; Zelentsov, ?year:103.

DESCRIPTION OF 4TH INSTAR LA VAE (n = 7)

Body length 7.6 - 9.4 mm (n = 2), head capsule 855 (752-922), pale yellow with a black occipital margin. The mental teeth, inner teeth and apical half of apical tooth of mandible and apex of premandible all dark brown. Remainder of mandible and premandible yellow-brown.

<u>Antenna</u>. (Fig. 63a). Five segmented, segment lengths 226 (203-240); 22.6 (21-25); 18.2 (16-24); 6.9 (5.5-8); 5.8 (5-7.5). Antennal ratio 4.23 (3.73-4.77). Antennal spine 32 - 36. Subsidiary spine 6 - 8 on apex of second antennal segment. Lauterborn organs absent. Ring organ 14 (10-18) from base of first antennal segment, point of insertion of distal seta on first segment 153 (147-158) from base of segment.

<u>Labrum</u> (Fig. 63b). SI seta palmate with three or rarely four lobes. SII, SIII and SIV normal. Numerous labral spines all simple. Pecten epipharynx of three subequal spines. Five or six broad chaetulae laterales at most weakly serrate but usually simple. Two distinct simple chaetulae basales present. Premandible 133 (126-140) long, simple, without beard.

<u>Mandible</u> (Fig. 63e). 287 (259-307) long, apical tooth 2.5 or more times longer than the combined width of the three inner teeth. Seta subdentalis present, characteristically shaped. Seta interna absent.

<u>Mentum</u> (Fig. 63c). Width of flattened mentum 211 (198-229). Broad median area consists of a median 'saddle-shaped' tooth and two pairs of broad teeth only weakly separated from each other. Five pairs of laterals. Ventromental plates

extending beyond outer mental teeth with a distinct beard of up to thirty setae beneath.

Maxilla (Fig. 63d). Palpiger strongly developed, apical seta 28 - 33 long. Simple lamellae on palpiger. Both simple and complex lamellae on galea, the complex lamellae resembling fused spines. Maxillary setae include broader serrate seta as well as narrower simple setae. Pecten galearis absent.

Abdomen. Procercus 117 (105-139) high by 63 (52-72) wide with one to four spurs on the anterior basal margin of the procercus. Seven subequal apical setae on the procercus of maximum length 837 (742-818). Hind parapod 360 - 370 (n = 2) anal tubule 110 (n = 1). Claws of anterior parapod golden, simple; claws of posterior parapod simple and dark brown to black. Longest body seta on thoracic segments 120 (106-137).

MATERIAL EXAMINED

OXFORDSHIRE: Aston Rowant National Nature Reserve, 13.iv.1977, leg. A.E. Stubbs (7 larvae, 2 reared to adult, 3 to pupae).

DISTRIBUTION AND ECOLOGY

The species is represented in the collections of the B.M.(N.H.) from many specimens from Wicken Fen (Cambridgeshire) and a few specimens from Scottish and southern English localities. Fittkau & Reiss (1978) cite records of the adults from the Pyrenees, Alps, France, Germany, Scandinavia, western U.S.S.R., Siberia and the Lake Baikal area.

Reiss (1968:240) found adults and pupae in Bodensee but makes no further comment on the ecology than to state that the species may have more than one generation each year.

On the available evidence it is only possible to say that obvius is found in standing water bodies of various sizes and trophic levels.

Psectrocladius barbimanus (Edwards)

Psectrocladius barbimanus (Edwards, 1929:333), Thienemann, 1937:4.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 9)

Body length 8.2 (7.2-9.0) mm (n = 3), head capsule 680 (636-731), yellow. Apical third of mandible, mentum and all but median ventral occipital margin dark brown. Premandible lighter brown.

Antenna (Fig. 64a). Five segmented, lengths 114 (108-124); 18.8 (17-21); 9.6 (8-13); 7.7 (6.5-9); 5.7 (5-6.5). Antennal ratio 2.74 (2.41-3.00). Antennal spine 38 (24-34) long, not extending to apex of third antennal segment. Subsidiary spine 10 (8-13) inserted subapically on the second antennal segment. Ring organ 8.5 (8-11) from base of first antennal segment, scar of distal seta insertion 17 (13-21) from base.

Labrum (Fig. 64b). SI with seven or eight lobes. SII and SIII normal for the genus, SIV indistinct. Numerous simple labral chaetae. Three (? always) simple chaetulae laterales present, two distinct apically branched chaetulae basales. Premandible 112 (108-119) long, simple.

Mandible (Fig. 64d). 218 (211-224) long, apical tooth shorter than combined width of three inner teeth. Seta subdentalis 22.5 (21-24) with weak apical hook. Seta interna with six branches, three outer branches apically serrate, three inner branches longer and simple.

Mentum (Fig. 64c). Flattened width 177 (153-190), paired median teeth lower than first lateral teeth each 18 - 22 wide. Five pairs of laterals, ventromental plates distinct with strong beard beneath.

Maxilla (Fig. 64e). Simple lamellae on palpiger. Apical seta of palpiger 6 - 9 long. Both simple and complex setae present on galea. Complex setae of basally fused spines lying ventrally on the galea. Pecten epipharyngis of fine teeth anterior to punctate area on galea. Maxillary setae simple.

Abdomen. Procerci 87 (79-92) high by 49 (42-58) wide, bearing postero-basally two spurs 8 - 11 long. Apically bearing 7 subequal setae of maximum length 887 (753-954). Lateral seta 71 (68-72) long, supra-anal seta 54 (47-66) long. The hind parapods are 318 (297-329) long and the anal tubules 44 (37-48) long by 22 (18-29) wide, simple. Claws of both anterior and posterior parapods yellow and simple. Longest setae on body 129 (116-148).

MATERIAL EXAMINED

CUMBRIA: Sunbiggin Tarn, 35/676 088, 240 m. o.d., 23.vi.1978, leg. C.H.C. Lyal (6 larvae reared to adult, 3 larvae).

DISTRIBUTION AND ECOLOGY

This species is infrequent in Britain, with only the holotype from London in the B.M.(N.H.) collections prior to this survey. However specimens have been seen from Hertfordshire (Rye Meads Sewage Works lagoons) and also from a woodland pool in Cheshire.

Wulker (1956:49) recorded specimens from East Greenland, Iceland, Lappland, W. Germany, France (Pyrenees) and literature references to British specimens. Fittkau & Reiss (1978) cite additional records from the Caucasus.

Reiss (1968:239) found the larvae between 0.5 and 12 m depth in Bodensee, and summarised the distribution of the species as boreoalpine, noting the absence of the species in southern and central Swedish lakes.

Psectrocladius edwardsi Brundin

Psectrocladius edwardsi Brundin, 1949:816

DESCRIPTION OF 4TH INSTAR LARVA (n = 1, head capsule only)

Head capsule length 614, pale yellow, lateral occipital margin brown with dorsal and ventral parts paler. Mentum and apical third of mandible brown-black.

Antenna (Fig. 65a). Five segmented, 103; 15.5; 7.5; 7.5; 6. Antennal ratio 2.82. Antennal spine 24 long, subsidiary 6 long, subapical on second antennal segment. Lauterborn organs present, weak, shorter than third segment. Ring organ 6 and scar of distal point of seta insertion 15 from base of first antennal segment.

Labrum. Indistinguishable from limbatellus (see Fig. 66b and description on page 283). SI seta with seven lobes. Premandible 93 long with single apical tooth.

Mandible (Fig. 65c). 195 long, apical tooth subequal to combined width of the three inner teeth. Seta subdentalis 22 long with apical hook. Seta interna with six branches; the outer two appear to be bluntly serrate.

Mentum (Fig. 65b). Flattened width 169, width of each median tooth 23. Notch between the two median teeth appears depper in edwardsi than limbatellus but this may be an artefact or a wear character. Five pairs of lateral teeth. Ventromental plates extend beyond outermost lateral teeth and have fine setae beneath (no more than 1 wide).

Maxilla (Fig. 65d). Lamellae on palpiger simple. Palpiger has shorter apical seta than in some other species in the genus. Both simple and complex lamellae on galea. The complex lamellae of fused spines are larger than in other species with broader spines. Pecten galeari of numerous fine spines. Maxillary setae include a single broad seta at the palpiger end of the row.

Abdomen. Missing.

COMMENTS

The pupae was identified using an unpublished key and description of Langton. This single specimen is very similar to limbatellus and it is difficult on the limited material available to decide which characters are of specific value and which are not. For this reason the species are not separated in the key and possible differences are instead listed below.

	edwardsi	limbatellus
Number of broad setae in maxillary seta row	One	Two or three
Outer branches of seta interna	Two bluntly serrate	All branches simple
Median mental teeth	Deeply separated	Weakly separated
Head capsule colour	Pale yellow	Darker yellow

MATERIAL EXAMINED

Site 2 (1 reared larva)

DISTRIBUTION AND ECOLOGY

See comments under limbatellus regarding unpublished manuscript by Langton which gives ecological date for edwardsi and limbatellus. The only locality for edwardsi in this survey, a garden fish pond, confirms Langton's conclusions on the ecology of the species.

Psectrocladius limbatellus (Holmgren)

Psectrocladius limbatellus (Holmgren, 1869:44).

DESCRIPTION OF 4TH INSTAR LARVAE (n = 6)

Body length 6.5 (5.6-7.0) mm (n = 4), head capsule 556 (540-604), yellow with lateral occipital margin, mentum and apical third of mandible brown or black.

Antenna (Fig. 66a). Five segmented, lengths 99 (95-108); 15.5 (13.5-17); 8.2 (8-9); 5.7 (5-6); 5.0 (4-5.5). Antennal ratio 2.91 (2.68-3.09). Antennal spine 32 (30-33), not extending to final segment. Small subsidiary spine present, shorter than weak Lauterborn organs. Ring organ low on first antennal segment, point of insertion of dorsal seta 11 - 15 from base of first segment.

Labrum (Fig. 66b). SI seta with seven or eight lobes, terminally rounded. SII and SIII normal for the genus, SIV very small. Pecten epipharynx of three broad spines. Four simple chaetulae laterales and two terminally branched chaetulae basales. Premandible 103 (95-108) long, simple.

Mandible (Fig. 66d). 194 (182-205) long, apical tooth subequal to or slightly longer than the combined width of the three inner teeth. Seta subdentalis 20 - 23 long with apical hook. Seta interna with six simple branches.

Mentum (Fig. 66c). Flattened width of mentum 157 (145-166), width of a single median tooth 24.5 (23-26). Paired median teeth each with nipple-like projection. Five pairs of lateral teeth. Ventromental plates distinct with broader setae than usual beneath (up to 2 wide).

Maxilla. Very similar to that of edwardsi (see Fig. 65d and description on page 281). The only difference observed, which may not be of specific value, is that there are two or three broad maxillary setae at the palpiger end of the row of maxillary setae. In *edwardsi* (only 1 specimen examined) there is only a single broad seta.

Abdomen. Procercus (Fig. 65e) 78 (68-84) high by 44 (39-55) wide with two or three distinct spurs up to 10 long and a few smaller tubercles. Seven apical setae up to 837 (689-911) long. Lateral seta 40 (29-52) long.

Hind parapods 262 (233-307) long, anal tubules 217 (191-243) by 51 (42-63), simple. Claws on both anterior and posterior parapods pale yellow and simple. Longest body setae 120 long.

MATERIAL EXAMINED

Site 23 (1 reared to adult, 5 larvae)

DISTRIBUTION AND ECOLOGY

The confusion between this species and the closely related *edwardsi* Brundin has only recently been resolved by Langton (unpublished memorandum 1977). The identification of the pupae and adult males of these two species in this survey is based upon characters discovered by Langton. Ecological differences were also found which are borne out by the observations here but it is not appropriate to discuss Langton's unpublished observations in this study.

The sole site in which *limbatellus* was found in this study is a small, high, cold oligotrophic tarn. Fourth instar larvae were found below a 3 or 4 cm thickness of ice.

Psectrocladius octomaculatus Wulker

Psectrocladius octomaculatus Wulker, 1956:15.

Psectrocladius calcaratus Edwards, 1929 sensu Thienemann, 1934:154 (misidentification)

DESCRIPTION OF 4TH INSTAR LARVAE (n = 9)

Body length 6.3 (4.8-6.9) mm (n = 3), head capsule 623

(551-667) um, yellow. Apical third of mandible, apical third of premandible, mentum and lateral margins of occipital margin dark brown.

Antenna (Fig. 67a). Five segmented, lengths 89 (84-95); 16.7 (14-21); 8.7 (8-10); 5.6 (4-7); 5.7 (4-7). Antennal ratio 2.47 (2.09-2.80). Antennal spine 29 (20-34), not extending to the apex of the final antennal segment. Subsidiary spine 8 (6-10) long, inserted subapically on the second antennal segment. Ring organ present about 5 from base of the basal antennal segment, and the scar of the insertion of the most dorsal seta 13 - 15 from the base.

Labrum (Fig. 67b). SI plumose with 5 or 6 lobes, SII and SIII normal, SIV very small or absent. Labral chaetae numerous, simple. Pecten epipharyngis of three subequal spines. Five or six simple chaetulae laterales, two distinct terminally branched chaetulae basales. Premandible 96 (84-106) long, simple.

Mandible (Fig. 67d). 210 (198-221) long, apical tooth subequal to combined width of three inner teeth. Seta subdentalis 22 (18-24) long with a notched apex. Seta interna of five or six simple branches.

Mentum (Fig. 67c). Width of flattened mentum 181 (168-190), paired median teeth bearing a hump and each tooth the width of two laterals. Five pairs of laterals, ventromental plates distinct with a weak beard beneath.

Maxilla (Fig. 67e). Simple lamella present on palpiger. Apical seta on palpiger elongate up to 18 long. Both simple and complex lamellae present on galea. The complex lamellae of basally fused spines are widely distributed on the ventral surface of the galea. Pecten gallearis of fine teeth present at the anterior edge of a strongly punctate area. Maxillary setae simple.

Abdomen. Procercus 59 (55-63) high by 36 (26-42) bearing postero-basally two or three spines up to 10 long as well as a variable number of smaller tubercles. The procerci bear apically five strong seta of maximum length 729 (572-773), and two finer setae. The upper lateral seta is 66 (53-79) long, the supra-anal seta up to 106 long.

Posterior parapods 243 (190-318), anal tubules 130 (110-159) long by 61 (42-74) wide, simple. Claws of posterior parapods brown, of anterior parapods yellow; all claws simple. Longest body seta up to 105 long.

MATERIAL EXAMINED

Site 15 (7 larvae reared to adults, 3 unreared larvae).

DI TRIBUTI N AND ECOLOGY

Psectrocladius octomaculatus is here recorded for the first time from the British Isles from the single locality. Wulker (1956:48) in describing the species records it from a number of localities frequently arising from misidentification of the immatures based on adult identifications by Goetghebuer. These localities are Swedish Lappland and the German Alps, and further localities include the Black Forest and Norway. He summarises that this is a boreo-alpine species.

The ecology of the larvae is poorly known, but pupal skins in Lappland were found in a number of different standing water bodies including boggy pools, but in the Alps and Black Forest pupae and larvae have been found in habitats including springs and ditches, frequently at altitudes over 1,000 m.o.d. Site 13 is a muddy spring beside a faster stream at 380 m.o.d.

Psectrocladius psilopterus (Kieffer)

Psectrocladius psilopterus (Kieffer, in Kieffer & Thienemann, 1906:144); Thienemann in Kieffer & Thienemann, 1906:149.
? _Psectrocladius simulans_ (Johannsen, 1937:67); Pankratova, 1970:218; Zelentsov, ?year:115.

DESCRIPTION OF 4TH INSTAR LARVA (n = 12)

Body length 5.2 mm (n = 1), head capsule 534 (518-604), pale brown-yellow with occipital margin brown-black except for pale ventral part. Lateral mental teeth dark brown, median tooth paler. Inner three teeth of mandible black, apical tooth pale brown, remainder of mandible yellow. Premandible light brown.

Antenna (Fig. 68a). Five segmented, lengths 119 (111-130); 19.2 (15-21); 9.5 (8-11); 7.7 (6.5-9.5); 5.7 (5-6.5). Antennal ratio 2.85 (2.58-3.33). Antennal spine 30 (24-34), subsidiary spine 6.8 (6-8) subapical on second antennal segment. Lauterborn organs weak, shorter than third segment. Ring organ 6 (5.5-8), scar of insertion of dorsal seta 20 (16-26) from base of first antennal segment.

Labrum (Fig. 68b). SI with 4 to 6 lobes, usually five, these lobes pointed. SII and SIII normal for the genus, SIV very small or absent. Pecten epipharyngis of three subequal spines. Chaetulae laterales of four or five simple scales, two chaetulae basales each with branched apices. Premandible 101 (90-109) long, with a single tooth broader than usual in the genus.

Mandible (Fig. 68e). 180 (159-201) long. Apical tooth longer than combined width of the three inner teeth. Seta subdentalis 19 (17-20) long with characteristic hook. Seta interna with six branches, the outer three bluntly dentate.

Mentum (Fig. 68d). Flattened width 167 (159-180), median tooth 60 (53-63) with a median saddle easily lost in worn specimens. Five pairs of lateral teeth. Ventromental plates distinct extending beyond outer lateral teeth and with numerous fine setae beneath.

Maxilla (Fig. 68e). Numerous lamellae on palpiger. No long apical seta on palpiger. Both simple and complex lamellae on galea, the complex lamellae of fused spines less numerous than in some species of Psectrocladius. Pecten labralis present consisting of fine teeth. One of the maxillary setae slightly serrate, but no broad setae present. A modified appendix present as in obvius.

Abdomen. Procercus 60 (58-63) high by 39 (37-42) wide with up to five small scales antero-bas lly. Apically there are five strong setae and usually two finer, shorter setae. The maximum length of the longest seta is 819 (798-840), the lateral seta 48 (37-58).

On the only specimen available for study the posterior parapod was 160 long, and the broad anal tubule of similar length. The claws of the anterior parapods yellow, those of the posterior parapods light brown, both simple.

MATERIAL EXAMINED

Site 11 (16 reared to adult); Site 48 (6 larvae, 5 reared to adult); EAST SUSSEX: Ashdown Forest, Lake in Isle of Thorns, 3.viii.1977, leg. P.S. Cranston (1 larva reared).

COMMENTS

psilopterus was identified here fro the pupa and adult male using keys of Wulker (1956) and Langton (unpublished). The species as understood here is very similar to simulans (Johannsen) as described by Roback (1957:90) and Zelentsov

(? year:115). The only differences between Zelentsov's description and that presented here is that the first antennal segment is shorter in these specimens (119 against 16?) and Zelentsov shows two serrate chaetulae laterales. If this latter character is correct this is the only species possessing this character in the genus Psectrocladius and would clearly separate simulans from psilopterus.

DI. RIBUTI N ND .OLO Y

Adults of psilopterus are widely distributed in Britain and Europe but there have probably been misidentifications of the species despite the distinctive pupa and adult.

The larvae are apparently characteristic in standing waters so at first sight the large numbers in Site 48 is surprising. However these larvae are probably ffom the Caban Coch reservoir 400 metres up river from the site. The larvae were found in thick growths of algae covering the stones in the river rather similar to the algal cover in the stagnant ditch at Site 11.

Psectrocladius sordidellus (Zetterstedt)

Psectrocladius sordidellus (Zetterstedt, 1838:814); Thienemann, 1944:628.

Psectrocladius stratiotis Kieffer, 1908:706; Potthast, 1914:325; Gouin, 1936:170; Thienemann, 1944:593.

DESCRIPTION OF 4TH INSTAR .ARVAE (n = 7)

Body length 5.7 - 7.4 mm (n = 2), head capsule length 568 (508-604), yellow with occipital margin pale brown scarcely darker than the head capsule. All teeth of mentum and api al third of mandible equally dark brown.

Antenna (Fig. 69a). Five segmented, lengths 90 (87-93); 16.6 (15-18); 8.5 (6.5-10); 5.2 (4.5-6); 5.0 (4-5.5). Antennal ratio 2.56 (2.41-2.76). Antennal spine 29 (26-32) not extending beyond fifth antennal segment. Subsidiary spine subapically on second antennal segment 9 (8-11) long. Ring organ 5 - 8, scar of dorsal seta in ertion 18 - 21 from base of first antennal segment.

Labrum (Fig. 69b). SI with a very variable number of lobes, from five to nine. SII and SIII normal for the genus, SIV small but present. Pecten epipharyngis of three subequal spines. Chaetulae laterales simple, four or five in number. Two chaetulae basales present, each terminally branched. Premandible broader than usual 89 (85-93) long with a single apical tooth.

Mandible (Fig. 69c). 190 (182-196) long, apical tooth shorter than combined width of three inner teeth. Seta subdentalis 19 (16-21) long with apical hook. Seta subdentalis with six or seven branches (? all) simple.

Mentum (Fig. 69d). Flattened width of mentum 149 (138-159). Two rounded median teeth without any projection, each tooth 20.5 (18.5-26) wide. Five pairs of median teeth (1 specimen has four on one side and five on the other). Ventromental plates distinct, extending beyond outer mental teeth and with a sparse beard of up to ten setae beneath.

Maxilla. Very similar to that of edwardsi (Fig. 65d). Lamellae on palpiger present. Palpiger without elongate apical seta. Both simple and complex lamellae on galea. The simple lamellae more pointed than usual in the genus. Pecten galearis of fine teeth present. Maxillary setae include a broader seta at the palpiger end of the row.

Abdomen. Procercus 53 (50-56) high by 33 (26-37) wide with 4 or 5 postero-basal spurs. These spurs are no more than 8 long and are less heavily sclerotised than in many other species in the genus. Apically the procercus bears 5 long setae of maximum length 750 (646-827) and two finer setae. Lat ral seta about 42 long, supra-anal ta 74 long.

Hind parapod 296 long (n = 1), anal tubules 67 (58-80) long by 34 (24-40) wide (n = 3). Claws on both anterior and posterior parapods simple, those on the anterior yellow-brown, tho e on the posterior yellow.

MAT I MIN D

ite 17 (5 larva reared to adult); ite 24 (2 larvae, 1 reared to pupa).

DI TRIBUTIO D COLOGY

dwards (1929:334) described _sordidellus_ as "rather common" and recorded _striti tis_ (as a pos ible variety of _sordidellus_) from two localities. The ritish useum (Natural istory) collections reflect this wide distribution of the species.

ulker (1956:52) summarises the distributi n in urope as ermany, France, Spain and Britain, but the species is almost certainly more widespread than these records sug e t.

The two localities in this survey are related: the second is the outflow from Malham Tarn (the first), within 800 metres of the Tarn and the larvae clearly ri inate from the Tarn. gain, angton (unpublished) summari es the ecolo y of th's species based upon his pupal exuvial records, but it is not appropriate to cite these findings here.

xxxiii. _Pseudorthocladius_ Goetghebuer

Pseudorthocladius Goetghebuer 1932:93; Thienemann and Kruger, 1939:246.

Type-species _Hydrobaenus curtistylus_ Goetghebuer, 1921 by subsequent designation of Goetghebuer, 1943:73 (but see Cranston, 1974:88, this designation needs a ruling by the I.C.Z.N.).

GENERI DIAGNOSIS (Based on literature and specimens examined)

Medium sized larvae, up to 6 mm long.

Antenna. Five segmented, third segment much smaller than fourth. Antennal ratio about 1. Antennal spine extends as far as or beyond terminal antennal segment. Lauterborn organs small, no longer than small third antennal segment. Ring organ distinct in first half of first antennal segment.

Labrum. SI serrate (not as strongly divided as a plumose seta). Zavrel (1937:1) describes a species apparently belonging to this genus in which the branches of SI were apparent on both sides of the seta. In Thienemann and Kruger's (1939) description and the specimens examined the SI seta only has spines on the inner margin. SII, SIII and SIV as normal. Very weak labral lamellae present between the bases of the SI. Labral chaetae reduced so that there are apparently only spines present on the labrum.

Pecten epipharyngis of three fine spines, chaetulae laterales three or four blunt spines, chaetulae basales of three or four simple spines. Premandible simple but with a distinct inner bulge (? tooth).

Mandible. Apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis very small, not extending beyond the inner margin of the mandible. Seta interna present, all branches strongly pectinate. The branches are divided into long and short groups.

Mentum. Paired median teeth, taller than four pairs of lateral teeth. The third and fourth lateral teeth are subequal in height. Ventromental plates small without setae beneath.

Maxilla. Palpiger small, bisensillae well developed. Maxillary setae long, one or more may be terminally serrate.

Pecten galearis and lamellae on the palpiger and galea absent.

Abdomen. 'nterior parapods reduc d and fused but bearing claws and small setae. Posterior parapods narrow and separate bearing few claws. Procerci small, placed posteriorly on the preanal segment and bearing two apical setae, one as long as a third of the boly. Anal tubules with one or two constrictions as long as posterior parapod.

COMMENTS AND SYSTEMATIC STATUS

The short third antennal segment indicates that this genus belongs to the Metriocnemini, while the presence of parapods and procerci (although modified) indicates that the genus is amongst the more plesiomorphic within the tribe. Compared with genera such as Heterotrissocladius and Paraphaenocladius (q.v.) which have a number of plesiomorphic characters Pseudorthocladius shows several apomorphies including the fusion of the anterior parapods, the reduction in size of the procerci and the number of procercal setae (although the remaining one is very long). There is also some trace of the posterior projection of the procerci and the ventral direction of the posterior arapods as fo nd in Gymnometriocnemus, Bryophaenocladius and Paraphaenocladius. The SI seta is only weakly branched co pared to the strongly plumose seta of many of the plesiomorphic genera, and resembles the SI seta of .elenisella and some Limnop yes.

aether tentatively placed Pseudorthocladius with Limnophyes, and Parachaetocladius a the sister group of all the Metriocnemini which lack procerci. The characters of the larva noted above suggests that this placement is correct.

Pseudorthocladius cfr. *curtistylus* (Goetghebuer)

? *Pseudorthocladius curtistylus* (Goetghebuer, 1921:28); Thienemann & Kruger 1939:246.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 6)

Medium sized larvae, 4.7 (4.2-5.1) mm long, head capsule 251 (233-280) um long. Head capsule brown with darker mentum, mandibles and premandibles.

Antenna (Fig. 70a). Five segmented lengths 24.8 (21-27); 10.4 (10-11); 2.4 (2-3); 8 (6-10); 4.6 (4-5). Antennal ratio 0.99 (0.86-1.13). Antennal spine 32 (28-36) long extending beyond fifth antennal segment. A bulbous subsidiary spine about 5 long is inserted subapically on the second antennal segment. The distinct ring organ is 10 - 12 from the base of the first antennal segment.

Labrum (Fig. 70b). SI seta with a few blunt branches on the inner margin (? only on inner). SII, SIII and SIV developed normally. Labral lamellae between bases of SI weakly sclerotised. Pecten epipharyngis of three short, sometimes blunt spines. Chaetulae laterales distinctive, three or four in number, broad and blunt. Up to four chaetulae basales visible near the ungula, including one chaetula much larger than the others. Ungula somewhat rectangular rather than U shaped. Premandible 56 (53-63) long with a sometimes notched terminal tooth and a distinct inner projection at about half the length of the mandible. No premandibular beard.

Mandible. (Fig. 70c). 80 (74-92) long, apical tooth shorter than combined width of the three inner teeth. Seta subdentalis very short not extending beyond the margin of the mandible. Seta interna present with seven branches, four short, three long, all pectinate.

Mentum (Fig. 70d). Width of flattened mentum 77 (74-84), width of paired median teeth 23.6 (21-27). Four pairs of lateral teeth, third and fourth subequal. Ventromental plates present, small, not extending beyond outer mental teeth and without setae beneath.

Maxilla. As generic diagnosis except that all the maxillary setae appear to be simple.

Abdomen (Fig. 70e). Procercus 12 (10-13) high by 10 (8-11) wide bearing apically one seta length 1230 (950-1430). Lateral seta 32 (31-34) long, weak. Hind parapod 95 - 105 long, anal tubules 60 - 70 long and 34 - 38 maximum width with one median constriction. Supra-anal seta absent. Anterior parapods fused bearing simple claws. Posterior parapods separate bearing golden yellow claws, fewer than usual and simple.

MATERIAL EXAMINED

EAST SUSSEX: Ashdown Forest, Broadstone Stream, 51/41.32., no date, leg. A. Hildrew (Site 9 of this survey).

COMMENTS, DISTRIBUTION AND ECOLOGY

This species is only tentatively assigned to _curtistylus_ since it differs slightly from Thienemann & Kruger's (1939) description and differs strongly in its ecology. Examination of material identified by Thienemann shows that these differences based on the descriptions are correct. These are the number of constrictions in the anal tubules, the serrate seta on the maxilla and the setae on the preanal segment (Thienemann & Kruger, 1939: fig. 2).

Of the three British species of _Pseudorthocladius_ only the larva of _curtistylus_ is described. In Europe _filiformis_ is recorded from flowing waters, while _curtistylus_ is found in mosses such as _Sphagnum_. The locality in which these larvae were found is relatively unusual in the low pH with a thick coating of iron bacteria covering the benthos and fallen leaves. Unfortunately subsequent visits to the site have not resulted in the collection of any live larvae for rearing, so the identity of the species must remain in doubt.

xxxiv. Pseudosmittia Goetghebuer

Pseudosmittia Goetghebuer, 1932:126; Strenzke, 1950:281-309.

Type-species Spaniotoma angusta Edwards, 1929, by designation of Edwards (1932:141).

GENERIC DIAGNOSIS (Based on Strenzke, 1950 and examination of two undetermined specimens in the B.M.(N.H.)

Small to medium sized larvae up to 5 mm long.

Antenna (Fig. 71a). Variable number of antennal segments distinguishable, though never more than four. Whole antenna short, no longer than half the mandibular length. Antennal spine long, as long as the mandible. Lauterborn organs indistinct, ring organ present about midway on the first antennal segment.

Labrum and palatum (Fig. 71b). Both SI and SII setae bifid. SIII and SIV normal. Labral chaetae simple or serrate, often numerous. Pecten epipharyngis of three spines which are usually simple but may be serrate. Chaetulae laterales simple, chaetulae basales present. Premandible with two to four teeth, distinct beard present (? in all species).

Mandible (Fig. 71c). Apical tooth shorter than combined width of the three inner teeth. Seta subdentalis weak or absent. Seta interna absent.

Mentum (Fig. 71d). One median tooth of variable shape, sometimes with a weak median indentation, sometimes with a median projection. Four pairs of lateral teeth. Ventromental plates distinct but not extending beyond the outer teeth of the flattened mentum. A second pair of plates may be present. No setae beneath.

Maxilla (Fig. 71e). ensillae on galea and palpiger weakly developed. Galea more elongate than usual, without lamellae (? always). Maxillary setae short and simple.

Abdomen. Anterior parapods present, fused, bearing claws (Fig. 71f). Posterior parapods either weak or absent. Procerci absent but one short seta present on each side in the position of the procerci. Anal tubules always present, two pairs, sometimes longer than the posterior parapods.

COMM NT AI D Y TEMATIC T TU

Pseudosmittia shares the bifid SI and SII with Camptocladius but can be separated by the possession of anal tubules, fused anterior parapods, and separate posterior parapods. Both genera are clearly members of the etriocnemini with the extreme reduction in abdominal features and antenna. Genera with these similar apomorphic characters include Thalassosmittia, Parasmittia and mittia which have a similar mentum, fused anterior pa apods and no procerci. The presence of a premandibular beard (not noted by previous authors) separates Pseudosmittia from all these related genera.

MATE IAL XAMINED

Site 30 (1 larva); SU EX: Ashdown Forest, 51/41.32, A ril 1975, leg. A. Hildrew (1 larva); RUTLAND: utland ater, 16.1.1978, leg. A. Brown (1 larva).

DI TRIBUTI N AND ECOLOGY

The species of the genus Pseudosmittia are mostly terrestrial or semiterrestrial, with only a few species found in aquatic habitats. Pseudosmittia oxoniana Edwards and Pseudosmittia *ruttneri* Strenzke (neither on the British list) are both aquatic, and adults and pupae of a species related to these have been taken by the author from Malham Tarn. It is possible that the specimens from Site 30 and Rutland Water belong to this species, but the Ashdown Forest (stream) specimen belongs to a second species, possibly terrestrial.

xxxv. *Rheocricotopus* Thienemann & Harnisch

Rheocricotopus Thienemann & Harnisch, 1932:135.

Type-species *Chironomus effusus* Walker, 1856:180 designated by Brundin, 1956:118.

GENERIC DIAGNOSIS

Medium sized larvae, up to 6.5 mm long. Frequently with brown striations on the thoracic segments of the fourth instar larvae.

Antenna. Five segmented with the segments consecutively smaller until the fifth segment which is slightly longer than, or subequal to the fourth. Lauterborn organs present, distinct but shorter than the third antennal segment. Antennal spine clearly bifid, the outer branch not extending beyond final antennal segment. Subsidiary spine present, small. Ring organ present low on first antennal segment.

Labrum. SI bifid with the two branches not fully separated. The two branches either subequal or the outer branch somewhat longer. SII long and fine, SIII short and stubby, SIV normal. Pecten epipharyngis of three spines of variable width. Chaetulae laterales simple, three or four in number. Two chaetulae basales also simple. Premandible with one apical tooth and no beard.

Mandible. Apical tooth shorter than the combined width of the three inner teeth. Seta subdentalis present, characteristically shaped with an apical hook. Seta interna present, five or six branches, either simple or with bluntly plumose apices.

Mentum. Paired median teeth with five distinct pairs of laterals. Each median tooth may have a small accessory tooth closely appressed or may be simple. Ventromental plates broad, extending beyond the outer mental teeth, and with numerous setae beneath.

Maxilla. Palpiger small with mostly indistinct sensillae. Galear lamellae present with sometimes complex bases. Pecten galearis well developed. Maxillary setae simple with the antaxial seta sometimes strongly triangular in shape.

Abdomen. Procerci higher than wide, usually with a distinct median posterior spur, and bearing apically up to five setae. Both sets of parapods normally developed bearing claws. Claws on anterior parapods with some inner teeth. Anal tubules short. Variable length setae on the body.

COMMENTS AND SYSTEMATIC STATUS

The generic description above is based upon examination of the three species described below. The larvae of the other two British species have not been found but a fourth species *glabricollis* (Meigen) has been poorly described as a larva (as *gouini* Goetghebuer) by Gouin. These descriptions, together with that of a Nearctic species described by Saether, suggests that *Rheocricotopus* is a well defined homogeneous genus in the larval stage.

Saether (1977:86) placed *Rheocricotopus* with *Psectrocladius*, *Paracricotopus*, *Mesocricotopus* and *Nanocladius* as the sister group of the *Cricotopus* group and the *Orthocladius* groups combined. The antennal structure indicates that *Rheocricotopus* belongs with the non-Metriocnemini but it is not clear from the larva where the enus belongs amongst these genera. There are many plesiomorphic characters amongst the larvae of *Rheocricotopus* including the wide ventromental plates and the numerous setae below the plates. The apomorphic character which Saether uses to unite the genera cited above is the presence of a spur on the procerci, but this is not pre ent in some of the enera, and the larvae of *Mesocricotopus* is not yet known. A further apomorphic character not cited by aether (loc.cit.) which unites *Rheocricotopus* and *Psectrocladius* is the distinctive seta subdentalis with an apical hook. Until the other genera can be examined in more detail the relationships of *Rheocricotopus* and *Psectrocladius* must remain in doubt.

KEY TO THE KNOWN BRITISH SPECIES OF RHEOCRICOTOPUS

1 Median mental teeth each with distinct outer tooth closely fused to the median tooth (Fig. 74d)........... 2
Median mental teeth simple (Fig. 73c) 3

2 Scales of pecten epipharyngis subequal, relatively narrow (Fig. 74b). Antaxial seta of maxilla at least four times as high as wide (Fig. 74e)...*fuscipes* (Kieffer)
Outer scales of pecten epipharynx broader than median scale (Fig. 72b). Antaxial seta of maxilla less than three times as high as broad (Fig. 72e) ....*chalybeatus* (Edwards)

3 Paired median mental teeth as dark as remainder of mentum .... *effusus* (Walker)
Paired median mental teeth paler than remainder of mentum .... *glabricollis* (Meigen)*

* Not seen (based on published description of Gouin (1936:168)).

atripes (Kieffer) (= foveatus Edwards) is not known as a larva.

Rheocricotopus chalybeatus (Edwards)

Rheocricotopus chalybeatus (Edwards, 1929:331).

DESCRIPTION OF 4TH INSTAR LARVAE (n = 7).

Body length (n = 1) 4.8 mm, head capsule 423 (381-470), yellow with occipital m rgin, mentum, apical two thirds of mandible and apical half of prementum dark brown.

Antenna (Fig. 72a). Five segmented, len ths 59 (55-63); 19.6 (18-21); 5.4 (5-6.5); 4.3 (4-4.5); 5.2 (5-5.5). Antennal ratio 1.72 (1.59-1.82). Antennal spine 28 (24-32) long, not extending beyond final antennal segment. ubsidiary spine 3 - 5 long, subapical on second antennal segment. Lauterborn organs present, shorter than third antennal segment. Ring organ 5 - 7 from base of first antennal segment.

Labrum and palatum (Fig. 72b). I bifid, each branch subequal. Pecten epipharynx of three spines, the median one narrower than the two outer ones. Three chaetulae laterales, ? chaetulae basales. Premandible 61 (56-66) long, simple.

Mandible (Fig. 72c). 119 (110-127) long with the apical tooth shorter than the combined width of the three inner teeth. Characteristic shaped seta subdentalis. Seta interna of five or six branches, each bluntly pectinate. Seta on outer margin weak.

Mentum (as in fuscipes, see Fig. 74d). idth of flattened mentum 92 (80-96). Paired median teeth with small outer tooth closely apressed. Five pairs of lateral teeth. Ventromental plates well developed with numerous setae beneath.

Maxilla (Fig. 72e). Few galear lamellae, apparently simple. Pecten gale ris with larger teeth than in the other two species examined. Antaxial seta with base broad,at most three times longer than wide. None of the maxillary ~e ae serrate.

Abdomen. Procerci approximately 26 high by 18 wide bearing apically 3 or 4 setae of maximum length 487. Strong spur present (Fig. 72d). Length of posterior parapods, anal tubules and supra-anal setae not determinable on the material examined. Claws of anterior parapod all terminally toothed except for the longest claws. Claws of posterior parapod simple, golden. Longest body seta 128 (116-137) long.

MATERIAL EXAMINED

Site 11 (1 reared to adult); Site 12 (6 reared to pupae or adult); Site 40 (1 reared to adult).

DISTRIBUTION AND ECOLOGY

Prior to this study *chalybeatus* was only known in Britain from the type-series from six widely distributed localities in England. The larvae do not appear to have been described previously although there are records of the species from several localities in Europe, including Scandinavia, the Alps, France and Germany. Lehmann (1971:489) summarises the distribution as Europe, with the exception of southern Europe and describes the ecology (with reference to the River Fulda) as rheophilic reaching the highest abundance in the potamal although in an earlier publication (1969:354) he mentions the rare occurrence in the upper reaches and the epirhithron and the higher abundance in the meta- and hyporhithron as well as the potamal.

The British material examined comes from two different types of habitats. The single specimen from Site 11 is from a spring high on basic rocks on Dartmoor, while the remaining sites are from the middle reaches of rivers. Site 8 is a chalk river, while Site 40 is a similar sized river flowing on the basic rocks on the west side of Dartmoor.

Rheocricotopus effusus (alker)

Rheocricotopus effusus (alker, 1856:180) ? not Lindégaard-Petersen 1972:485.

DESCRIPTION O 4TH IN .A. LA V. (n = 6)

Body length 4.8 (4.4-5.2), head capsule 430 (402-445) yellowi h-brown, occipital margin, mentum and part of postmentum, mandible and apical half of premandible darker brown.

Antenna (Fig. 73a). Five segmented, lengths 60 (55-64); 13.6 (13-14.5); 9.4 (8-10); 5.7 (5-6); 5.8 (5-6). Antennal ratio 1.74 (1.67-1.79). Antennal spine 30 - 33 long not extending beyond fifth antennal segment. Subsidiary spine about 5 long subapically on second antennal segment. Ring organ about 5 from base of first antennal segment.

Labrum and palatum (ig. 73b). I bifid with the inner branch slightly shorter than the outer br nch. SII, SIII and SIV built as usual for the genus. Pecten epipharynx of three scales, relatively broad and subequal. Four chaetulae late ales, ? chaetulae basales. Premandibles simple 71 (67-75) long.

Mandible (Fig. 73d). 134 (129-140) long, apical tooth shorter than combined width of the three inner t eth. Characteristic seta subdentalis present. Seta interna present, five or six branches all apparently simple.

Mentum (Fig. 73e). Paired median teeth ithout lateral accessory teeth. Five pairs of laterals. Ventromental plates present, extending beyond outer teeth of flattened mentum, bearing numerous setae beneath.

Maxilla (ig. 73e). Palpiger short, sensillae present but small. Galear lamellae present apparently with multiple small spines at base. Pecten galearis distinct with more, smaller teeth than chalybeatus. Antaxial seta with a broad base, less than three times as high as wide.

Abdomen. Procercus 27 (26-28) high by 17 (15-18) wide bearing on the median posterior margin a distinct spur as in *fuscipes* (Fig. 74f). Apical seta of procercus 4 or 5, maximum length 160. Hind parapods 185 (170-195) long. Claws of anterior parapods with few inner teeth. Anal tubules short (difficult to ee on exuviae). Body setae short, or absent.

MATERIAL EXAMINED

Site 19 (3 larvae, 1 reared to adult); ite 22 (3 reared to pupae).

COMMENTS

The species described by Lindegaard-Petersen (1972:486) as *Rheocricotopus effusus* based on associated pupal skins determined by ehmann is not the same as the species described here. In several characters this des ription differs from all known *Rheocricotopus* including the mandible with an elongate apical tooth, n rm l shaped seta subdentalis and SI shape. This may be a misassociation and be a *Psectrocladius* or if it is a *Rheocricotopus* it may be *glabricollis* which is poorly described.

DISTRIBUTION AND ECOLOGY

Prior to this study the species had been recorded f om a few scattered localities in Britain, rarely more than one specimen from each locality. Like *chalybeatus* this species is apparently widely spread throughout urope.

Lehmann (1971:489) found this sp cies to be abundant in the River Fulda and describ d the species as rheobiont and oxybiont. He cites Thienem nn (1950:129) finding *effusus* in springs and moss in streams, and later (1954:330) calling it a "krenoxen Formen". oth the upland Yorkshire localities in which this species has been found in the resent study are rich in springs, in fact the s cond locality (ite 22) is the place of emergence of an underground river, and the first site has many springs in the river bed and in the tributaries. From the limited evidence presented here it is suggested that the species is krenophilic.

<u>Rheocricotopus fuscipes</u> (Kieffer)

<u>Rheocricotopus fuscipes</u> (Kieffer, 1909:45)

<u>Rheocricotopus dispar</u> (Goetghebuer, 1913:151)

DESCRIPTION OF 4TH INSTAR LARVAE (n = 10)

Body length 5.2 (4.5-6.2), head capsule length 420 (381-466). Yellow with occipital margin black and mentum, apical two thirds of mandible and apical half of premandible dark brown.

<u>Antenna</u> (Fig. 74a). Five segmented, lengths 61 (53-63); 14.3 (13-16); 7.8 (6-9); 4.9 (4-5.5); 5.4 (5-6). Antennal ratio 1.81 (1.66-1.94). Antennal spine 27 (?23-34), subsidiary spine about 4 long, subapical on second antennal segment. Ring organ 2 - 4 from base of first antennal segment.

<u>Labrum</u> (Fig. 74b). SI bifid, each branch subequal. SII long and narrow, SIII short, SIV normal. Pecten epipharyngis of three subequal, relatively narrow spines. 3 or 4 chaetulae laterales, 2 chaetulae basales, all simple. Premandible 68 (61-74) long, simple.

<u>Mandible</u> (Fig. 74c). 132 (117-140) long, apical tooth shorter than combined width of the three inner teeth. Typical seta subdentalis present. eta interna of five or six branches, each bluntly plumose.

<u>Mentum</u> (Fig. 74d). Flattened width 104 (97-110). Paired median teeth with partially fused small accessory teeth and five pairs of laterals. Ventromental plates distinct extending

beyond outer mental teeth and with numerous setae beneath.

Maxilla (Fig. 74e). Palpiger small, galear lamellae present with apparently complex bases resembling fused spines. Pecten galearis present with teeth similar to *effusus*, smaller than *chalybeatus*. None of the maxillary setae are as strongly triangular as in the other two species described: the maximum height of the antaxial seta is at least four times the width.

Abdomen. Procercus (Fig. 74f) 26.5 (22-32) high by 19 (14-21) wide with a strong spur in the middle of the posterior side and bearing apically five setae of maximum length 349 (275-420). Procercus more heavily sclerotised on the posterior edge (stippling in figure). Hind parapods 198 (169-233) long, anal tubules not distinguishable in exuviae or whole larvae. Claws of anterior parapods bear a few inner teeth, less than in the other two species examined. Longest body seta 74 (60-83) long.

MATERIAL EXAMINED (Virtually all reared at least to pupa)
Site 3 (4); Site 14 (4); Site 21 (12); Site 26 (2); Site 29 (8); Site 34 (1); Site 36 (8); Site 37 (6); Site 40 (2); Site 46 (1); Site 49 (2); OXFORDSHIRE: Cuddesdon, 42/595 025, 1.iv.1978, leg. R.W. Crosskey, (ex cocoon of *Simulium spinosum*) (1 larva); HAMPSHIRE: Matley Wood Bog, 41/334 078, 22.xi.1977, leg. P.S. Cranston (1 larva); EAST SUSSEX: Broadstone stream, no date, leg. A. Hildrew (3 larvae) (Site 9 of this study).

DISTRIBUTION AND ECOLOGY

Adult *fuscipes* have been collected throughout Britain but according to Fittkau and Reiss in Limnofauna Europaea the species is less widely distributed in Europe than *effusus*. This may be due to misidentification in the genus prior to the revision of the adult males and pupae (Lehmann 1969) or may reflect a genuine difference in the relative abundances of the species between Britain and western Europe.

The larvae of fuscipes was found in nearly all stretches of running water examined in this survey with the exception of the spring zones and some of the high fast streams. The largest numbers were found in streams with thick growths of algae on stones, and this agrees with Lehmann's (1971:489) observations. He summarises the ecology of the species as eurythermic and eurytopic living on stones and plants. There are also records of fuscipes from standing waters including Bodensee (Reiss cited in Lehmann, 1969:356).

Lindegaard-Petersen (1972:485) found the species to be a spring form in Linding A with maximum numbers in April. In this study fourth instar larvae were found at all times of the year with the greatest numbers in the early months of the year.

xxxvi. Smittia Holmgren

Smittia Holmgren, 1869:47

Phaenocladius Kieffer in Thienemann, 1921:845.

Euphaenocladius Thienemann, 1934:31; Strenzke, 1950:845.

Type-species Chironomus brevipennis Boheman, 1865:575 by monotypy.

GENERIC DIAGNOSIS (Based on published descriptions and examination of undetermined B.M.(N.H.) material)

Larvae small to medium sized, head capsules relatively small.

Antenna. Four segmented (some figures show five segments). Second antennal segment usually at least as long as the first, two or three terminal segments reduced. Whole antenna longer than half the length of the mandible. Weak Lauterborn organs may be visible and a distinct ring organ present. Antennal spine well developed but not extending beyond apex of antenna.

Labrum and palatum, SI setae plumose each branch deeply incised. Remaining S setae simple, SIII very weak. Labral chaetae serrate or simple. Chaetulae laterales simple, chaetulae basales weak or absent. Premandible with two apical teeth and a variably developed inner tooth. No premandibular beard.

Mandible. Apical tooth shorter than combined width of the three inner teeth. Seta subdentalis small but present, seta interna with some terminally plumose branches.

Mentum. A single median tooth which may be domed or with a median nipple and five pairs of lateral teeth. Ventromental plates weakly developed without setae beneath. There may be a projection or tooth at the base of the outermost mental teeth.

Maxilla. Sensillae on galea and palpiger reduced. No lamellae on galea (? always), a few on base of palpiger. No pecten galearis. Maxillary setae reduced in number and size, simple.

Abdomen. Procercus absent without setae in the place. Posterior parapods reduced but bearing simple claws. Anterior parapods basally fused but with numerous fine spines on the basal part and several simple claws at the divided apex of the parapod. Anal tubules are reduced but usually visible.

COMMENTS AND SYSTEMATIC STATUS

The antennal structure and absence of the procerci indicate that this genus belongs amongst the more apomorphic genera of the tribe Metriocnemini. Saether (1977:86) placed Parasmittia and Smittia combined as the sister group of the marine genera of Metriocnemini centred on Clunio. For discussion of the position of Smittia relative to Clunio see page 98.

Smittia ? contingens (Walker)

Smittia ? contingens (Walker, 1856:191)

Smittia ? aquatilis Goetghebuer, 1921:88; Thienemann & Strenzke, 1941:245.

DESCRIPTION OF 4TH INSTAR LARVA (n = 1)

Body length 2.2 mm, head capsule 190 um, pale brown with occipital margin slightly darker and mentum, mandible and apical half of premandible darker brown.

Antenna (Fig. 75a). Four segmented, lengths 16; 25; 1; 1.5. Antennal ratio 0.58. Antennal spine 28 long. Ring organ 5 from base of first antennal segment, weak Lauterborn organs present but apparently no subsidiary spine.

Labrum and palatum (Fig. 75b). As generic diagnosis. SI with about five spines, labral chaetae serrate and simple. Three chaetulae laterales, each simple. Chaetulae basales apparently absent. Premandible 37 long with two subequal apical teeth and a broad small inner tooth.

Mandible (Fig. 75c). 65 long with apical tooth shorter than the three inner teeth. Seta subdentalis weak, seta interna with six or seven branches, some of which are terminally serrate or plumose. Setae on mandible weak.

Mentum (Fig. 75d). Width of not fully flattened mentum 50, width of median tooth 13. Median tooth with a median nipple. Ventromental plates weak without setae beneath.

Maxilla (Fig. 75e). Sensillae on palpiger distinct but those on galea smaller than usual. No lamellae on galea, two or three on base of palpiger. Maxillary setae short and reduced in number. No pecten galearis.

Abdomen. Procercus absent. Anterior parapods fused basally (Fig. 75f), bearing fine spines on the base and a few pale yellow simple claws on the separated apex. Posterior parapods separate bearing brown simple claws. Anal tubules short. A few sparse short body setae present.

MATERIAL EXAMINED

Site 30 (1 larva, questionably 4th instar)

COMMENTS

In several publications Thienemann suggested that *aquatilis* Goetghebuer and *contingens* (Walker) are synonyms following the questioned synonymy of Edwards, 1929:361. In 1941:253 Thienemann and Strenzke state that the adult midge which emerged from the larva they described was *Smittia contingens* (Walker), yet they described the larva as *Smittia aquatilis* Goetghebuer, apparently a junior synonym of *contingens*.

The larva described here is similar in many respects to *aquatilis* sensu Thienemann and Strenzke (1941) but differs in the number of antennal segments. Thienemann and Strenzke illustrate a five segmented antenna with the terminal three segments very reduced and this specimen described here has only four segments. It is possible that Thienemann & Strenzke are mistaken - the terminal segments are very small but the material has not been traced for close examination.

Smittia aquatilis Goetghebuer, as understood by the European workers, is, as the name suggests, an aquatic species, one of the few *Smittia* found in this habitat. The larva differs only slightly from that of *aterrima* (Meigen) a typical terrestrial *Smittia* species, and it is probable that the species is secondarily aquatic as with some *Pseudosmittia* species.

xxxvii. Synorthocladius Thienemann

Synorthocladius Thienemann, 1935:211.

Type-species Dactylocladius semivirens Kieffer, 1909:48, by original designation.

GENERIC DIAGNOSIS

Small larvae, up to 4 mm long.

Antenna. Various authors have interpreted the number of antennal segments differently. Between the second and the apical segment the intermediate segment often appears to be divided, although there is not the distinct break in the sclerotisation of the wall usually seen between segments. If the antenna is interpreted as five segmented, the third segment is longer than either the second or the fourth and the apical segment is very small. The antennal spine is long, often extending beyond the apical antennal segment. The ring organ is very low on the first antennal segment and the Lauterborn organs are very small.

Labrum. All S setae simple although SIV apparently absent. SIII broader and longer than usual in the Orthocladiinae. Pecten epipharyngis of three blunt smooth scales. Three or four short chaetulae laterales, chaetulae basales absent. The labral margin, ungula and basal sclerite are all strongly sclerotised, as is the premandible. Premandible with an indistinct apical tooth and a broad inner tooth.

Mandible. Apical tooth shorter than combined width of the three inner teeth. Seta subdentalis long, seta interna absent. One strong spine just proximal to the seta subdentalis on the inner margin of the mandible.

Mentum. Two tall median teeth and four pairs of laterals. Ventromental plates absent. Strong tufts of setae arising in a star shape from just outside the outermost lateral teeth.

These setae do not appear to be homologous with the beard present in other species of Orthocladiinae, arising as they do from a central area rather than from beneath the ventromental plates. Many of the setae appear to be directed inwards under the mentum unlike the beard in other genera of Orthocladiinae.

Maxilla. Antaxial setae short, simple. One sensilla basiconica well developed and elongate similar to *Eukiefferiella.*

Abdomen. Procerci about as high as wide, weakly sclerotised, bearing apically five or six setae. Anal tubules with dorsal pair slightly longer than ventral pair, and medially constricted. The dorsal pair are subequal to the posterior parapods.

Body with plumose and simple setae alternating, two pairs of each on each segment on abdominal segments I - VII, absent on the most posterior segments.

COMMENTS AND SYSTEMATIC STATUS

Synorthocladius is probably a monospecific genus: the generic diagnosis is based upon the species *semivirens.*

Saether (1977:86) suggests that *Synorthocladius* is the sister group of *Orthocladius* based on apomorphies of the female genitalia. The apparent separation of the genus from *Eukiefferiella* and *Cardiocladius* by Saether is surprising in view of the apomorphic characters shared by these genera in the larval stage. These are the simple SI setae, the broad blunt premandible, the inner margin of the mandible with spines and the general structure of the epipharynx.

Larval structures shared between *Eukiefferiella* and *Synorthocladius* include the elongate maxillary sensilla basiconica and the stellate abdominal setae of *Synorthocladius* may be derived from the terminally branched setae sometimes found in *Eukiefferiella calvescens/verralli* group. Larval structures thus suggest that *Synorthocladius* may be closely related to Eukiefferiella, and there are features of the pupa and adult male which do not refute this suggestion.

Synorthocladius semivirens (Kieffer)

Synorthocladius semivirens (Kieffer, 1909:48); (Pagast, 1933:297); (Dorier, 1933:185-197); Thienemann, 1935:211.

DESCRIPTION OF 4TH INSTAR LARVAE (n = 12)

Body length 2.8 (2.5-3.2) (n = 6) mm; head capsule 329 (286-371) um. Head capsule pale yellow brown with mandible, mentum, occipital margin, labral margin, ungula, basal sclerite and premandible all dark brown.

Antenna. (Fig. 76a). (see generic diagnosis). Segment lengths 61.7 (56-67); 13.7 (13-14.5); 27 (26-30); 3.2 (3-4). If the third segment is divided the lengths are 20 (18-21); 7 (5-8). Antennal ratio 1.40 (1.33-1.51). Antennal spine 60.5 (42-74), subsidiary spine 7 - 8. Ring organ 2 - 4 from base of first antennal segment.

Labrum (Fig. 76b). As generic diagnosis with premandible 49 (43-58) long (Fig. 76c).

Mandible (Fig. 76d). 96 (84-106) long with apical tooth short. Seta subdentalis more proximally sited on the mandible than usual and 18 (14-22) long. 12 (11-14) long spine situated just below the seta subdentalis. Seta interna absent.

Mentum (Fig. 76f). Flattened mentum 60 (53-67) wide, paired median mental teeth 15 - 17 wide. Ventromental plates not extending beyond outer mental teeth. Long setae beneath mentum (see comments under generic diagnosis).

Maxilla (Fig. 76e). Palpiger short with tetrahedral lamellae on the outer edge of the palpiger. No lamellae on the galea, but one of the sensillae basiconicae well developed. Antaxial setae short and simple, at least one seta appears rounded.

Abdomen. Procercus 13.4 (13-15) high by 13 (12-14) wide, bearing apically five or six setae of maximum length 392 (350-466). Lateral seta 45 (40-50) long, supra-anal seta absent. Posterior parapods 146 (116-171) long, dorsal anal tubules about 150 long by 14 wide, medially slightly constricted.

Setae on abdominal segments I - VII as in Fig. 76g with stellate setae alternating with simple setae, two pairs of each on each segment. Claws on anterior and posterior parapods both golden brown and simple.

MATERIAL EXAMINED

Site 4 (1 reared); Site 9 (5 larvae); Site 10a (3 reared, 1 larva); Site 40 (2 reared); Site 43 (5 reared, 3 larvae); Site 50 (1 reared, 1 larva).

DISTRIBUTION AND ECOLOGY

Adults of this species have been found throughout Britain and middle to northern Europe as far as the Arctic Circle. Similarly the larvae have been known for many years and have been recorded frequently in the literature. Mackey (1976a:245) in recording the larvae from the River Thames reviews the previous records of the larvae from the surface of stones in running waters (Berg, 1948:177; Lindegaard-Petersen, 1972:481; Lehmann, 1971:490). Reiss (1964:232) finding the pupae and adults from Bodensee mentions the previous records from standing waters including those of Meuche (1939:481) and Ehrenberg (1957:125) who found the species in the emergent stone and algal zone of east Holstein lakes.

Lehmann (1971:490) found the larvae of semivirens on the mud crust on stones in the River Fulda with a maximum abundance in the potamal zone. Mackey (loc.cit.) states that observations on the larval biology are contradictory because although many studies suggest that the larvae demand moving water the larvae are also found in the littoral of lakes. This is a familiar problem when comparing faunas in Britain with those on the continent of Europe. The size of many of the lakes in Europe means that wave action on the littoral zone gives rise to similar conditions to those in running waters, and similar faunas are frequently found.

Mackey gives information on the size distribution of the larvae in the Thames throughout the year and shows maximum numbers in the Acorus zone were found in March/April and again in late May. In the Nuphar zone (Mackey, 1977:70) the largest population occurred in the autumn.

In the course of this study semivirens larvae were found in eight sites, all moderate sized streams with stony beds. The species was only very abundant in Broadstone stream (ite 9), where it is second only to Heterotrissocladius marcidus in abundance in this iron-rich stream.

xxxviii. Thalassosmittia Strenzke & Remmert

Thalassosmittia Strenzke & Remmert, 1957:270.

Type-species Camptocladius thalassophilus Bequaert & Goetghebuer 1913:373 by original designation.

GENERIC DIAGNOSIS (Based upon the original description of Strenzke & Remmert)

Medium sized larvae, up to 5 mm long.

Antenna. Five segmented, the fourth segment longer than the third and the first segment scarcely higher than broad. Antennal spine shorter than flagellum, two branched with the inner branch extending to the end of the third antennal segment. Subsidiary spine present subapically on the second segment. Indistinct Lauterborn organs present. Ring organ present near apex of first antennal segment.

Labrum. SI setae divided into three or four branches with a strong central branch. SII and SIII simple, rather broader than usual in the Metriocnemini. SIV small. Labral lamellae between the bases of the SI heavily sclerotised and divided into two strong spines. Labral chaetae both simple and serrate. Pecten epipharynx of three blunt scales which are partially fused at the base. Chaetulae laterales of two types: the anterior two or three resemble the scales of the pecten epipharynx, and below and posterior to these are two pairs of pointed spines. Chaetulae basales of two simple spines. Premandible with one apical tooth and two rounded inner teeth. No premandibular beard.

Mandible. Apical tooth scarcely longer than any of the four inner teeth. Seta subdentalis present extending to the innermost tooth. Seta interna with outer branches serrate, inner ones simple.

Mentum. Dome shaped median tooth with four pairs of lateral teeth, decreasing evenly in size. The median tooth is twice the width of the first laterals. Ventromental plate present but not extending beyond outer teeth of flattened mentum.

Abdomen. Anterior parapods present, fully divided, with simple claws. Procerci absent but a thickened seta in the place. Posterior parapods separate and bearing simple claws. Anal tubules absent. Supra-anal seta present.

COMMENTS AND SYSTEMATIC ST TUS

See comments on page 98 on "Clunionini" for discussion of the marine genus of Orthocladiinae.

DISTRIBUTION AND ECOLOGY

The European species I. thalassophila is known as an adult from Belgium, England, France and Germany. The species is a typical marine littoral zone inhabitant. Strenzke & Remmert (1957:271) found the larvae amongst Enteromorpha in rock pools on the German North Sea coast.

The author has observed adults swarming in the intertidal zone on the Channel coast but no larvae were found.

xxxix. Thienemannia Kieffer

Thienemannia ieffer, 1909:49

Symmetriocnemus Thienemann, 1937:30

Type-species Thienemannia gracilis Kieffer, 1909:49 by monotypy.

GENERIC DIAGNOSIS (Based upon poor descriptions of otthast, 1915:341 (as Metriocnemus clavaticornis)and parck, 1922:101 (as Thienemannia gracilis).

Small larvae, up to 4 mm long.

Antenna. Five segmented, longer than half the length of the mandible. Fourth segment longer than the third but the terminal three segments all short. Antennal ratio distinctly higher than 1. Antennal spine long but not extending beyond terminal. antennal segment. Lauterborn organs present, langer than in most Metriocnemus. Ring organ present in basal third of first antennal segment.

Labrum and palatum. SI plumose with serrate labral plates between the bases. Premandible not described, but Saether (1977:81) infers that the premandibular beard present in Metriocnemus is also present in Thienemannia.

Mandible. Inadequately described.

Mentum. Paired median mental teeth small, clearly .lower than first of five pairs of lateral teeth.

Maxilla. Sensillae of palpiger and galea apparently weakly developed (Potthast loc. cit. Figure 127). Numerous relatively short maxillary setae.

Abdomen. Procercus present bearing apically six or s even setae. One of the lateral setae is more strongly developed than usual in the *Metriocnemus*-related genera.(Potthast, loc.cit. Figure 125). Posterior parapods long, supra-anal seta long. Anterior parapods normally developed.

COMMENTS AND SYSTEMATIC STATUS

In the absence of adequate descriptions of the larvae of the only described Palaearctic species, *gracilis*, it is difficult to comment on the systematic status of the genus. It is clear however on the existing evidence that the genus is very close to *Metriocnemus* and the separation may not prove to be valid. The pupa and adult male bears out this belief, but further material must be examined in more detail before accepting this possible synonymy.

The single species *gracilis* has been recorded from springs and small streams in many countries of western Europe, but never in large numbers.

xl. *Thienemanniella* Kieffer

Thienemanniella Kieffer, 1911:187

Type-species *Corynoneura clavicornis* Kieffer, 1911, by designation of Goetghebuer in Goetghebuer & Lenz (1939:7).

GENERIC DIAGNOSIS

Small larvae, no more than 3 mm long.

Antenna. (Fig. 77d). Five segmented, the fourth and fifth, and rarely the third, small. The second segment is usually darkened. The whole antenna is about half the length of the head capsule (Fig. 77a). Lauterborn organs and antennal spine very small. Ring organ present, and mark of insertion of seta.

Labrum and palatum (Fig. 77b). All S setae simple. Pecten epipharynx with five fine spines. Chaetulae laterales with one pair strongly serrate. Chaetulae basales absent? Premandible with one apical tooth, and a distinct beard.

Mandible (Fig. 77c). Apical tooth subequal to the first of four inner teeth. Seta interna of six plumose branches. eta subdentalis weak or absent.

Mentum (Fig. 78a-e). Either two or three median teeth. Ventromental plates small (? absent) without setae beneath.

Maxilla (Fig. 77e). Sensillae on palpiger small, on galea larger. Galear surface with many fine setae. Maxillary setae (? always) finely serrate. No pecten galearis, apparently no appendix.

Abdomen. Only two thoracic segments; the meso- and metathoracic segments are fused. Procercus small bearing apically four or five setae. Anterior and posterior parapods separate, anal tubules pointed, shorter than the posterior parapods. A strong, simple, somewhat darkened seta arises from the ventral basal half of the posterior parapod.

COMMENTS AND SYSTEMATIC STATUS

For discussion of the relationship between Corynoneura and Thienemanniella and the Orthocladiinae see under Corynoneura (Page 100). Larval Thienemanniella retain some of the more plesiomorphic character states of the Orthocladiinae compared with Corynoneura. These include the five segmented antenna, the presence of a seta subdentalis and seta interna and simple premandible.

Distinctive apomprphic characters shared by the two genera include the structure of the chaetulae laterales, the brush of fine setae on the galea or palpiger base, the fused meso- and metathoracic segments and the ventrobasal spine on the posterior parapods.

As in Corynoneura the palatum of Thienemanniella appears to be modified for possible filter feeding (see page 101).

KEY TO THE K C N LA V E OF BRI ISH THIENEMANNI LLA

1 Second antennal segment pale. Body segments bearing long setae each as long as half the segment length .... fusca (Kieffer)
Second antennal segment dark. No long body setae 2

2 Two median teeth on the mentum (Fig. 78c) ...... species A
Three median teeth on the mentum (Fig. 78d) 3

3 Head capsule dark brown. First antennal segment less than 90 um long ....clavicornis Kieffer
Head capsule yellow or yellow-brown, never very dark. First antennal segment over 90 um long 4

4 Lateral mental teeth evenly decreasing in size from the outer median teeth to the most lateral teeth (Fig. 78e) .... species B
First lateral teeth clearly lower than a slope of even decreasing size from the median teeth to the outer teeth (Fig. 78d) .... species C

Thienemanniella clavicornis Kieffer

Thienemanniella clavicornis Kieffer, 1911:187

? Thienemanniella vittata Edwards, 1924 sensu Thienemann, 1941:232 not Edwards.

DESCRIPTION OF 4TH INSTAR LARVA (n = 3)

Body length 2.1 mm (n = 1), head capsule 275 (254-291) um, brown, occipital margin black, remainder of mentum, mandible and premandible scarcely darker than head capsule. Second antennal segment dark brown or black.

Antenna. Five segmented, len·ths 82.7 (80-85); 26 (25-27); 18 (17-19); 2; 3.3 (3-4). Antennal ratio 1.66 (1.63-1.69). Antennal spine weak 18 long (n = 1), Lauterborn organs present but small. ing organ 40 (39-42), point of seta insertion 63 (59-66) from base of first antennal segment.

Labrum and palatum. As generic diagnosis, premandible 37 - 40 long.

Mandible. 59 (54-64) long, outer apical tooth no longer than any of the four inner teeth. Seta interna with five or six plumose branches.

Mentum (Fig. 78a). 35 (34-37) wide with three subequal median teeth.

Maxilla. As generic diagnosis.

Abdomen. rocercus 11 - 13 high by 11 - 12 wide, darkly pigmented and bearing apically four setae of maximum length (broken in all cases) 124 long, dark. Posterior parapods and anal tubules not measurable. Claws of posterior parapod yellow and simple, those of the anterior parapod yellow-brown with very small inner teeth. Ventrobasal seta on posterior parapod 29 (26-32) long, pale brown.

MATERIAL EXAMINED

Site 34 (1 larva); Site 49 (1 reared to pupa); Site 50 (1 reared to male).

DISTRIBUTION AND COLOGY

Thienemanniella clavicornis Kieffer, like most species in the genus has been recorded only relatively infrequently in Britain and Europe. Fittkau and Reiss (1978) note only patchy distribution through Europe, but the evidence of recent collecting by the author in Britain suggests that the species is in fact quite widely distributed from Devon to North Yorkshire, with more records from higher ground than lowland south-east England.

Schlee (1967:16) states that the larvae were numerous in the rheokrene of the River Fulda (west Germany) but unless the larva which Thienemann briefly described as _? vittata_ (1941:232) is in fact _clavicornis_, the larva has not been previously described and the ecology is poorly known. All three sites from which the species was collected in this country were fast flowing, cold rivers.

Thienemanniella fusca (Kieffer)

Thienemanniella fusca (Kieffer, 1924:54).

? _Thienemanniella morosa_ (Edwards, 1924)

DESCRIPTION OF 4TH INSTAR LARVA (n = 1)

Body length not measurable, head capsule 249 um, pale yellow-brown, with a continuous black occipital margin and the mentum and mandible scarcely darker than the surrounding head capsule. All antennal segments pale yellow.

Antenna (Fig. 78d). Five segmented; lengths 70; 25; 3; 2; 3; third segment, unusually for the genus, as short as the fourth and fifth segments. Antennal spine 8 long, Lauterborn organs distinct,as long as the third segment. Ring organ 23, site of insertion of seta 46 from base of first antennal segment.

Labrum and palatum. As generic diagnosis. Premandible 35 long with a distinct beard.

Mandible (Fig. 78c). 64 long with outer apical tooth no longer than the first of four inner teeth. Seta subdentalis 4 long, seta interna with six plumose branches.

Mentum (Fig. 77b). Three median teeth (in figure the middle tooth is apparently worn). Five pairs of lateral teeth, ventromental plates weak, no setae beneath.

Maxilla. As generic diagnosis but difficult to discern the setae.

Abdomen. Procercus 24 high by 18 wide bearing apically four setae of maximum length 344. Lateral seta of procercus 92 long, supra-anal seta 127 long, both longer and thicker than usual in the genus. Apparently no ventrobasal seta on the posterior parapod. Numerous stout dark setae on the body of maximum length 130 um. Posterior parapod claws yellow, simple; those of anterior parapod yellow with fine inner teeth on all but the shortest claws.

MATERIAL EXAMINED

Site 41 (1 reared to pharate female)

COMMENTS, DISTRIBUTION AND ECOLOGY

This distinctive larva was identified by comparison with the description by Zavrel in Thienemann, 1936:209 of *Thienemanniella fusca* Kieffer. Although the description is brief, the larva and pupa are so distinctive as to render it unlikely that there is confusion with any other species. These distinctive characters include the short third antennal segment, long body setae, pale second antennal segment and *Metriocnemus*-like pupa with tubercles on the posterior margin of the abdominal segments. Edwards (1929) suggested that Kieffer's *T. fusca* may be a junior synonym of his (1924) species *morosa* based on the published description of the adult, but no one to the author's knowledge has pursued this possible synonymy. Fittkau and Reiss (1978) do not list *T. fusca* but it is not clear whether this is by omission or because of suspected synonymy with *morosa*. Kieffer described the species from Lunz (Austria) and Thienemann (1944) stated that *fusca* is found in the moss of waterfalls in the Alps and on weirs in North Germany.

The only locality in which the single specimen was found was a weir on the River harfe in North Yorkshire, an interesting, although hardly statistically valid, similarity of habitat.

Thienemanniella species A

? Thienemanniella cfr. claviforceps Kieffer, 1925, sensu Thienemann, 1941:232.

DESCRIPTION OF 4TH INSTAR LARVA (n = 3)

Body length 2.6 mm (n = 1), head capsule 301 (265-330), pale yellow-brown, occipital margin black, mentum, mandible and second antennal segment brown.

Antenna. Five segmented, lengths 94 (88-98); 29.3 (27-32); 25.7 (25-26); 3; 4.3 (4-5). Antennal ratio 1.50 (1.47-1.56). Antennal spine very short. Ring organ 47 (42-53), point of seta insertion 72 (66-78) from base of first antennal segment. Lauterborn or ans present but weak.

Labrum and palatum. As generic diagnosis; premandible 43 (42-45) long with distinct beard.

Mandible. 83 (82-84) long with outer tooth no longer than the first of the four inner teeth. Seta subdentalis very weak, seta interna with six plumose branches.

Mentum (Fig. 78c). Two median teeth and five pairs of laterals, evenly decreasing in height. Flattened width 46 (45-48). Ventromental plates weak without setae beneath.

Maxilla. As generic diagnosis.

Abdomen. Procercus (n = 2) 12 - 13 high by 8 - 9 wide bearing apically four setae of maximum length 201 - 243. Lateral seta of procercus and supra-anal setae fine and short, as usual for the genus. Ventro-basal seta of the posterior parapod 29 - 30 long, golden, simple. Claws on posterior parapods yellow-brown, simple; those on anterior parapods yellow with a few inner teeth. Anal tubules and posterior parapods not measurable on exuviae.

MATERIAL EXAMINED

Site 32 (2 larvae, 1 reared to pupa); Site 47 (1 larva).

COMMENTS

This larval type with only two median mental teeth is unusual in the genus Thienemanniella and has only been described before for the species flaviforceps Kieffer, by Thienemann (1941:232). This species is not on the British list, and there are several British species without described larvae so it is unwise to comment on the identity of this larva.

The two sites in which this larva was found are both deep rivers running through clay in south-eastern England. The flow rate was slow in both sites and there was little weed growth in the turbid rivers.

Thienemanniella species _

DESCRIPTION OF 4TH INSTAR LARVA (n = 4

Body length 2.3 - 2.5 mm (n = 2), head capsule 306 (296-318), yellow, with occipital margin black and mentum, mandible and second antennal segment dark brown.

Antenna. Five segmented, lengths 100.7 (98-103); 31.5 (29-33); 25.5 (24-27); 2.2 (2-3); 3.7 (3-4). Antennal ratio 1.61 (1.48-1.75). Antennal spine slight, ring organ 54 (53-55) point of insertion of seta 76 (74-79) from base of first antennal segment. Lauterborn organs present but weak.

Labrum and palatum (Fig. 77d). As generic diagnosis. All 8 setae simple. Pecten epipharyngis of five spines. First chaetulae laterales developed into serrate setae. Premandible 33 - 40 long with a distinct beard.

Mandible. 78 (77-79) long with outer apical tooth no longer than the first of four inner teeth. Seta subdentalis short, seta interna of six plumose branches.

Mentum (Fig. 78d). Three median teeth as a group somewhat longer than the remaining lateral teeth, such that a line from the outermost median tooth to the fifth lateral tooth shows the first laterals to be shorter than the others. Ventromental plates weak, no setae beneath.

Maxilla (Fig. 77e). As generic diagnosis. Numerous setae on anterior margin of galea. Three finely serrate maxillary setae, apparently no appendix.

Abdomen (n = 2). Procercus 16 - 18 high by 13 wide, bearing apically four setae of maximum length 243 - 250. Lateral seta of procercus weak. Posterior parapods 169 - 238 long, anal tubules simple, tapering to a point, 58 - 60 long. Ventro-basal spine on posterior parapod 32 - 34 long, simple, pale brown. Claws on posterior parapod yellow, simple; those on anterior parapod yellow-brown with fine inner teeth.

MATERIAL EXAMINED

Site 29 (2 larvae, 2 reared to pupae).

COMMENTS

Examination of specimens reared to Thienemanniella lutea (Edwards, 1924) in the collections of the F.B.A. suggests that they are the same larval type as species _ in this work. However with only a small proportion of the larvae of British species reared to adult males it would be unwise to ascribe a species name to this larva.

Thienemanniella species C

DESCRIPTION F 4TI IN TA L VA (n = 1)

Body len th 3.3 mm, head capsule 339 um, pale yellow, with occipital margin dark brown and mentum, mandible and second antennal segment brown.

Antenna. Five segmented; lengths 106; 32; 24; 2; 3. Antennal ratio 1.74. Antennal spine not visible. Ring organ 63, site of in ertion of seta 70 from base of first antennal segment. Lauterborn organ present but small.

Labrum and palatum. As generic diagnosis.

Mandible. 71 long with apical (outer) tooth no longer than any of the four inner teeth. eta subdentalis very small, seta interna of six plumose branches.

Maxilla. As generic diagnosis.

Abdomen. Procercus 17 high by 15 wide, bearing apically four setae of maximum length 258. Late al seta weak and short. Posterior parapods 180 long, anal tubules very weak. Ventro-basal spine of posterior parapod 3? long, yellow. Claws of posterior parapod pale yellow and simple; those of anterior parapod yellow-brown and may be simple (difficult to determine in exuvium).

MATERIAL EXAMINED

Site 21 (1 larva).

COMMENTS

Emergence traps over the stream (Site 21) only collected adult *Thienemanniella majuscula* (Edwards, 1924:183), and it is possible that species C in this survey belongs to this species. However, as with the other unascribed species of *Thienemanniella* in this survey must remain in doubt until definitely associated males can be found.

Thienemanniella majuscula was previously known only from the type-series from two south-eastern English localities. Numerous specimens were taken from emergence traps over Site 21 in North Yorkshire, but no comments can be made on the ecology of the species.

xli. *Trissocladius* Kieffer

Trissocladius Kieffer in Kieffer & Thienemann, 1908:3.

Type-species *Trissocladius brevipalpis* Kieffer (in Kieffer & Thienemann, 1908) by designation of Edwards (1929:309).

GENERIC DIAGNOSIS (see Comments below)

Medium to large larvae. Body colour blood-red.

Antenna. Said to be five segmented but figure of Chernovskii (1949:Fig. 131) suggests possible seven segmented antenna like *Heterotrissocladius* (Fig. 37a) and *Paratrissocladius* (Fig. 62a). Lauterborn organs small, ring organ in basal quarter of first antennal segment. Antennal blade as long as flagellum.

Labrum. SI plumose, other S setae simple. Pecten epipharyngis of three simple scales. Premandible with two apical teeth and broad inner teeth.

Mandible. Apical tooth shorter than combined width of three inner teeth. Seta interna and seta subdentalis present.

Mentum. Two median teeth lower than the first of six pairs of laterals. Ventromental plates extend beyond mentum, no setae beneath.

Abdomen. Procerci caudally sclerotised with six or seven apical setae. Parapods well developed, anal tubules about half as long as posterior parapod.

COMMENTS AND SYSTEMATIC STATUS

Trissocladius is recorded from Britain from a single adult male *brevipalpis* and the genus as restricted by Saether

(1976:163) now comprises two infrequently collected species.

The generic diagnosis above is based upon published descriptions as summarised by Saether (1976:164) since no larval material has been found. The descriptions used are those of Kieffer & Thienemann (1908), Potthast (1915), Chernovskii (1949), and Pankratova (1970).

Saether (1976:23) based only on the male argues that _Trissocladius_ may be the sister group of _Zalutschia_, but in the absence of the female, and without full examination of the pupa and larva this cannot be more than tentative.

DISTRIBUTION AND ECOLOGY

The single British record of _brevipalpis_ is from East Sussex. This species is also recorded from elgium, ermany, Finland, Sweden and the U.S. . aether summarises the ecology of the species as a mud tube dweller living in puddles and emerging early in the ye r (March to May).

xlii. _alutschia_ Lipina

Zalutschia Lipina, 1939:106; Saether, 1976:180

Type-species _Zalutschia zalutschicola_ Lipina, 1939:96, by monotypy.

GENERIC DIAGNOSIS (based on Saether's diagnosis (1977:180)).

Small to medium sized larvae, up to 7 mm long, head capsule up to 580 um long.

Antenna. Six segmented, each segment consecutively smaller, the sixth very fine. Blade of varying lengths. Lauterborn organs present, smaller than third antennal segment. Ring organ present.

Labrum. SI plumose, all other S setae simple. Pecten epipharyngis of three simple spines. Premandible with two apical teeth and one inner tooth.

Mandible. Apical tooth only slightly shorter than width of three inner teeth. Seta interna present, seta subdentalis present with apical notch.

Mentum. Double median tooth as high or higher than six pairs of lateral teeth. Ventromental plates broad, extending beyond outer mental teeth and with setae beneath.

Maxilla. Sensillae on palpiger and galea distinct. Numerous lamellae on galea, both simple and complex. Pecten galearis present. Maxillary setae both simple and weakly serrate. Appendix may be present.

Abdomen. Procerci bear 6 or 7 apical setae. Parapods well developed, as are the anal tubules which may be longer than the posterior parapods.

COMMENTS AND SYSTEMATIC STATUS

Dowling (in press) records a species of *Zalutschia* from Irish bogs, other than this only one specimen is known from Britain, an unidentified species mentioned on page 331 . The generic diagnosis is therefore based on the recent revision of Saether (loc. cit.).

Saether places *Zalutschia* as the sister group of the poorly known *Trissocladius*, both genera being amongst the more plesiomorphic of the non-Metriocnemini. The fourth antennal segment being longer than the third and the presence of all body appendages indicate that the genus belongs with the non-Metriocnemini. The plumose SI seta and broad ventromental plates with setae beneath indicate that *Zalutschia* is amongst the more plesiomorphic genera, while the six segmented antenna shows relationships with both *Paratrissocladius* and *Heterotrissocladius*. Saether (1976:14-32) discusses the phylogeny of *Zalutschia* and related genera.

MAT_RIAL EXA.INAD

Site 15 (1 larva reared to female). Identified with ~aether (1976:183-193) as species near lingulata lingulata ~aether, 1976 This subspecies is described from several North American localities but there are slight differences between this specimen and lingulata lingulata. Unfortunately in remounting the specimen the larval head capsule was damaged and parts including the antenna and mandible were lost. The specimen is therefore not figures or described. The single locality is a boggy spring high on Dartmoor (Devon).

xliii. Genus undetermined.

acutilabis onstantinov

Genus indet. acutilabis Konstantinov, 1948 (not seen); Pankratova, 1970:323.

DESCRIPTION OF 4TH IN THE LARVA (n = 1)

Body length 5.1 mm, head capsule 530 um, yellow-brown with occipital margin scarcely darkened and mentum and mandible nearly black.

Antenna (Fig. 79a). Five segmented; lengths 43; 11; 11; 11; 4. Antennal ratio 1.30. Antennal spine 43 long, subsidiary spine 6 long, inserted subapically on the second antennal segment. Ring organ 7 from base of first segment. Lauterborn organs very distinct, slightly longer than the second antennal segment and with distinct striations. On the dorsallateral side external to the base of the antenna is a sclerotised extension of the head capsule, as in Camptocladius (Fig. 9a).

Labrum (Fig. 79b) and palatum. All S setae simple, the SI setae arising from distinct tubercles. SII as long as SIII. Labral chaetae long and sinuous, simple. Pecten epipharyngis of three large scales. Chaetulae laterales and chaetulae basales not distinguishable on poor preparations. Ungula strongly sclerotised. Premandible with a single apical tooth and a broad inner tooth. No eard pre ent.

Mandible (Fig. 79e). 185 long with apical tooth slightly shorter than the combined width of the three inner teeth. eta subdentalis very small, seta interna with five or six fine branches, each very finely serrate or plumose. Outer margin of mandible with a single crenulation near the base of the anterior seta. Inner margin smooth.

Mentum (ig. 79d). A single elongate median tooth, often very worn. In unworn specimens, two lateral teeth can be seen. Ventromental plates small without setae beneath

Maxilla (Not ade uately visible on any specimen to figure). Sensillae on pal iger small, those on galea large and distinct. No pecten galearis. Maxillary setae simple and long. No appendix visible.

Abdomen. Procercus 25 high by 27 wide bearing apically five setae of maximum length 487. Lateral seta of procercus 101 long. Posterior parapod not measurable, anal tubules 169, simple, rounded.

Claws of posterior parapods brown, simple; those of anterior parapod yellow with distirct inner teeth. l_4 seta on abdominal segments I to VI or VII developed into a setal brush with at least fifty translucent branches, at most 137 long.

MATERIAL EXAMINED

CLWYD: Glan-y-wern, River Clwyd, 11.v.1978, leg. F.B.A. River Survey, (F.B.A. Coll., via L.C.V. Pinder). Also seen (but too poorly prepared for measurement) POWYS: Newbridge-on-Wye, River Wye, .vii.1978, leg. D. Morris. Further material from Site 43 coll. J. Francis has been seen but was not available for measurement.

COMMENTS

This distinctive larva has not, to the author's knowledge, been reared since Konstantinov's description in 1948, yet the larva has been found on a number of occasions in several countries since. This larva is known from U.S.S.R., Britain and Canada (aether pers.comm.) and the frequency of occurence in Britain (although not collected in this survey) implies that the adult is likely to be a described species although to which genus it belongs is uncertain.

The presence of a setal brush on abdominal segments suggests that this is a Cricotopus: the simple SI seta is not incompatible (vide brevipalpis and ?obnixus)but the strongly developed tubercles at the base of the SI setae are different from described Cricotopus, as are the strongly developed Lauterborn organs. If the pecten epipharyngis is correctly interpreted (and this is not certain) the species must belong to the subgenus Cricotopus while the aberrant species belong to the more apomorphic subgenus Isocladius.

Further evidence conflicting with the possible placement in Cricotopus is the shape of the pupal thoracic horn within the fourth instar larva from the River Clwyd. This is subconical with a tapering at the base: unlike any described Cricotopus or other Orthocladiine known to the author.

Gut contents of several of the larvae examined have consisted of subequal length fibres initially believed to be sponge spicules but more likely to be fibres of wood. The shape of the mentum is so distinctively shaped that an unusual diet is suggested and it is possible that the larva bores into submerged wood. However examination of submerged wood at

Site 43 did not reveal any acutilabis although several larvae were found by J. Francis in routine Surber sampling at the same time of year.

Unfortunately none of the larvae of acutilabis collected in Britain have been preserved alive and the identity of this enigmatic larva must remain in doubt until it can be reared.

CHAPTER 7

ECOLOGICAL AND PHYLOGENETIC SUMMARY

1. Phylogeny and ecology

In the preceding chapter the phylogeny of the 41 genera of Orthocladiinae found in Britain is discussed and as much data as is available on the distribution and ecology of the 91 described species is cited. For those genera containing predominantly or totally terrestrial, semiterrestrial or marine species the ecology is discussed at the generic level. The validity of discussing any aspect of the ecology of a genus may be questioned, (see the final section of this chapter) but there is evidence that the evolution of the Orthocladiinae has involved changes in larval habitat and many of these changes correspond with the evolution of supra-specific taxa.

The primitive (plesioeic) larval habitat is postulated to be cold running water with conditions of relatively stable temperature, water velocity and dissolved oxygen concentration. This habitat, although frequently chosen by the more plesiomorphic subfamilies of Chironomidae cited on page 6, is less usual in the Orthocladiinae where it is retained largely in the more primitive genera such as *Brillia*, *Cardiocladius* and *Eukiefferiella*. Certain genera have been able to move into slowly moving and standing waters which have an increased risk of elevated temperatures and reduced oxygen concentrations. These genera include the more apomorphic non-Metriocnemini such as *Psectrocladius* and most of the genera of the '*Orthocladius* + *Cricotopus*' series of genera. One genus in the last group (*Halocladius*) has become marine - an unusual habitat amongst the insects but one which has apparently evolved four times in the family Chironomidae. These marine groups are: part of

Tanytarsus (Chironominae), the majority of the subfamily Telmatogetoninae and, in the subfamily Orthocladiinae, the genera *Halocladius* and *Clunio* and its relatives. *Halocladius* is clearly a close relative of *Cricotopus* and is believed to be the sister genus. The genus is therefore likely to have had a freshwater ancestry, quite different from the postulated evolution of the marine *Clunio* and relatives from the terrestrial Metriocnemini.

All the known terrestrial and semiterrestrial larval Orthocladiinae belong to the apomorphic tribe the Metriocnemini. The more plesiomorphic genera within this tribe are separable from nearly all other larval Orthocladiinae by the relatively elongate fourth antennal segment compared with the third segment. These genera which retain all their body appendages have many of the character states believed to be plesiomorphic within the Orthocladiinae such as plumose SI seta, presence of labral lamellae near the anterior margin of the labrum and large ventromental plates often extending beyond the outer teeth of the mentum. Many of these genera have aquatic larvae while others are hygropetric or semiterrestrial. Larval Metriocnemini have evolved to fill a greater range of niches than any other Chironomidae. The more plesiomorphic genera such as *Heterotrissocladius*, *Heleniella* and *Heterotanytarsus* are lotic as are the larvae of the two most advanced genera *Thienemanniella* and *Corynoneura*. However within the Metriocnemini there is a number of genera with predominantly terrestrial species. These include *Bryophaenocladius*, *Gymnometriocnemus* and the genera centred on *Smittia*. Saether (1977) postulated that these genera, together with those centred on *Clunio* (see page 98) form a monophyletic group. Aquatic larvae in *Smittia* and

Pseudosmittia which have the characteristic reduced body appendages of the more apomorphic Metriocnemini are very likely to be secondarily aquatic having evolved from terrestrial ancestors. This is analagous to the freshwater species in the genus *Telmatogeton* (Telmatogetoninae) which are postulated to have become secondarily freshwater only on Hawaii, having evolved from a marine ancestor.

ii. Generic limits in the Orthocladiinae

It is not the intention in this section to discuss the wider aspects of the generic limits in Chironomidae, but to make some observations based upon the examination of the larvae described in this thesis.

As stated on page 20, although there is much agreement amongst present day workers on the generic limits within the Chironomidae, there are further problems to be resolved particularly amongst the monospecific and species-poor genera. Although Brundin (1956) reviewed many of the small genera erected by Kieffer, certain of these genera erected for aberrant adults were not considered. One of the most frequent causes of modification of the adults in Chironomidae is the adoption of ground mating, as opposed to swarming. This habit is fairly widespread in many different groups of Chironomidae and many similar modifications are found, particularly in the adult males. These morphological modifications are discussed by Cranston (in press) in relation to aberrant genera in the Tanytarsini and include hypopygial enlargement, hypopygial torsion, antennal reduction (number of segments and plume), reduction in number of facets of the eye and reduction in relative length of mid-leg and shortening of the wing or even brachypterism.

This complex of characters linked with a behavioural change in the adult is not of any supra-specific evolutionary significance but has arisen on a number of occasions in response to adverse environmental conditions which make aerial swarming unsuccessful. These conditions include dwelling in areas where high winds are expected and where being blown from the swarming site would mean failure to reproduce. These conditions are found in the Arctic and Antarctic and on small islands and many species dwelling in these areas show the complex of adult morphological characters associated with the loss of swarming habit. Although it is clear that these modifications are not of evolutionary significance at the supra-specific level, new genera have been described frequently for these 'aberrant' species, principally by Kieffer. In the Orthocladiinae such a case in point is Dolichoprymna, erected for a Metriocnemus-like species from the Arctic. The resolution of the correct generic placement of these aberrant species must rest with the examination of the immature stages which are not affected by the environmental conditions which modified the adult midge.

In a similar manner genera have been erected for aberrant larvae without regard for the characters of the adult and pupa which may indicate the true relationships of the species in question. Examples of genera erected on aberrant larvae in the Orthocladiinae include Plecopteracoluthus erected for larvae which are ectoparasitic on North American Plecoptera nymphs. Although the larvae are quite distinctive, Saether (1977) recognised that the pupae and adults belonged to the genus Nanocladius and that Plecopteracoluthus warranted no more than subgeneric status. Although the close examination of pupae and adults, particularly of species from outside the British Isles, lies outside the ambit of this study it appears that some genera in the Orthocladiinae may not warrant generic status as in the case cited above. Notable amongst these is the genus Epoicocladius erected for a species ectoparasitic on Ephemeroptera nymphs and with a larva modified for this way of life. Characters in the adult and pupa suggest that this genus is very close to Parakiefferiella (see page 145 for fuller comments). Two further genera which appear to have been erected without regard for characters in all stages of the life history are Paralimnophyes (page 254) and Thienemannia (page 318). They are close to or possibly synonyms of Limnophyes and Metriocnemus respectively. The formal synonymy of these genera must however await a more detailed knowledge of the range of characters found in the larvae and pupae of Limnophyes and Metriocnemus and, in the case of Thienemannia, closer examination of the poorly described larva and pupa.

From the examples illustrated above it would appear that the pupae might be the most reliable indicator of phylogenetic relationships in the Orthocladiinae and to an extent this may be true. However, within certain genera which appear quite homogeneous on the basis of the adults (male and female) and larvae, the pupae may show a greater variation of characters than in any of the other stages. Discussions with other chironomid taxonomists including Fittkau, Pinder, Reiss and Saether shows that there is some agreement on generic delimitation based upon apomorphies in two stages of the life history. The undoubted apomorphies of the larval Epoicocladius do not themselves justify generic ranking; a unique synapomorphy of adult or pupa must also be found. Future work on the possible synonymy of the genera cited on the previous page should take into account the above argument and characters of all stages of the life cycle should be considered before erecting or synonymising genera.

iii. Why identify larval Chironomidae to species?

In Chapter 1.ii. the potential ecological importance of the Chironomidae was briefly discussed. As with most freshwater organisms the larval Chironomidae have been considered by biologists studying aquatic ecosystems. Much of this work has been related to studies of water quality and the search for either indicator organisms or the calculation of diversity indices.

Sladecek (1973a) in a lengthy review of the use of indicator organisms points out that there has been no widespread acceptance of the use of indicator species in Britain or North America, although the system is widely used in the U.S.S.R. and western Europe. After tracing the history of classification of aquatic organisms as indicators of water quality since 1870, Sladecek lists 33 points of criticism of what he terms the 'saprobic system' These objections range from that of subjectivity, particularly of the classifications of the indicator species, through discrepancies between the ecology of the species in different geographic areas, excessive complication of classification and the absence of keys. Perhaps the most telling criticisms from British limnologists were those levelled by Hynes (1970) who stated that the concept of indicator organisms proving the existence of pollution is wrong since these very species are often found in waters unpolluted by man. Macan (1961) said the system needed more facts and criticised the excessive rigidity of the system, while Brinkhurst (1968) believed that reports in plain language could convey far more information than the restrictive system.

Bartsch & Ingram (1966) comment on the limited application of the saprobic system in the United States and make a point which is just as pertinent for the compilation of most of the diversity indices used by limnologists. For instance they state "It is basic to the use of indicator organisms that they be identified as to species, because, whatever their indicator capacities may be, it is presumed to be at the species level and not at higher taxonomic echelons." These authors do not suggest the need for better taxonomy but state that "... taxonomy has become an unattractive specialism in this age of rockets and outer space. These taxonomic difficulties ... are amongst the greatest drawback of the saprobic system."

In contrast to the pessimism of Bartsch and Ingram, two other American biologists Resh & Unzicker (1975) stress the importance of good taxonomy at the species level in water pollution studies. Within the North American context they recommend the use of caddis as control indicators giving the following reasons for their choice:

1. Caddis contain species both tolerant and intolerant of pollution,
2. There is a workable adult taxonomy,
3. There are available techniques for association of adults and immatures.

Although their most telling criticisms of the methodology of some aquatic biologists are perhaps most appropriate to their North American colleagues some of their concluding remarks are pertinent "The time and effort spent on identifying specimens' genus (sic) and in developing endless and often meaningless faunal lists for environmental impact statements should be shifted to associating immature and adult aquatic insects and to develop identification keys. If this were done the species lists prepared in the future would not merely be taxonomic exercises but valuable tools in the biological assessment of water quality."

Sladecek (1973) considered the three most frequently used indices in Britain (Trent, Lothians and Chandler's Biotic Score) to be based on the saprobic system. Although this is not the place to discuss this controversy it is clear that identification to species level is necessary for the majority of the indices involving indicator organisms.

Hellawell (1978) summarises the use of data on diversity of aquatic communities: models of the structure of communities and indices of diversity are frequently used in pollution studies since environmental stress often changes diversity and structure of the community. Changes in diversity indices may be used to estimate the degree of stress which may be due to pollution. Although Hurlbert (1971) states that "... species diversity has become a non-concept - it conveys no information because it has been defined in so many ways ..." Hellawell (loc.cit.) describes in detail the various indices that are in use and subjects the data of Learner et.al. (1971) and Hynes (1970) to pollution indices, six diversity indices and seven comparative indices. He comments on the usefulness of each of the indices and includes notes on the taxonomic requirements of each test. In several cases it is stated that species recognition is necessary but it is not necessary to name the taxon and this is felt to be taxonomically easier. This may be true for some groups of aquatic organisms but is unlikely to be the case for the Chironomidae, so it must be assumed that for the majority of indices the recognition of the taxa and the naming of the species are linked.

The characteristics which make caddis suitable as indicator organisms (Resh & Unzicker)(loc.cit.) also seem to be true of the Chironomidae. In addition, however, there are a greater number of Chironomidae which are tolerant to pollution and they are therefore of greater value as indicators of pollution. They may also be more easily and speedily reared compared with the Trichoptera. The impending availability of pupal keys as well as the key presented here should enable identification of more than 75 per cent of the Orthocladiinae, a greater proportion of the fauna than in the British Trichoptera.

There is however a number of disadvantages to the use of Chironomidae either as indicator species or in diversity indices in pollution studies. Foremost is the preparation time of microscope slides for identification of the larvae. Since larval Chironomidae are ubiquitous in most aquatic ecosystems the preparation time may become prohibitive. The need to make slide preparations for identification of aquatic groups has not, however, been a deterrent to algologists or those who study crustaceans or oligochaetes.

Another problem frequently mentioned with the use of larval Chironomidae is that they are difficult to identify even when they are mounted on slides. The existence of adequately illustrated keys with details of terminology explained should alleviate this problem. The experience of Saether (pers.comm.) in North America was that the provision of keys and the identification of voucher specimens for workers led to a high standard of identifications. Experience suggests that this also applies in this country although this opinion is so far based only upon circulated keys to the genera and the response to these keys.

A point concerning the use of any group as indicators is the need to retain voucher collections preferably deposite Museums. The absence of this historic material makes it diffi if not impossible to interpret which species earlier workers have been examining and much valuable ecological information is lost. Attempts to trace earlier collections of identified larval Chironomidae from the British Isles has been a time-consuming and largely fruitless task. Resh and Unzicker (1975) state that this is often the case in the United States for collections of aquatic organisms. If any group of aquatic invertebrates is to have any value as indicator organisms it will be necessary for voucher collections to be retained so that in the light of new taxonomic information older ecological findings can be revised.

In concluding this section evidence has been presented that Chironomidae may be of use as indicators (as species or communities) of the state of water quality, but that problems exist, partly of a taxonomic nature and partly of a technical nature. It is the belief of the author that these problems are not insurmountable and are compensated for by the wide pollution tolerances exhibited by different species in the family.

REFERENCES

BECKER, T. (1908). Dipteren der Kanarischen Inseln. Mitt.zool. Mus.Berl. 4:1 - 180.

BERG, K. (1948). Biological studies on the River Susaa. Folia limnol.scand. 4:1 - 318.

BIRKETT, N.L. (1957). Notes on a small collection of Chironomidae made in the Kendal district. Entomologist's mon.Mag. 93:145 - 149.

BÖHEMAN, C.H. (1865). Spetsbergens Insekt-Fauna. Öfvers.K. VetenskAkad.Förh.Stockh. 22: 563 - 577.

BOTNARIUC, C. & ALBU, P. (1971). Chironomidae (Diptera) from Retezat Massif of the southern Carpathians, Romania. Can.Ent. 103: 471 - 476.

BRINKHURST, R.O. (1968). Discussion to Tumpling. Suggested classification of water quality based on biological characteristics. 4th.Int.Conf.Water Poll.Res., Prague. 1 - 16: 1 - 2 (not seen).

BRUNDIN, L. (1949). Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. Ein Beitrag zur Kenntnis der bodenfaunistischen Charakterzüge schwedischer oligotropher Seen. Rep.Inst.Freshwat.Res.Drottningholm 30: 1 - 914.

(1956). Zur Systematic der Orthocladiinae (Dipt., Chironomidae). Rep.Inst.Freshwat.Res.Drottningholm 37: 5 - 185.

(1956a). Die bodenfaunistischen Seentypen und ihre Anwenbarkeit auf die Südhalbkugel. Zugleich eine Theorie der produktionsbiologischen Bedeutung der glazialen Erosen. Rep.Inst.Freshwat.Res.Drottningholm 37: 186 - 235.

(1966). Transantarctic relationships and their significance evidenced by chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. K.svenska VetenskAkad.Handl. 11: 1 - 472.

BRYCE, D. (1960). Studies on the larvae of the British Chironomidae (Diptera), with keys to the Chironominae and Tanypodinae. Trans.Soc.Br.Ent. 14: 19 - 62.

(1963). Chironomidae in "The insects of the Malham Tarn Area". Proc.Leeds phil.lit.Soc.Sci.Sect. 9: 15 - 91.

BRYCE, D. & HOBART, A. (1972). The biology and identification of the larvae of the Chironomidae (Diptera). Entomologists Gaz. 23: 175 - 217.

CHERNOVSKI, A.A. (1961). Identification of larvae of the midge family Tendipedidae. (Translated by E. Lees, edited K.E. Marshall). National Lending Library for Science and Technology, Boston Spa, Yorkshire.

COE, R.L. (1950). Family Chironomidae. In Kloet, G.S. & Hincks, W.D. A checklist of British Insects. 1st edition, Diptera. Handbk.Ident.Br.Insects. 9: 121 - 206.

COOK, E.F. (1949). The evolution of the head in the larvae of the Diptera. Microentomology 14: 1 - 57.

COQUILLET, D.W. (1910). The types of the North American genera of Diptera. Proc.U.S.natn.Mus. 37: 499 - 647.

CRAIG, D.A. (1969). The embryogenesis of the larval head of Simulium venustum Say (Diptera: Nematocera). Can.J.Zool. 47: 495 - 503.

CRANSTON, P.S. (1975). Corrections and addition to the list of British Chironomidae (Diptera). Entomologist's mon.Mag. 110: 87 - 95.

(1976). "Chironomidae" In Kloet, G.S. & Hincks, W.D. A checklist of British Insects. 2nd edition (revised). Part 5. Diptera & Siphonaptera. Handbk.Ident.Br.Insects. 11 (5): 12 - 21.

(1979). The development stages of Limnophyes globifer (Lundström) (Diptera: Chironomidae). Hydrobiologia (in press).

(1979a). A redescription and generic reassignment of the adults of Halotanytarsus tika Tourenq, 1975. Annls.limnol. (in press).

DEGEER, C. (1776). 394 - 400 Mémoires pour servir à l'histoire des insectes. 6: viii + 523 pp. Stockholm.

DEJOUX, C. (1978). Recherches sur les Chironomides d'Afrique francophone. Chironomus 2: 3 - 6.

DISNEY, R.H.L. (1975). Two interesting additions to the list of Chironomidae (Dipt.) for the Malham Tarn area of Yorkshire. Entomologist's mon.Mag. 111: 173.

DITTMAR, H. (1955). Ein Sauerlandbach. Untersuchungen an einem Wiesen-Mittelgebirgsbach. Arch.Hydrobiol. 50: 305 - 552.

DORIER, A. (1933). Les metamorphoses de quelques Orthocladiinae recueillis en Dauphiné. Trav.Lab.Hydrobiol.Piscic.Univ. Grenoble 25: 191 - 202.

DOWNES, A. (1970). in Fallis, A.M. editor, "Ecology and physiology of parasites. A symposium. Univ.Toronto Press. Adam Hilger Ltd. London, 258 pages.

(1974). The feeding habits of adult Chironomidae. Ent. Tidskr.Suppl. 95: 84 - 90.

DOWNES, J.A. & COLLESS, D.H. (1967). Mouthparts of the biting and blood-sucking types in Tanyderidae and Chironomidae (Diptera). Nature, Lond. 214: 1355 - 1356.

EASTOP, V. & VAN EMDEN, H.F. (1972). in Aphid Technology edited by van Emden. Academic Press, London and New York.

EATON, A.E. (1875). Breves dipterarum uniusque lepidopterarum Insulae Kerguelensi indigenarum diagnoses. Entomologist's mon.Mag. 12: 58 - 61.

EDWARDS, F.W. (1924). Some British species of Corynoneura (Diptera: Chironomidae). Entomologist's mon.Mag. 60: 182 - 189.

(1924a). On the British species of Thalassomyia and Cardiocladius (Diptera: Chironomidae). Entomologist's mon.Mag. 60: 203 - 207.

(1929). British non-biting midges (Diptera, Chironomidae) Trans.R.ent.Soc.Lond. 77: 279 - 430.

(1937). Chironomidae (Diptera) collected by Prof A. Thienemann in Swedish Lappland. Ann.Mag.nat.Hist. 10(20): 140 - 148.

FABRICIUS, J.C. (1794). Entomologia systematica emendata et aucta 4: 472 pp. Hafniae (Copenhagen).

FAHY, E. (1972). Taxonomic observations on the larvae of Eukiefferiella calvescens Edw. and E. verralli Edw. (Diptera: Chironomidae). Ent.Tidskr. 93: 30 - 35.

FITTKAU, E.J. (1954). Trichocladius nivalis Goetgh. (Chironomidenstudien III). Ber.limnol.Flussstn.Freudenthal. 6: 17 - 27.

(1962). Die Tanypodinae (Diptera: Chironomidae). Die tribus Anatopyniini, Macropelopiini und Pentaneurini. Abh.Larvalsyst.Insekten 6: 1 - 453.

(1968). Eiolomyia amazonica n.gen. n.sp. eine flugfähige Chironomide (Diptera) mit einem Hypopygium inversum. Amazoniana 1: 259 - 265.

(1973). Friedrich Lenz 14.9.1889 - 7.9.1972. Christiana Albertina, Kieler Universitats Zeitshrift 15: 91 - 92.

(1974). Ichthyocladius n.gen., eine neotropische Gattung der Orthocladiinae (Chironomidae, Diptera) deren larven epizoisch auf Welsen (Astroblepidae und Loricariidae) leben. Ent.Tidskr.Suppl. 95: 91 - 106.

FITTKAU, E.J. & LEHMANN, J. (1970). Revision der Gattung Microcricotopus Thien. u. Harn. (Dipt. Chironomidae). Int.Rev.ges.Hydrobiol.Hydrogr. 55: 391 - 402.

FITTKAU, E.J. & REISS, F. (1978). Chironomidae in Limnofauna Europaea. Gustav Fischer Verlag, tuttgart and New York. xvii + 532pp. 404 - 440.

FITTKAU, E.J., SCHL.., D. und REISS, F. (1967). Chironomidae in Limnofauna Europaea. Gustav Fischer Verlag, Stuttgart and New York. 346 - 381.

FREEMAN, P. (1955). A study of the Chironomidae (Diptera) of Africa south of the Sahara. I. Bull.Br.Mus.nat.Hist.Ent. 4: 1 - 67.

(1956). A study of the Chironomidae (Diptera) of Africa south of the Sahara. II. Bull.Br.Mus.nat.Hist.Ent. 4: 287 - 368.

(1964). Notes on Chironomidae (Diptera,: Nematocera). Proc.R.ent.Soc.London (B) 33: 147 - 150.

GOETGHEBUER, M. (1912). Etudes sur les Chironomides de Belgique. Mém.Acad.r.Belg.Cl.Sci. 3: 1 - 26.

(1913). Description de Chironomides nouveaux récoltès en Belgique. Annls Biol.lacustre 6: 143 - 172.

(1921). Chironomides de Belgique et specialement de la zone de Flandres. Mém.Mus.r.Hist.nat.Belg. 8: 1 - 211.

(1927). Les Cricotopus de Belgique (Dipt., Chironomides) Bull.Annls Soc.r.ent.Belg. 67: 51 - 54.

(1932). Diptéres (Nématocères). Chironomidae IV. Orthocladiinae, Corynoneurinae, Clunioninae, Diamesinae. Faune Fr. 23: 1 - 204.

(1935). Ceratopogonidae et Chironomidae nouveaux ou peu connus d'Europe (sixième note). Encycl.ent.Ser. B.II. Diptera 8: 3 - 14.

(1938). Ceratopogonidae et Chironomidae nouveaux ou peu connus d' urope (huitième note). Bull.Annls.Soc.r.ent.Belg. 78: 56 - 64.

(1940-1950). Tendipedidae (Chironomidae) Part f. Subfamilie Orthocladiinae. A. Die Imagines. Fleig.palaearkt.Reg. 13g: 1 - 208.

(1943). Faunule diptérologique des bois, en Flandres. Biol.Jaarb. 10: 56 - 70.

(1944). Ceratopogonidae et Chironomidae nouveaux ou peu connus d'Europe (douzième note). Biol.Jaarb. 11: 35 - 44.

GOETGHEBUER, M., HUMPHRIES, C.F. and FITZGERALD, A.M. (1949). Metamorphosis of the Chironomidae. I. A description of the larvae, pupae and imagines of some members of the genus Smittia (Kieff.), of the larvae of Orthocladius crassicornis (Goetgh.) and of the imago of Orthocladius flaveolus (Goetgh.) Hydrobiologia 1: 410 - 424.

GOUIN, F. (1936). Metamorphosis de quelques Chironomides d'Alsace et de Lorraine avec la description de trois espèces nouvelles par M. Goetghebuer. Revue fr.Ent. 3: 151 - 173.

(1959). Morphology of the larval head capsule of some Chironomidae (Diptera: Nematocera). Smithson.misc.Collns. 137: 175 - 201.

GOWIN, F. (1943). Orthocladiinen aus Lunzer Fleissgewässern. II. Arch.Hydrobiol. 40: 114 - 122.

HALIDAY, A.H. (1855). Descriptions of insects figured, and references to plates illustrating the notes on Kerry insects. Nat.Hist.Rev.Proc. 2: 59 - 64.

HALL, R.E. (1961). The Chironomidae of three chalk streams in southern England. Proc. 11th Int.Kongr.Ent.Wien 1960 1: 178 - 181.

HAMILTON, A.L. (1965). An analysis of a freshwater benthic community with special reference to the Chironomidae. Ph.D. Thesis, Dept. Zoology, University of British Columbia. (not seen).

HASHIMOTO, H. (1976). Non-biting midges of marine habitats (Diptera: Chironomidae) in 'Marine Insects' editor L. Cheng, North Holland Publishing Company.

HELLAWELL, J.M. (1978). Biological Surveillance of Rivers. Water Research Centre, Stevenage. 332 pp.

HENNIG, W. (1950). Die larvenform der Dipteren. 2 Teil. vii + 458 227 - 374. Akademie - Verlag, Berlin (2nd edition, 1968 seen).

(1966). Phylogenetic systematics. University of Illinois Press, Chicago, Ill. 263 pp.

(1968). Kritische Bemerkungen uber den Bau der Flügelwurzel bei den Dipteren und die Frage nach der Monophylie der Nematocera. Stuttg.Beitr.Naturk. 193: 1 - 23.

HENSON, H. (1957). The larva, pupa and imago of Hydrobaenus ephemerae Kieff. (Chironomidae, Diptera). Hydrobiologia 9: 25 - 37.

HINTON, H.E. (1960). A fly larva that tolerates dehydration and temperatures from -270°C to 102°C. Nature, Lond. 188: 336 - 337.

HIRVENOJA, M. (1973). Revision der gattung Cricotopus van der Wulp und ihrer Verwandten (Diptera: Chironomidae). Ann.zool.fenn. 10: 1 - 363.

HOLMGREN, A.E. (1869). Bidrag til Kannodomen om Beeren Eilands och Spetsbergens Insekt-Fauna. K.svenska VetenskAkad.Handl. 8: 1 - 55.

HRABĚ, S. (1947). Prof. Dr. Jan
Věst.čsl.zeměd.Mus. 11: 18 -

HUMPHRIES, C.F. (1938). The chironom
See, the relative density of its
period. Arch.Hydrobiol. 33: 535 -

(1951). Metamorphosis of the Chironomi
of the imago, larva and pupa of 46)
Goetghebuer, and of the larva and pupa o
trifascia Edwards. Hydrobiologia 3: 209 -

HUMPHRIES, C.F. and FROST, W.E. (1937). River Liffer
The chironomid fauna of submerged mosses.
43 (B): 161 - 181.

HYNES, H.B.N. (1970). The ecology of running waters. Liverpool University Press, Liverpool. 555 pp.

INSTITUTE OF TERRESTRIAL ECOLOGY/NATURE CONSERVANCY COUNCIL (1977). A conservation review. The selection of biological sites of national importance to nature conservation in Britain, editor D. Ratcliffe. Cambridge University Press, Cambridge. (2 vols.)

JOHANNSEN, O.A. (1937). Aquatic Diptera. III. Chironomidae: Subfamilies Tanypodinae, Diamesinae and Orthocladiinae. Mem.Cornell Univ.agric.Exp.Stn. 205: 3 - 84.

(1937a). Aquatic Diptera. IV. Chironomidae: Subfamily Chironominae. Mem.Cornell Univ.agric.Exp.Stn.210: 3 - 56.

KIEFFER, J.J. (1906). Description de nouveaux dipteres nematoceres d'Europe. Annls Soc.scient.Brux. 30: 311 - 348.

(1906a). Description d'une genre nouveau et de quelques espèces nouvelles de Diptères de l' Amerique du Sud. Annls Soc.scient.Brux. 30: 349 - 358.

(1906b). Diptera Fam. Chironomidae. in P. Wytsman (editor) Genera Insectorum 42: 1 - 78.

(1908). Description de deux nouveaux Chironomides. Bull. Acad.r.Belg.Cl.Sci. 8: 705 - 707.

(1909). Diagnoses de nouveaux Chironomides d'Allemagne Bull.Soc.Hist.nat.Metz 26: 37 - 56.

(1911). Nouveaux Tendipédides du groupe Orthocladius (Dipt.) 1 note. Bull.Soc.ent.Fr. 8: 181 - 187.

(1911a). Nouveaux Tendipédides du groupe Orthocladius (Dipt.) 2 note. Bull.Soc.ent.Fr. 9: 199 - 202.

(1912). Nouveaux Chironomides (Tendipédidae) de Ceylan Spolia zeylan. 8: 1 - 24.

(1912a). Quelques nouveaux Tendipédides (Dipt.) obtenus d'eclosion. 1 note. Bull.Soc.ent.Fr. 17: 86 - 88.

(1913). Nouveaux Chironomides (Tendipédides) d'Allemagne. Bull.Soc.Hist.nat.Metz. (3 ser.) 4: 7 - 35.

(1913a). Chironomides et Cecidomyidae. In Result scient. Voy.Ch.Alluaud et R.Jeannel en Afrique orientale. (1911-1912) (1pt.) 1: 1 - 43.

(1921). Chironomides nouveaux ou peu connus de la région paléarctique. Bull.Soc.Hist.nat.Metz. 29: 51 - 109.

(1923). Chironomides nouveaux ou peu connus de la région Paléarctique (suite). Annls Soc.scient.Brux.Mem. 42: 138 - 180 (follows on from 1922, same volume, pages 71 - 128).

(1924). Chironomides nouveaux ou rares de l'Europe centrale. Bull.Soc.Hist.nat.Metz. 30: 11 - 110.

KIEFFER, J.J. (1906) in Kieffer, J.J. & Thienemann, A. Über die Chironomiden Gattung Orthocladius. Z.wiss.Insekt.Biol. 2: 143 - 156.

KIEFFER, J.J. (1908) in Kieffer, J.J. & Thienemann, A. Neue und bekannte Chironomiden und ihre Metamorphose. I. Neue und bekannte Chironomiden. Z. wiss.InsektBiol. 4: 1 - 10, 33 - 39, 78 - 84.

KITCHING, R.L. (1971). An ecological study of water-filled tree holes and their position in the woodland ecosystem. J.anim. Ecol. 40: 281 - 302.

KONSTANTINOV, . . (1948). K poznaniyu fauny Chironomidae basseina R. Amur. Novye vidy podsemeistva Chironomidae. Dokl.Akad.Nauk SSSR 62: 557 - 560 (not seen).

KOWNACKA, M. & KOWNACKI, A. (1967). Parametriocnemus boreoalpinus Gowin et Thienemann 1942 (Tendipedidae, Diptera) nowy gatunek dla Tatr. Acta hydrobiol., Krakow. 9: 187 - 191.

KREJTZER, R. (1940). Limnologisch-ökologische Untersuchungen an holsteinischen Kleingewassern. Arch.hydrobiol.Suppl. 10: 359 - 572.

KRUGER, F. & THIENEMANN, A. (1941). Terrestriche Chironomiden XI. Die Gattung Gymnometriocnemus Goetgh. (Mit einem Beitrag von M. Goetghebuer, Gent). Zool.Anz. 135: 185 - 195.

LAURENCE, B.R. (1954). The larval inhabitants of cow pats. J.anim.Ecol. 23: 234 - 259.

LEARNER, M.A., WILLIAMS, R., HARCUP, M. & HUGHES, B.D. (1971). A survey of the micro-fauna of the River Cynon, a polluted tributary of the River Taff (South Wales). Freshwat.Biol. 1: 339 - 367.

LEHMANN, J. (1969). Die europäischen Arten der Gattung Rheocricotopus Thien. und Harn. und drei neue Artvertreter dieser Gattung aus der Orientalis (Diptera: Chironomidae). Arch.Hydrobiol. 66: 348 - 381.

(1971). ie Chironomiden der Fulda. Systematische, okologische und faunistische Untersuchungen. Arch.Hydrobiol. Suppl. 37: 466 - 555.

(1972). Revision der europaischen Arten (Puppen ♂♂ und Imagines ♂♂) der Gattung Zukiefferiella Thienemann. Beitr. Ent. 22: 347 - 405.

LEWIS, D.J. (1973). Psychodidae and Phlebotomidae, 155 - 179, in K.G.V. Smith (editor), Insects and other arthoropods of medical importance, British Museum (Natural History), London.

LINDEGAARD-PETERSEN, C. (1972). An ecological investigation of the Chironomidae (Diptera) from a Danish lowland stream (Linding A). Arch.Hydrobiol. 69: 465 - 507.

LIPINA, N.N. (1928). Lichinki i kukolki chironomid. Ekologiya i sistematika. Izd.nauch.Inst.ryb.khoz. 3: 1 - 179 (not seen).

LUNDBECK, W. (1898). Diptera groenlandica. Vidensk.Meddr dansk naturh.Foren. 5: 236 - 314.

LUNDSTROM, C. (1915). Diptera Nematocera aus den arctischen Gegenden Sibiriens. Zap.imp.Akad.Nauk. 29: 1 - 33.

MACAN, T.T. (1949). Survey of a moorland fish-pond. J.anim.Ecol. 18: 160 - 186.

MACAN, T.T. & WORTHINGTON, E.B. (1959). Life in Lakes and Rivers. Collins, London. 272 pp.

MACQUART, J. (1826). Insectes Diptères du Nord de la France. I. Tipulaires. Mem.Soc.Sci.Agric.Lille. 1823/1824: 59 - 224.

MALLOCH, J.R. (1915). The Chironomidae or midges of Illinois, with particular reference to the species occurring in the Illinois River. Bull.Ill.St.Lab.nat.Hist. 10: 275 - 543.

McALPINE, J.F. (1965). Insects and related terrestrial invertebrates of Ellef Ringnes Island. Arctic 18: 73 - 103.

(1965a). Observations on anthophilous Diptera at Lake Hazen, Ellesmere Island. Can.Fld.Nat. 79: 247 - 252.

MEIGEN, J.W. (1804). Klassification und Beschreibung der europäischen zweiflugeligen Insekten (Diptera Linn.) Erster Band, Erste Abtheilung, xxviii + 152, zweite Abteilung, vi, + 153 - 314. Reichard, Braunschweig.

(1818). Systematische Beschreibung der bekannten europäischen zweiflugeligne Insekten. Teil I. xxxvi + 332 pp. Forstmann, Aachen.

(1830). Systematische Beschreibung der bekannten europäischen zweiflugeligen Insekten. Teil VI. xi + 401 pp. Schulz, Hamm.

MUCHE, A. (1939). ie Fauna im Algenbewuchs. Nach Untersuchungen im Littoral ostholsteinischer Seen. Arch.Hydrobiol. 34: 349 - 520.

MIALL, L.C. & HAMMOND, A.R. (1900). The structure and life-history of the Harlequin Fly (Chironomus). Clarendon Press, Oxford. 196 pp.

MORGAN, N.C. & WADDELL, A.B. (1960). Chironomidae (Diptera) new to Perthshire including some species new to Britain. Entomologist 93: 62 - 69.

MOZLEY, S.C. (1970) Morphology and ecology of the larvae of Trissocladius grandis (Kieffer) (Diptera, Chironomidae), a common species in the lakes and rivers of Northern Europe. Arch.Hydrobiol. 67: 433 - 451.

(1971). Maxillary and premental patterns in Chironominae and Orthocladiinae (Diptera: Chironomidae). Can.Ent. 103: 298 - 305.

MUNDIE, J.H. (1957). The ecology of Chironomidae in storage reservoirs. Trans.R.ent.Soc.Lond. 109: 149 - 232.

MURRAY, D.A. (1972). A list of the Chironomidae (Diptera) known to occur in Ireland, with notes on their distribution. Proc.R.Ir.Acad.Sect.B 72: 275 - 293.

NATIONAL ENVIRONMENT RESEARCH COUNCIL (1976). Report on the Role of Taxonomy in Ecological Research. Publication series B, No. 14. N.E.R.C., London. iv. + 48 pp.

OLIVER, D.R. (1968). Adaptations of arctic Chironomidae. Ann. zool.fenn. 5: 11 - 118.

(1977). Bicinctus-group of the genus Cricotopus Van der Wulp (Diptera: Chironomidae) in the Nearctic with a description of a new species. J.Fish.Res.Bd.Can. 34: 98 - 104.

PANKRATOVA, V.Ya. (1970). Lichinki i kukiki komarov podsemeistva Orthocladiinae fauny SSSR (Diptera, Chironomidae = Tendipedidae). Opred.Faune SSSR 102: 1 - 343.

(1970a). Key to the larvae of the genera of the subfamily Orthocladiinae. F.B.A. Transl. 54: 1 - 8 (Translation of generic key 1970).

PANZER, G.W.F. (1813). Faunae insectorum germanicae initiae oder Deutschlands Insekten. Heft 54 24 pp. Nürnberg.

PINDER, L.C.V. (1974). The Chironomidae of a small chalk stream in southern England. Ent.Tidskr.Suppl. 95: 195 - 202.

(1978). A key to adult males of British Chironomidae Scient.Publs Freshwat.biol.Ass. 37: 1 - 169, 189 figs.

PINDER, L.C.V. & CRANSTON, P.S. (1976). Morphology of the male imagines of Orthocladius (Pogonocladius) consobrinus and O. glabripennis with observations on the taxonomic status of O. glabripennis. Entomologica scand. 7: 19 - 23.

(1971a). Four new and unusual Chironomidae (Diptera) Can. nt. 103: 1799 - 1827.

(1975). Two new species of Heterotanytarsus Sparck with keys to Nearctic and Palaearctic species of the genus (Diptera: Chirono 1d e). J. ish. es.Bd.Can. 32: 259 - 270.

(1975a). Nearctic and Palaearctic Heterotrissocladius (iptera: Chironomidae). Bull.Fish. es.Bd.Can. 193: 1 - 67.

(1976). F vision of Hydrobaenus, Trissocladius, alutschia Paratrissocladius and some related genera (Diptera: Chironomidae). Bull.Fish.Res.Bd.Can. 195: 1 - 287.

(1977). Taxonomic studies on Chironomidae: Nanocladius, Pseudochironomus and the Harnischia complex. Bull. ish.Res. Bd. an. 196: 1 - 143.

(1977a). Female genitalia in Chironomidae and other Nematocera. Bull. ish. es. d.Can. 197: 1 - 209.

SANTO -ABREU, . (1918). Ensayo de una Monografia de los Tendipedidos de las Islas Canarias. Mems R.Acad.Cienc.Artes Barcelona 14: 159 - 326.

SAUNDERS, L.G. (1924). On the early stages of Cardiocladius (iptera: hiron midae). ntomologist's mon. ag. 60: 227 - 231.

SCHLE , D. (1966). Praparation und rmittlung von Messwerten an Chirono iden (Diptera). Ge ss. b ss. 41/2: 169 - 193.

(1968). Vergleichende Merkmals nalyse zur Morphologie und Phylogenie der Corynoneura - Gruppe (iptera: hironomidae). Zugleich eine allgemeine Morphologie der Chiron miden - Imago. Stuttg.Beitr. aturk. 180: 1 - 150.

SHILOVA, A.I. (1971). The study of Chironomid Systematics and Fauna in the oviet nion. imnologica, erlin 8: 9 - 12.

SLADECEK, V. (1973). System of ater uality from the Biolo ical Point of view. Arch. ydrobiol. rg.Limnol. 7: 1 - 218.

SOPONIS, A. (1977). A revision of the Nearctic species of Orthocladius (Orthocladius)van der ulp (Diptera: Chironomidae) em.ent. oc. an. 102: 1 - 187.

SPÄRCK, R. (1922). Beitrage zur Kenntnis der hironomidenmetamorphose I - IV. nt. eddr 14: 32 - 109.

SPÄRCK, . and T NEMA , A. (1924). 'Metriocnemus" ampullaceus var austriacus. Verh.int.ver.Limnol. 2: 222 - 223.

STAEGER, C. (1839). ystematisk fortegnelser over de i Danmark hidtil fundne Diptera. Naturhist. idsskr. 2: 549 - 600.

STR NZK , K. (1940). Terrestrische C ironomiden V. Camptocladius stercorarius e eer. Zool.Anz. 132: 115 - 123.

(1942). Terrestrische Chironomiden XII. Bryophaenocladius subvernalis Edw. Zool.Anz. 137: 10 - 13.

(1950). Systematik, Morphologie, und Ökologie der terrestrischen hironomiden. Arch. ydrobiol. uppl. 18: 207 - 414.

(1950a). Terrestrische Chironomiden XIV. "Limnophyes" flexuellus dw.. ool.Anz. 145: 101 - 111.

(1952). Terrestrische Chironomiden XV. Bryophaenocladius nidorum dw. eitr. nt. 2: 529 - 542.

(1957). Terrestrische Chironomiden XVI. Bryophaenocladius nitidicollis Goetgh. (Diptera: Tendipedidae: Orthocladiinae). Beitr. nt. 7: 398 - 411.

(1950a). Lebensform und phylogenese der terrestrischen Chironomiden. 15th Int. on r. ool. ect. 4: 1 - 4.

(1960). et morphose und Verwandtschaftsbeziehungen der Gattung Clunio Hal. (Dipt.). (Terrestrische Chironomiden XXIV) uomal.elain-ja kasvit. eur.van.kasvit.Julk. 22: 1 - 30.

SUBLETTE, J. . & UBLETTE, M. . (1965). Family Chironomidae (Tendi edidae) in A catalog of the iptera of America north of Mexi o. U. . ent. gric. andb. 276: 142 - 181.

(1973). a ily Chironomidae pp 289 - 422 in M. Delfinado & E.D. Hardy (editors) Catalogue of the Diptera of the Oriental Region. Vol. 1. Suborder ematocera 618 pp. University ress f awaii, Honolulu.

ULC, K. & , J. (1924). O epoikikych a parasitickych larvach hironomidu. Acta. oc. ci.nat.moravo-siles 1: 353 - 391.

TAYLO , T.H. (1 03). Note on the habits of hironomus (Orthocladius) sordidellus. Trans.ent. oc.Lond. 4: 521 - 523.

THIENEMANN, A. (1921). Die etamorphose der Chironomiden-Gattun en amptocladius, Dyscamptocladius and Paraenocladius mit Bemerkungen uber die Artdifferenzierung bei den Chironomiden uberhaupt. rch. ydrobiol. uppl. 2: 809 - 850.

(1926). ydrobiolo ische Untersuchungen an den kalten uellen und Bächen der albinsel Jasmund auf Rugen. Arch. Hydrobiol. 17: 221 - 336.

(1932). Chironomiden - Metamorphoses V. Die attung Cardiocladius Kieffer. Zool.Anz. 101: 81 - 90.

(1934). Chironomiden-Metamorphosen. VIII. Phaenocladius. Encycl.ent. 7: 29 - 46.

(1935). Chironomiden-Metamorphosen. X. Orthocladius-Dactylocladius (Dipt.) Stettin ent. Ztg. 96: 201 - 224.

(1936). Alpine Chironomiden. Arch. Hydrobiol. 30: 167 - 262.

(1936a). hironomiden-Metamorphosen. XI. Gattung Eukiefferiella. Stettin ent. Ztg. 97: 43 - 65.

(1936b). Chironomiden-Metamorphosen XIII. Die Gattung Dyscamptocladius T ienemann. Mitt. Dt. ent. Ges. 7: 49 - 54.

(1936c). Chironomiden-Metamorphosen. XIV. Die Orthocladiinen-gattungen Acricotopus, Trichocladius, Rheorthocladius. Festschr. 60 Geb. Prof. E. Strand, Riga 1: 531 - 553.

(1937). Chironomiden-Metamorphosen (Diptera). XV. Mitt. ent. Ges. Halle 15: 22 - 36.

(1937a). Chironomiden aus Lappland III. Beshreibung neuer Metamorphosen, mit einer estimmungstabelle der bisher bekannten etriocnemuslarven und-puppen. Stettin ent. Ztg. 98: 87 - 96.

(1937b). Arktische Chironomidenlarven und -puppen aus dem Zoologischen Museum, Oslo. Norsk. ent. Tidsskr. 5: 1 - 7.

(1938). hironomiden- etamorphosen. VI. Encycl. ent. 9: 87 - 96.

(1941). Lapplandische Chironomiden und ihre Wohngewasser. Arch. Hydrobiol. Suppl. 17: 1 - 253.

(1942). Trichocladius- rten aus den Lunzer Seen. Arch. Hydrobiol. 39: 294 - 315.

(1944). estimmungstabellen für die bis jetzt bekannten Larven und Puppen der rthocladiinen (iptera: Chironomidae). Arch. Hydrobiol. 39: 551 - 664.

(1945). reidrich rüger zum Gedachtnis. Arch. Hydrobiol. 41: 430 - 434.

(1950). Verbreitungsgeschichte der Süsswassertierwelt Europas. Versuch einer histori chen Tiergeographie der europaischen innengewasser. Binnengewasser 18: 1 - 809.

(1954). Chironomus. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Binnengewasser 20: 1 - 834.

THIENEMANN, A. HARNI CI, O. (1932). Chironomiden-Metamorphosen IV. Die attung Acricotopus v.d.W. Zool. Anz. 99: 135 - 143.

THIENEMANN, A. & KI FF , J.J. (1916). Schwedische Chironomiden Arch. Hydrobiol. Plankton. Suppl. 2: 483 - 554.

THIENEMANN, A. & KRUGER, F. (1937). Chironomiden aus Lappland II. *Orthocladius abiskoensis* Edwards and *rubicundus* Mg., zwei "Gruppen-Species" der Chironomiden. *Zool.Anz.* 117: 257 - 267.

(1939). Terrestrische Chironomiden II. *Zool. Anz.* 127: 246 - 253.

THIENEMANN, A. & STRENZKE, K. (1941). Terrestrische Chironomiden. VII. Die Gattung *Paraphaenocladius* Th.. *Zool. Anz.* 133: 137 - 146.

(1941a). Terrestrische Chironomiden. IX. *Euphaenocladius* Th.. *Zool. Anz.* 133: 244 - 253.

TOKUNAGA, M. (1932). Morphological and biological studies on a new marine chironomid fly, *Pontomyia pacifica* from Japan. Part 1: Morphology and taxonomy. *Mem.Coll.Agric.Kyoto Univ.* 19: 1 - 56.

(1939). Chironomidae from Japan (Diptera). XI. New or little-known midges, with special reference to the metamorphosis of torrential species. *Philipp.J.Sci.* 69: 297 - 345.

VERRALL, G.H. (1912). Another hundred new British species of Diptera. *Entomologist's mon.Mag.* 43: 20 - 27.

WALKER, F. (1856). *Insecta britannia*, Volume 3, xxiv + 352, London.

WILSON, R. (1977). Chironomid pupal exuviae in the River Chew. *Freshwat.Biol.* 7: 9 - 17.

WINNERTZ, J. (1846). Beschreibung einiger neuer Gattungen aus der Ordnung der Zweiflugler. *Stettin ent.Ztg.* 7: 11 -20.

WIRTH, W.W. (1949). A revision of the Clunioninae midges with descriptions of a new genus and four new species. *Univ. Calif.Publs Ent.* 8: 151 - 182.

WÜLKER, W. (1956). Zur Kenntnis der Gattung *Psectrocladius* Kieff. (Dipt. Chironom.). Individuelle Variabilitat, Grenzen, und Möglichkeiten der Artentrennung, Ökologie und Verbreitung. *Arch.Hydrobiol.Suppl.* 24: 1 - 66.

(1957). Uber die Chironomiden der *Parakiefferiella*-Gruppe (Diptera: Tendipedidae: Orthocladiinae). *Beitr.Ent.* 7: 411 - 429.

(1959). Drei neue Chironomiden-Arten (Dipt.) und ihre Bedeutung fur das Konvergenzproblem bei Imagines und puppen. *Arch.Hydrobiol.Suppl.* 25: 44 - 64.

WULP, F.M. van der (1874). Dipterologische aanteekeningen. *Tijdschr.Ent.* 17: 109 - 148.

ZAVREL, J. (1931). Praemandibeln einiger Dipteren-larven. *Archo zool.ital.* 1000 - 1004.

(1934). Prispevek k faune bystrin a jezer ve Vysokych Tatrach. _..h...lubu prir.., ..rno_ 17: 8 - 12.

(1937). Eine neue Trissocladiusart. _..pisy vydav.prir.Fak. ..asaryk.Univ._ 239: 1 - 12.

(1938). ohlavni dvojtvarnost larev a ku..el pakomaru. _Spis vydav. rir.rak. ..asaryk.Univ._ 257: 1 - 23.

(1939). re..andibuly larev nekterych Nematocer II. _Vest. csl. ool...ol._ 6/7: 518 - 533.

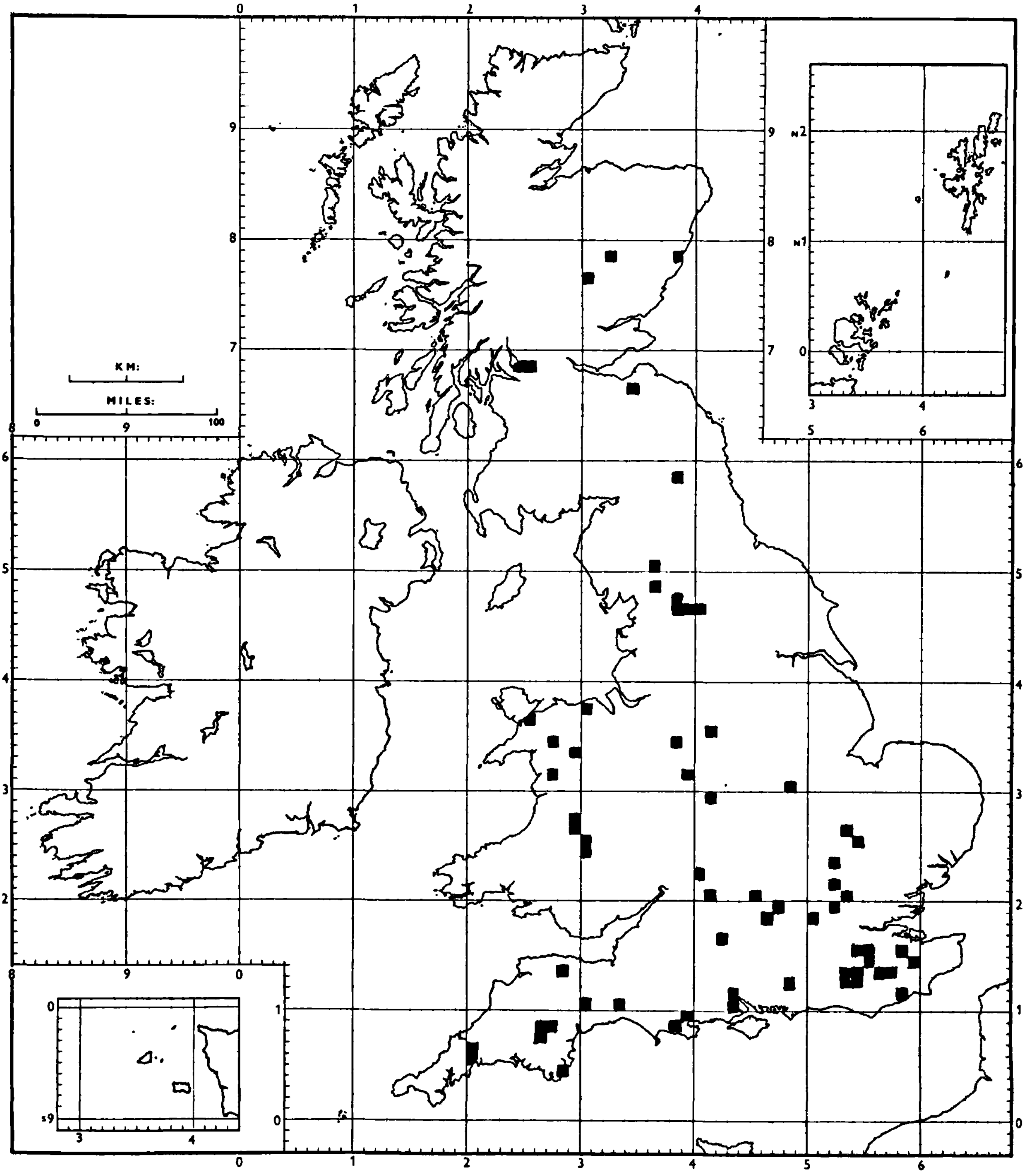
(1939a). hironomidarum larv e et nymphae II. (Genus _E..kiefferiella_ Th.). _Acta ..oc. ci.nat.moravo-siles._ 11: 1 - 29.

(1941). hironomidarum larvae et nymphae. IV. (..enus _Metriocnemus_ v.d. ulp.). _..cta ..oc. ci.nat.moravo-siles_ 13: 1 - 2..

ZETTERSTEDT, J. . (1°3). iptero..ogia candanaviae. Section 3 iptera, 477 - 868, in _Insecta Lapponica_ vi + 1140 pp. Leipzig.

(1850). _iptera Scandanaviae disposita et descripta._ IX. 3367 - 3710. Lund.

Appendix 1



Appendix 2

Range, Mean Body length

Head capsule

Antenna 1

2

3

4

5

6

7

A.R.

Spine

Subsid[i]ary

Distance to R.O.

Mandible l.

SSd

Si

Labrum S1

S2

S3

S4
Labral setae
Premandible

Mentum width

Hind PP

A.T,

Procercus h.

width

No of setae
Length (max)

Lateral setae

Supra-anal seta

Claws Hind Fore Hc colour

Figure 1

a. Arrangement of parts on a slide.

Abbreviations:

a. - abdomen

d. - collecting data

det. - determination

h. - head and antennae.

l. - legs from one side of body

la. - larva, head capsule and exuvium.

p. - pupal exuvium.

th. - thorax with legs from one side of body attached

w. - wings

b. Whole larva. Lateral view of *Eukiefferiella claripennis* (Lundbeck). (4th instar).

Abbreviations:

a.p. - anterior parapod

h. - head

p.p. - posterior parapod.

th. - thoracic segments (swollen in fourth instar)

c. Ventral view of head capsule of *Eukiefferiella brevicalcar* (Kieffer). Right mandible and maxilla removed.

Abbreviations:

a. - antenna.

l. - labrum.

m. - mandible.

ma. - maxilla.

me. - mentum

o.m. - occipital margin

p.m. - postmentum

Fig. 1

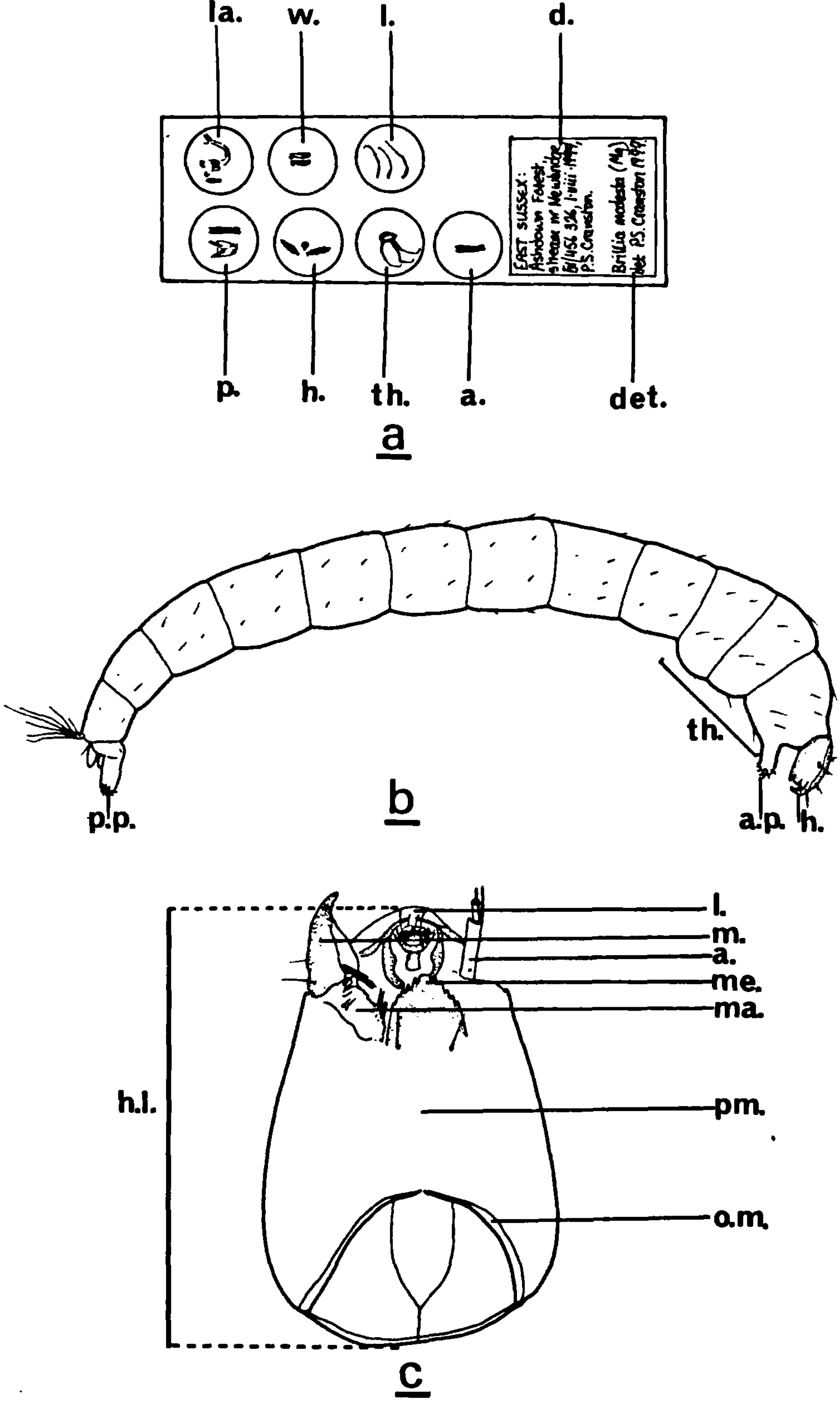


Figure 2

a. Frontoclypeus, labrum and palatum of *Psectrocladius psilopterus* Kieffer, dorsal view.

Abbreviations:

f.c. - frontoclypeus.

l. - labrum

l.m. - labral margin.

p. - palatum.

b. Labrum and palatum of *P. psilopterus* Kieffer, dorsal view with palatum lifted to same plane.

Abbreviations:

ch.l. - chaetulae laterales.

ch.b. - chaetulae basales.

l.ch. - labral chaetae.

l.m. - labral margin.

p.e. - pecten epipharyngis.

pm. - premandible.

SI - anterior seta of the labrum

SII - posterior seta of labrum.

SIII - smaller seta of labrum.

SIV - bisensillum of labrum.

u. - ungula.

Fig. 2

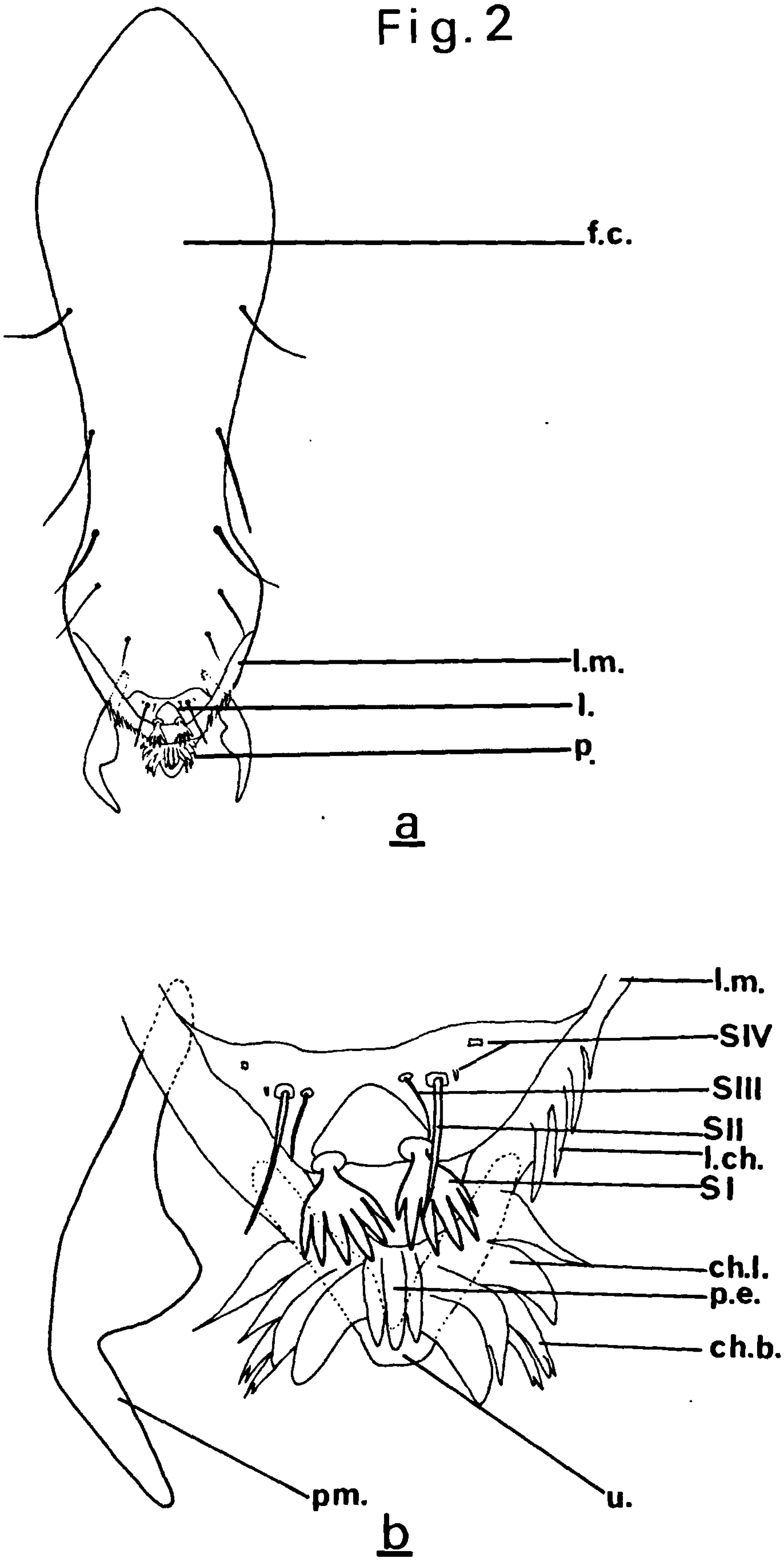


Figure 3

a. Antenna of *Cricotopus sylvestris* (Fabricius).

Abbreviations:

a.s. - antennal spine.

i.m. - intersegmental membrane.

L.o. - Lauterborn organ.

r.o. - ring organ.

s.l. - segment length.

s.s. - subsidiary spine.

b. Mandible of *Brillia modesta* (Meigen).

Abbreviations:

a. - length of apical tooth.

i. - combined width of inner teeth.

i.m. - inner margin of mandible.

s.i. - seta interna.

s.sd. - seta subdentalis.

Fig.3

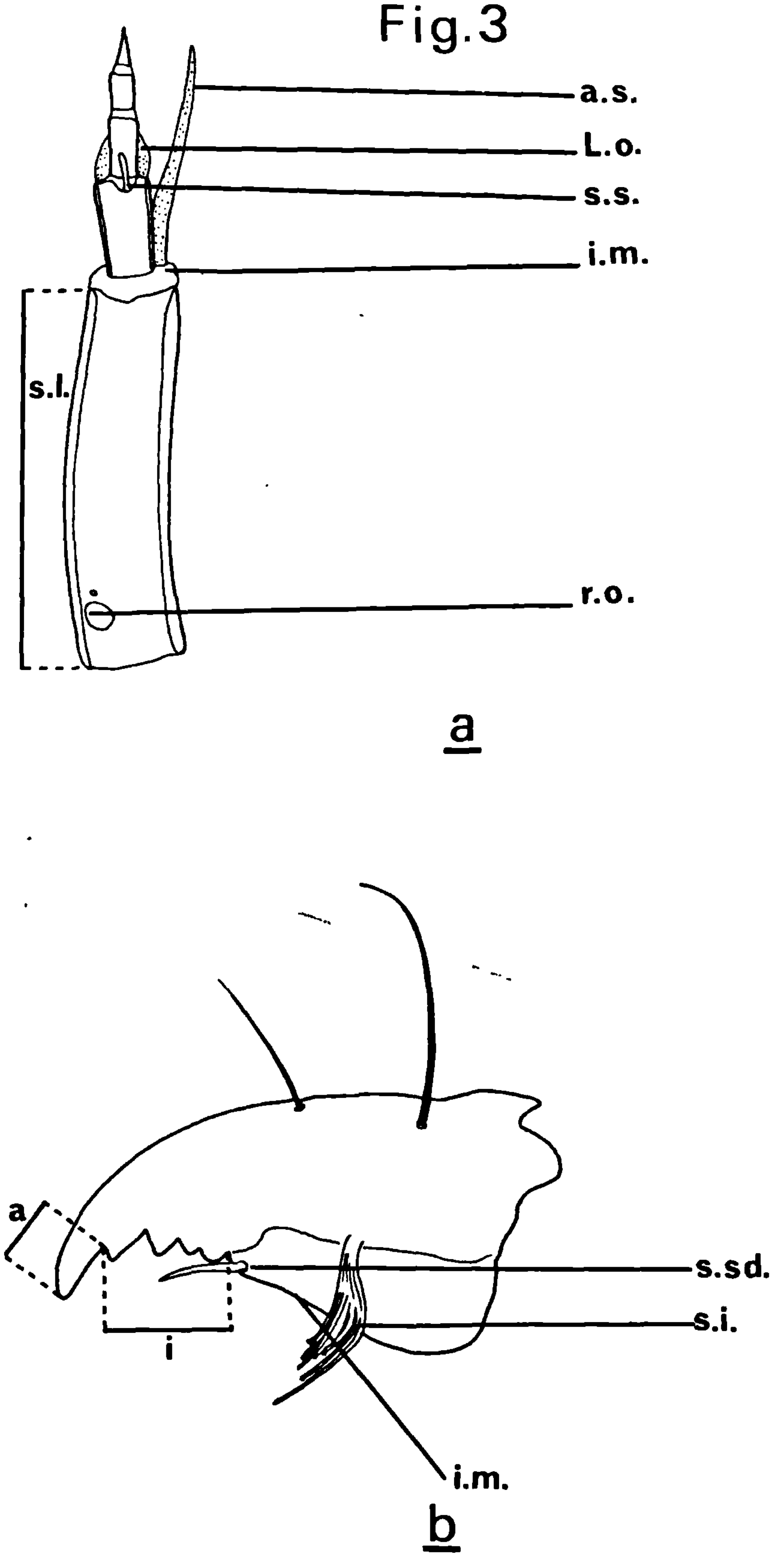


Figure 4

a. Maxilla of *Acricotopus* lucens (Zetterstedt).
Ventral view of left maxilla.

Abbreviations:

a. - appendix.

a.s. - apical seta of palpiger ("a" seta).

b. - sensilla basiconica.

g.l. - galear lamellae.

l.p. - (tetrahedral) lamellae on palpiger.

m.s. - maxillary setae.

p. - palpiger.

p.g. - pecten galearis.

r.o. - ring organ on palpiger.

b. Mentum of *Rheocricotopus fuscipes* (Kieffer).
Ventral view.

Abbreviations:

m. - mentum.

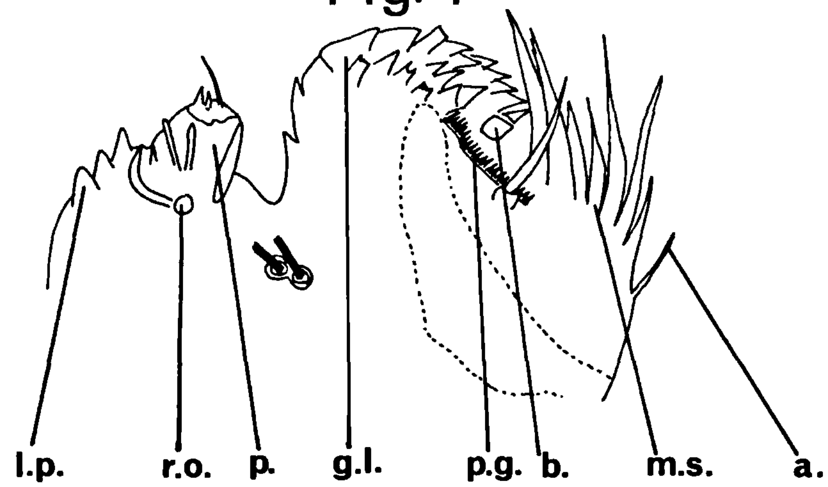
m.s. - seta at base of mentum.

m.w. - width of flattened mentum.

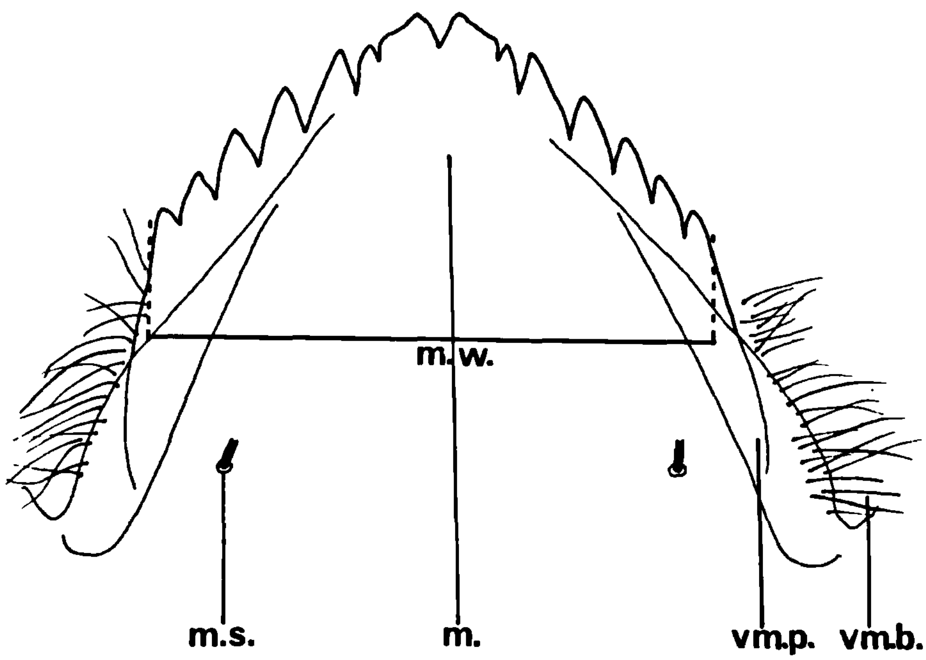
vm.b. - ventromental beard.

vm.p. - ventromental plates.

Fig. 4



a



b

Figure 5

a. Posterior segments of _Eukiefferiella minor_ (Edwards). Lateral view.

Abbreviations:

at. - anal tubule.

a. - length of posterior parapod.

b. - length of anal tubule.

c. - length of apical seta of procercus.

cl. - claws of posterior parapod.

p. - procercus.

p.p. - posterior parapod.

s.s. - supra-anal seta.

b. Procercus of _Psectrocladius psilopterus_ (Kieffer). Lateral view.

Abbreviations:

a.s. - apical seta of procercus.

h. - height of procercus.

l.l.s. - lower lateral seta of procercus.

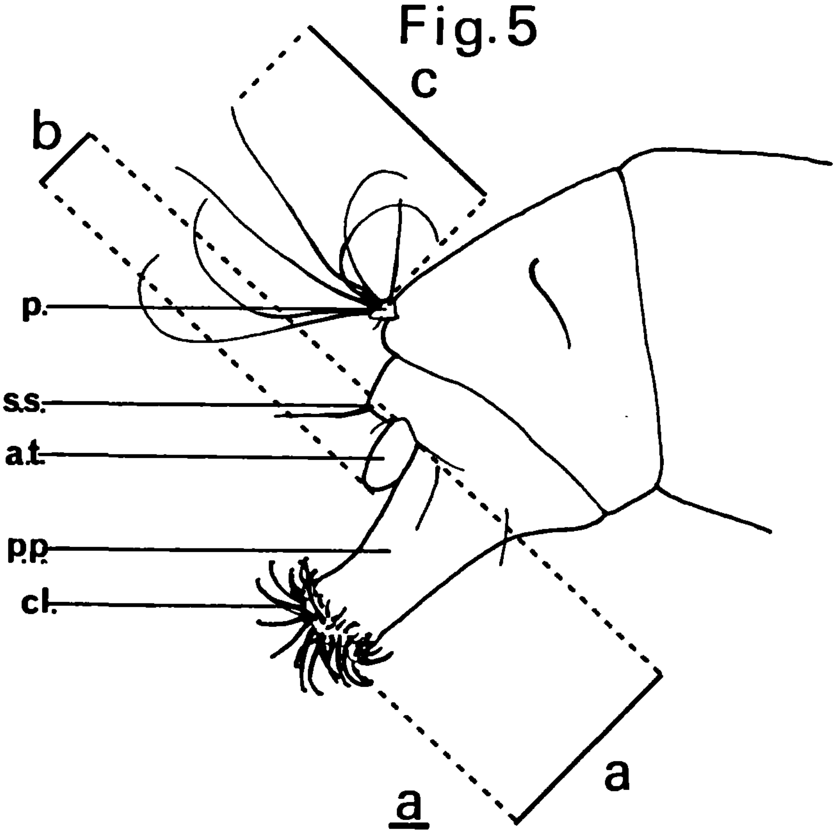
p. - procercus.

sp. - spurs on procercus.

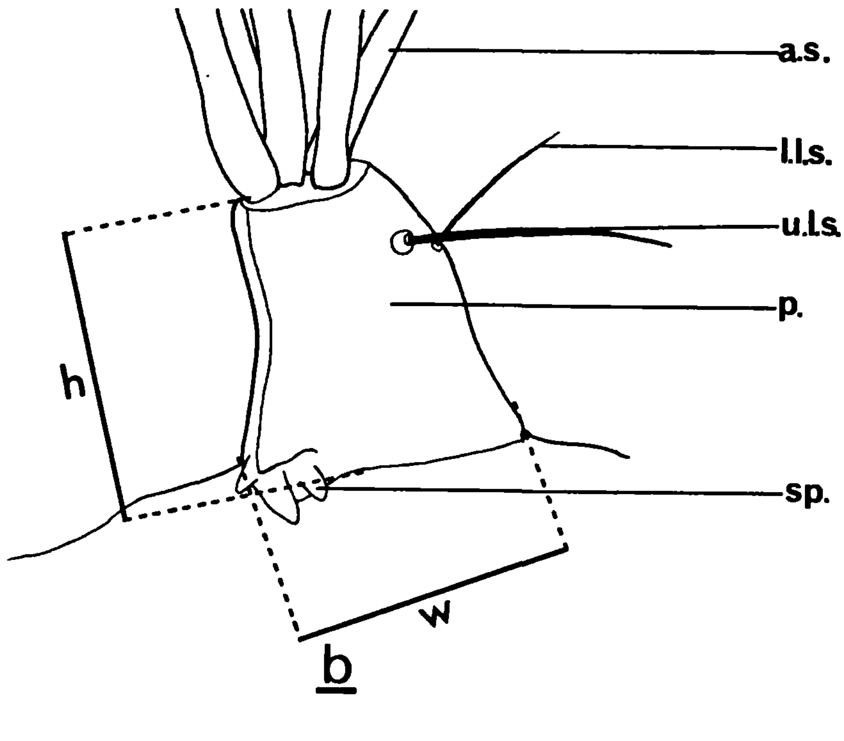
u.l.s. - upper lateral seta of procercus.

w. - width ~~of~~ procercus.

Fig. 5



a



b

Figure 6

Acricotopus lucens (Zetterstedt)

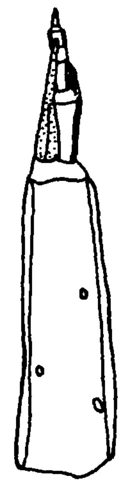
a - Antenna (Cil)

b - Labrum & palatum (Cil)

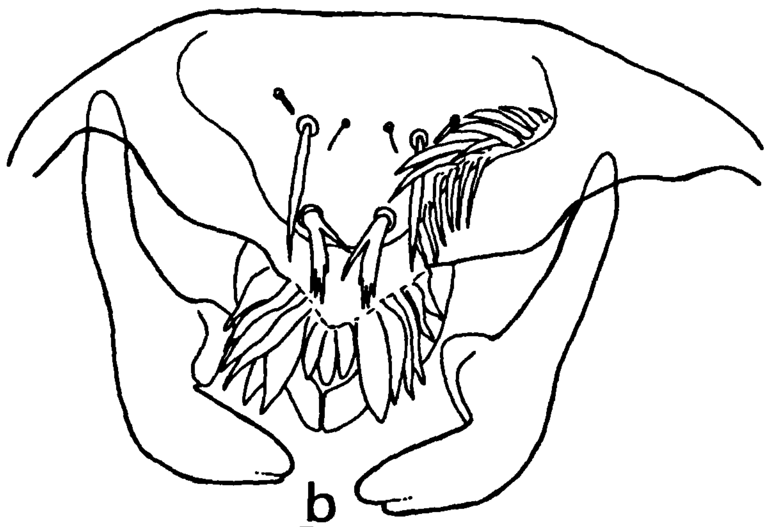
c - Mandible (Cil)

d - Mentum (Cil)

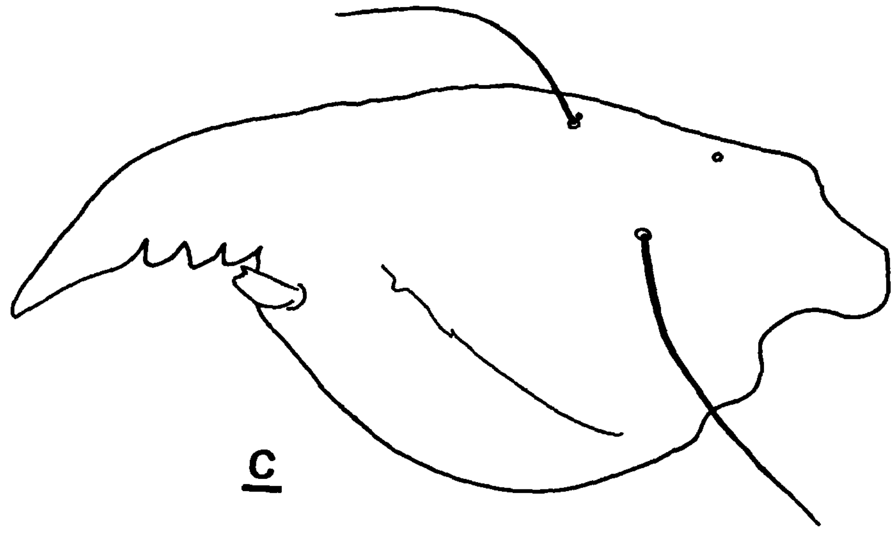
Fig. 6



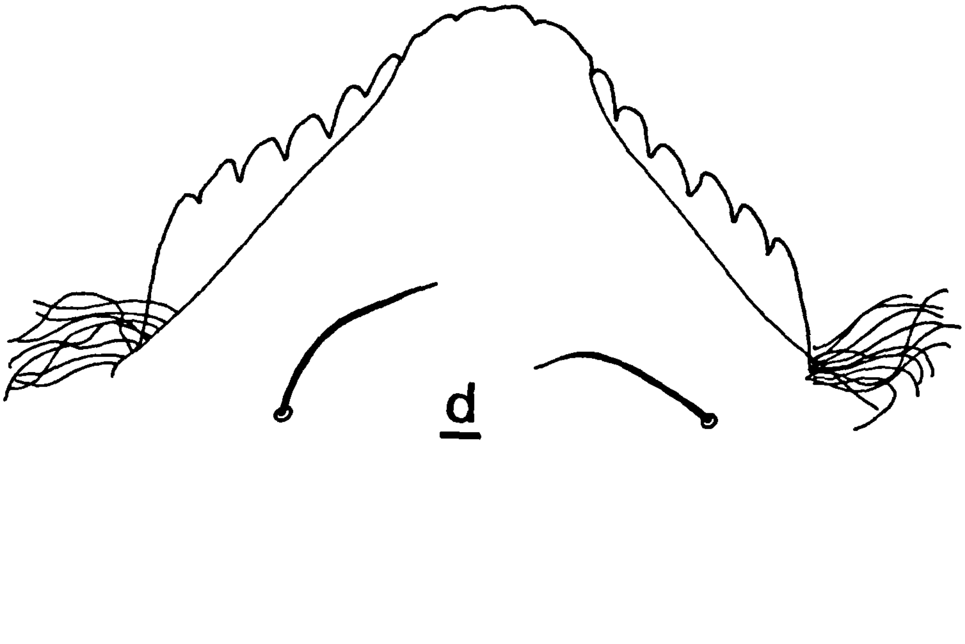
a



b



c



d

Figure 7

Brillia modesta (Meigen)

a - Antenna (oil)

b - Mentum and postmentum (100)

c - Dorsal area of head and labrum (400)

d - Labrum and palatum (Oil)

e - Mandible (400)

f - Mentum (400)

g - Maxilla (Oil)

Fig. 7

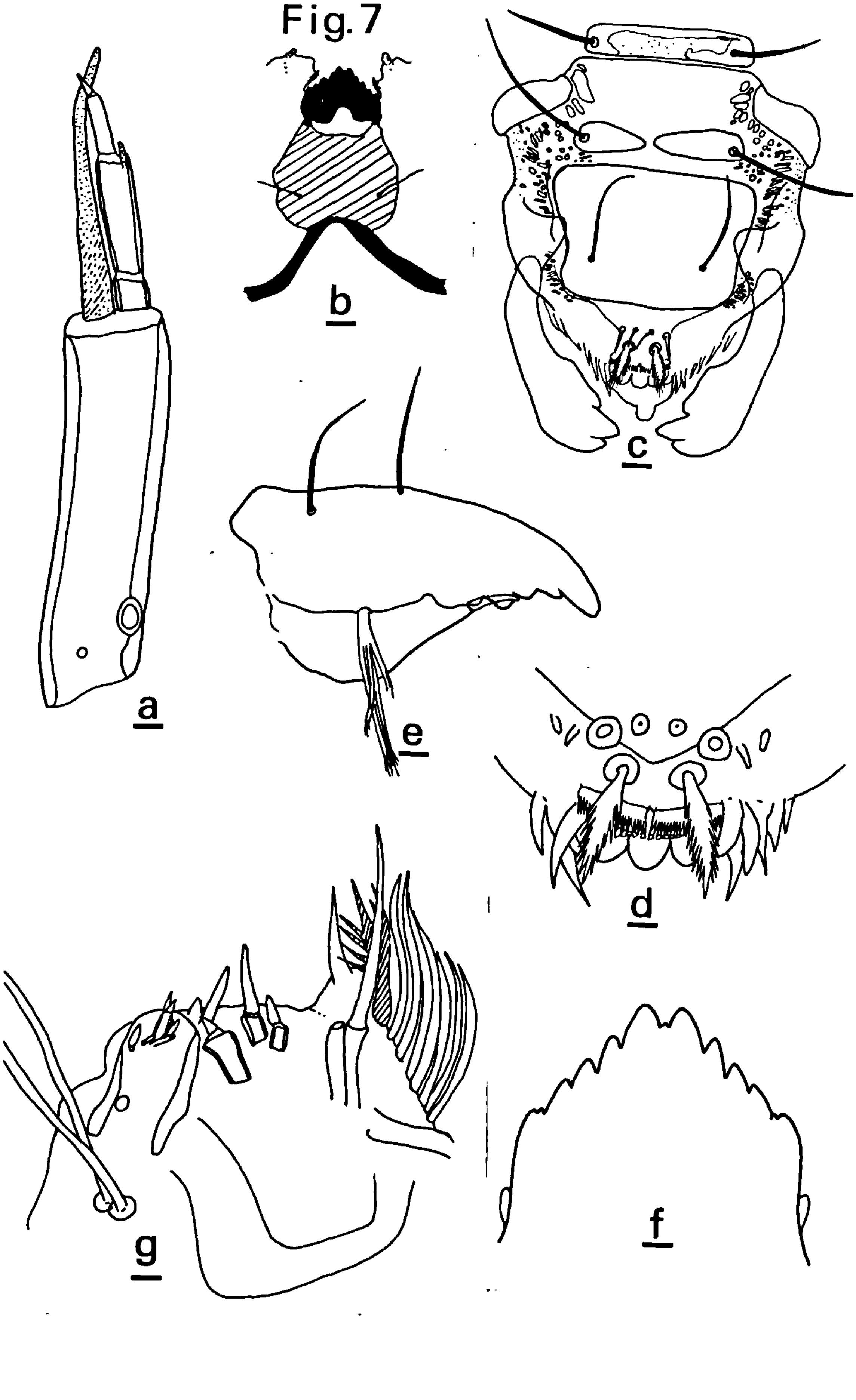


Figure 8

Bryophaenocladius

a. - Antenna of *B. xanthogyne* (Edwards). (Oil).

b. - Antenna of *B. subvernalis* (Edwards). (Oil).

c. - Labrum, palatum of *xanthogyne* (Edw).
(Oil, composite drawing).

d. - Mentum of *subvernalis* (Edw). (400)

e. - Mentum of *xanthogyne* (Edw). (400)

f. - Mandible of *xanthogyne* (Edw). (400)

g. - Posterior segments of *Bryophaenocladius muscicola* (Kieffer), det Thienemann (100)

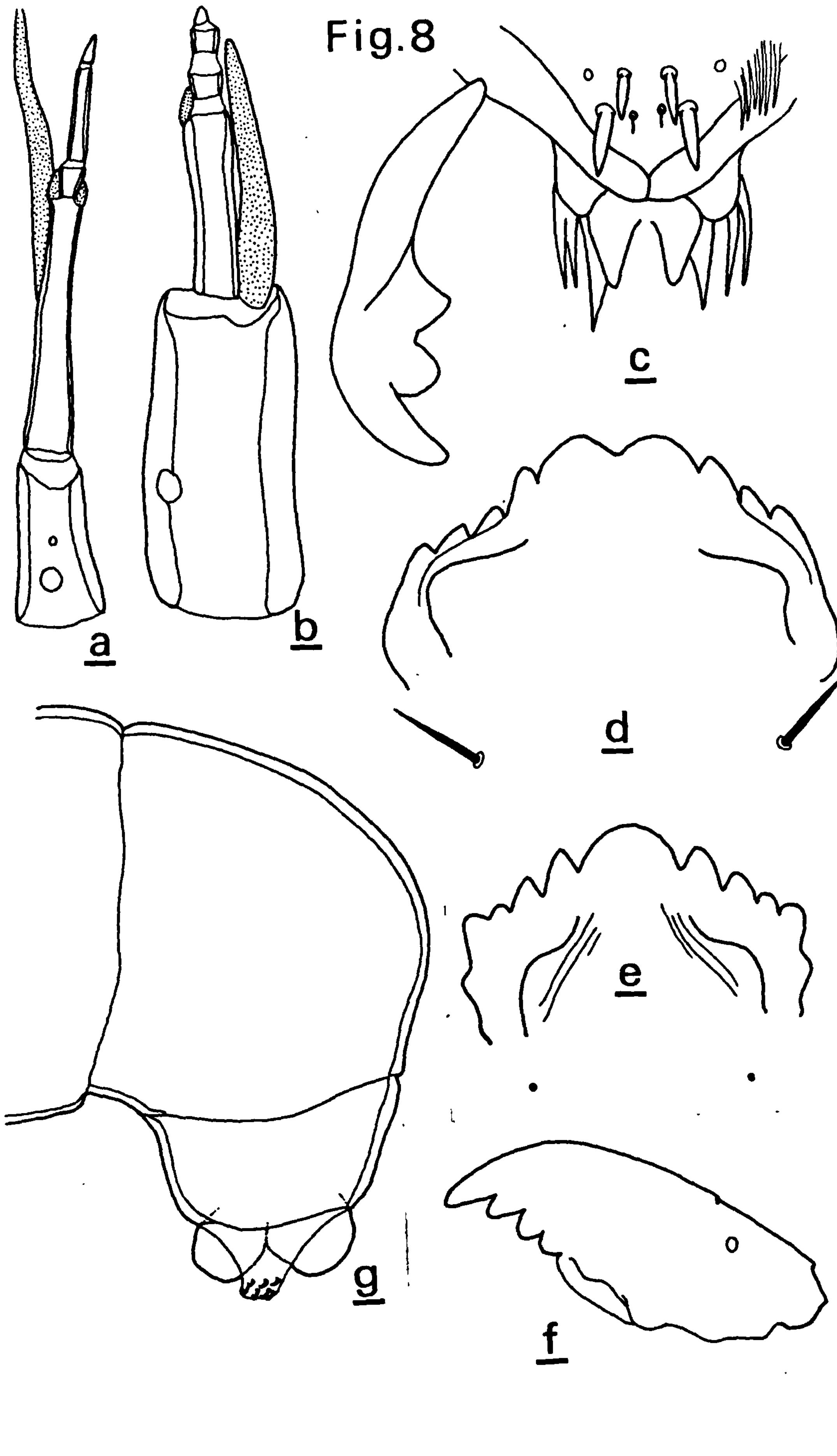


Fig.8
a
b
c
d
e
f
g

Figure 9

Camptocladius stercorarius Degeer

a - Right antenna, dorsal view (O11)

b - Labrum (O11)

c - Head and anterior parapods (100)

d - Anterior end (100)

e - Mentum (400)

f - Mandible (400)

g - Maxilla (O11)

Fig. 9

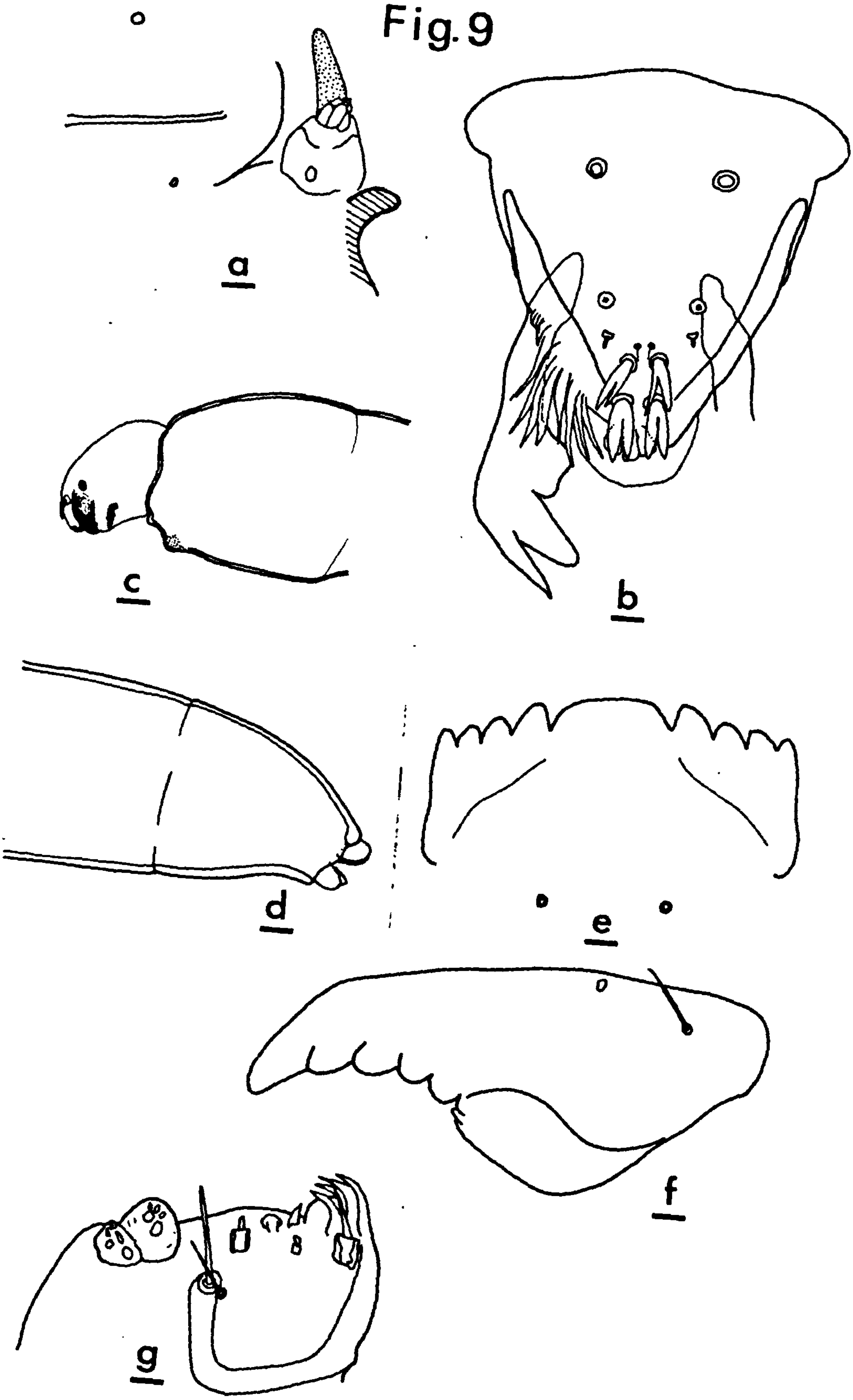


Figure 10

Cardiocladius

a - Antenna of *fuscus* (Oil)

b - Mandible of *fuscus* (400)

c - Mandible of *capucinus* (400), tilted slightly

d - Labrum and palatum of *fuscus* (Oil)

e - Mentum of *fuscus* (400)
(The least worn of four specimens but some wear particularly on first two pairs of lateral teeth)

f - Mentum of *capucinus* (unworn) (400)

Fig. 10

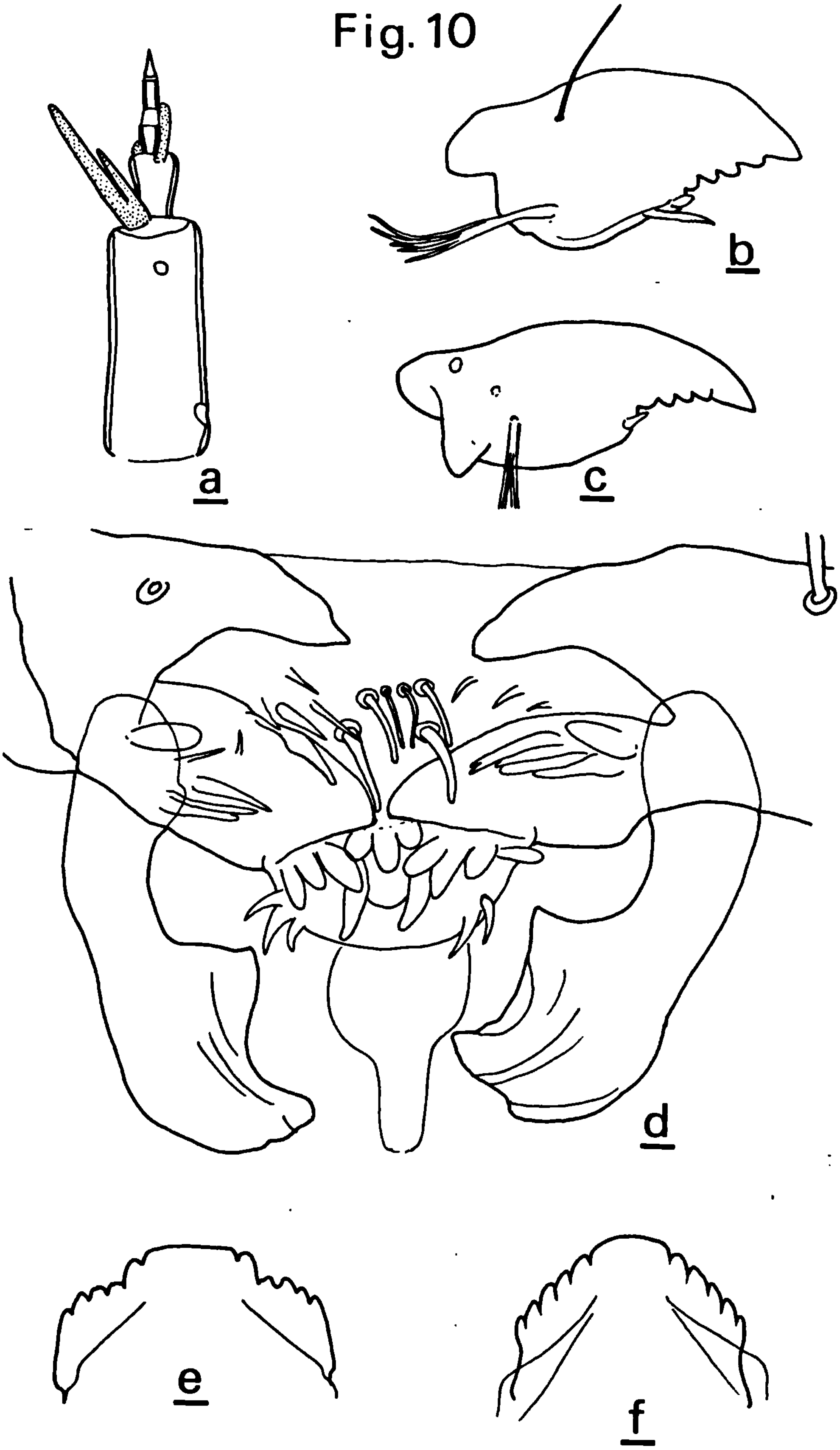


Figure 11

Chaetocladius

a. - Antenna of *suecicus* (Kieffer)(011)

b. - Labrum of *suecicus* (Kieffer), right SI not drawn (011)

c. - SI and labral lamellae of *dentiforceps* (Edwards) 2 (011)

d. - Mandible of *suecicus* (Kieffer) (400)

e. - Mentum of *suecicus* (Kieffer) (400)

f. - Maxilla of *suecicus* (Kieffer) (400)

1 *suecicus* drawn from material identified by Thienemann.

2 *dentiforceps* drawn from larva "associated" with adult *dentiforceps* determined Cranston.

Fig. 11

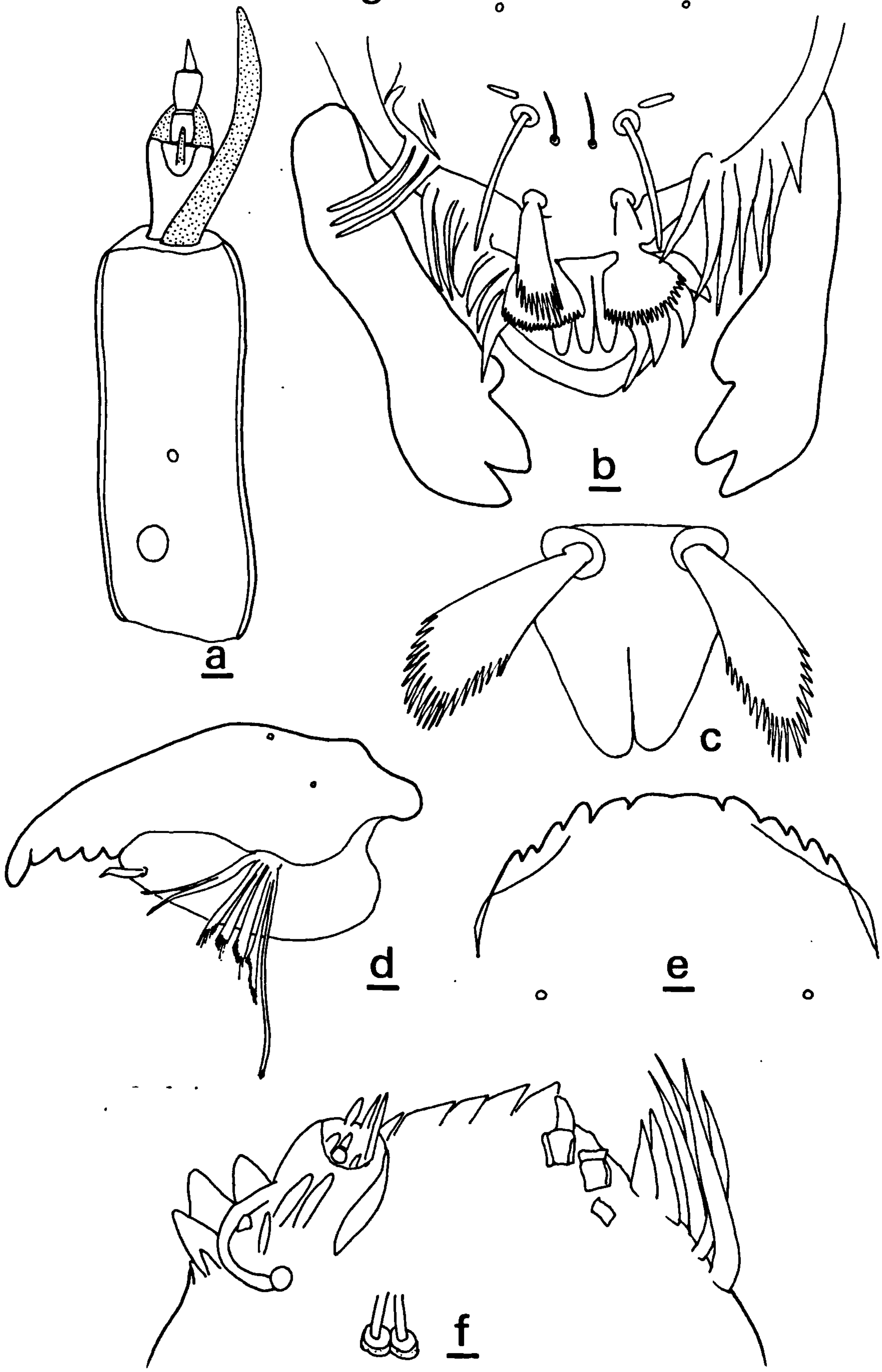


Figure 12

Clunio marinus Haliday

a. - Antenna (011)

b. - Labrum, palatum and premandibles (011).
(Premandibles with single apical tooth pointing upwards)

c. - Mandible (400)

d. - Mentum (400)

e. - Posterior segments (400)

Figure 13

Corynoneura

a. - Antenna of *C. lobata* (Edwards). (400)

b. - Dorsal view of head capsule of *Corynoneura scutellata* Winnertz. (200).

c. - Mandible of *Corynoneura lacustris* Edwards (011).

d. - Spine on ventral base of posterior parapod of *C. lobata* (011).

Fig.12

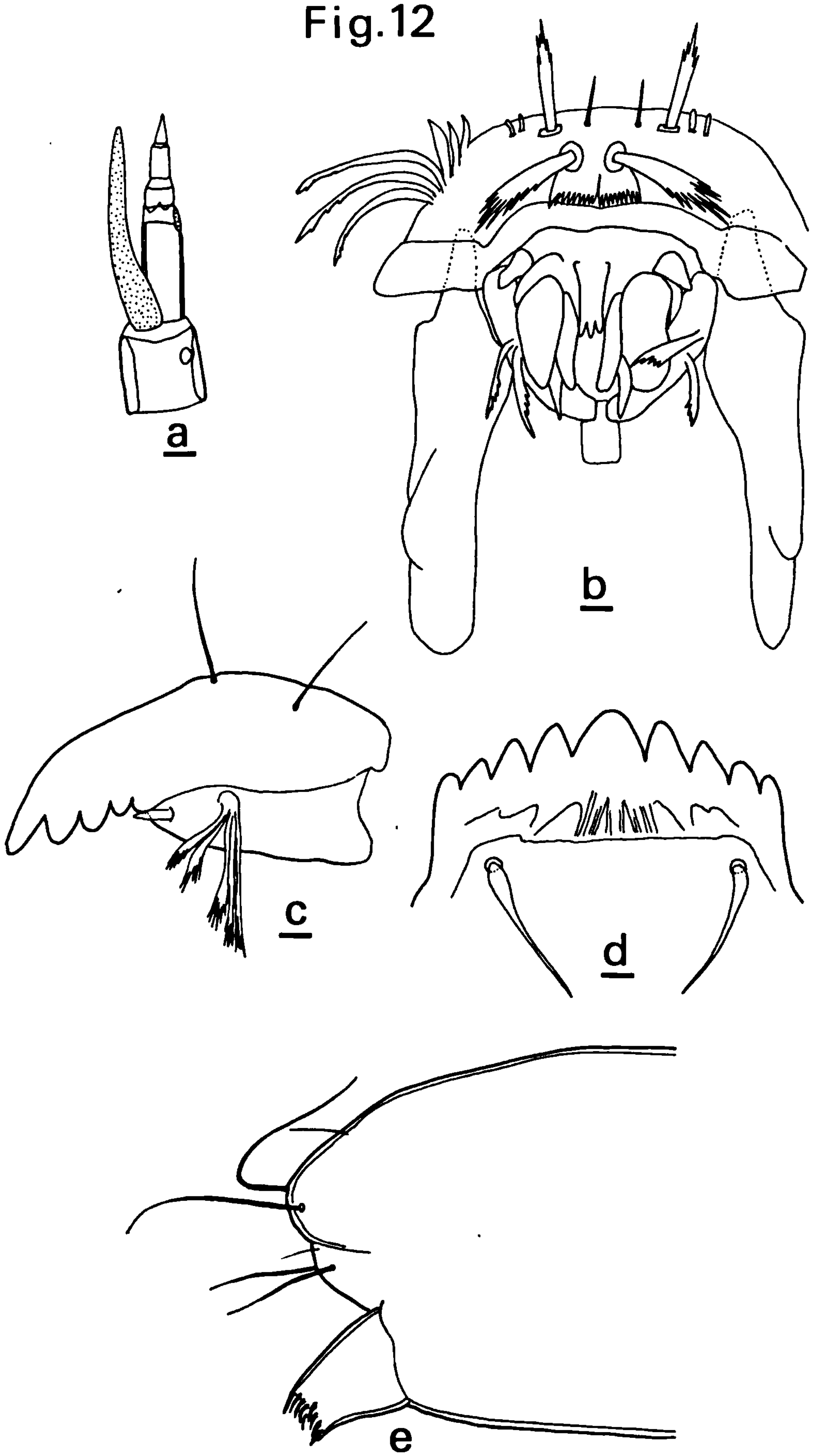


Fig.13

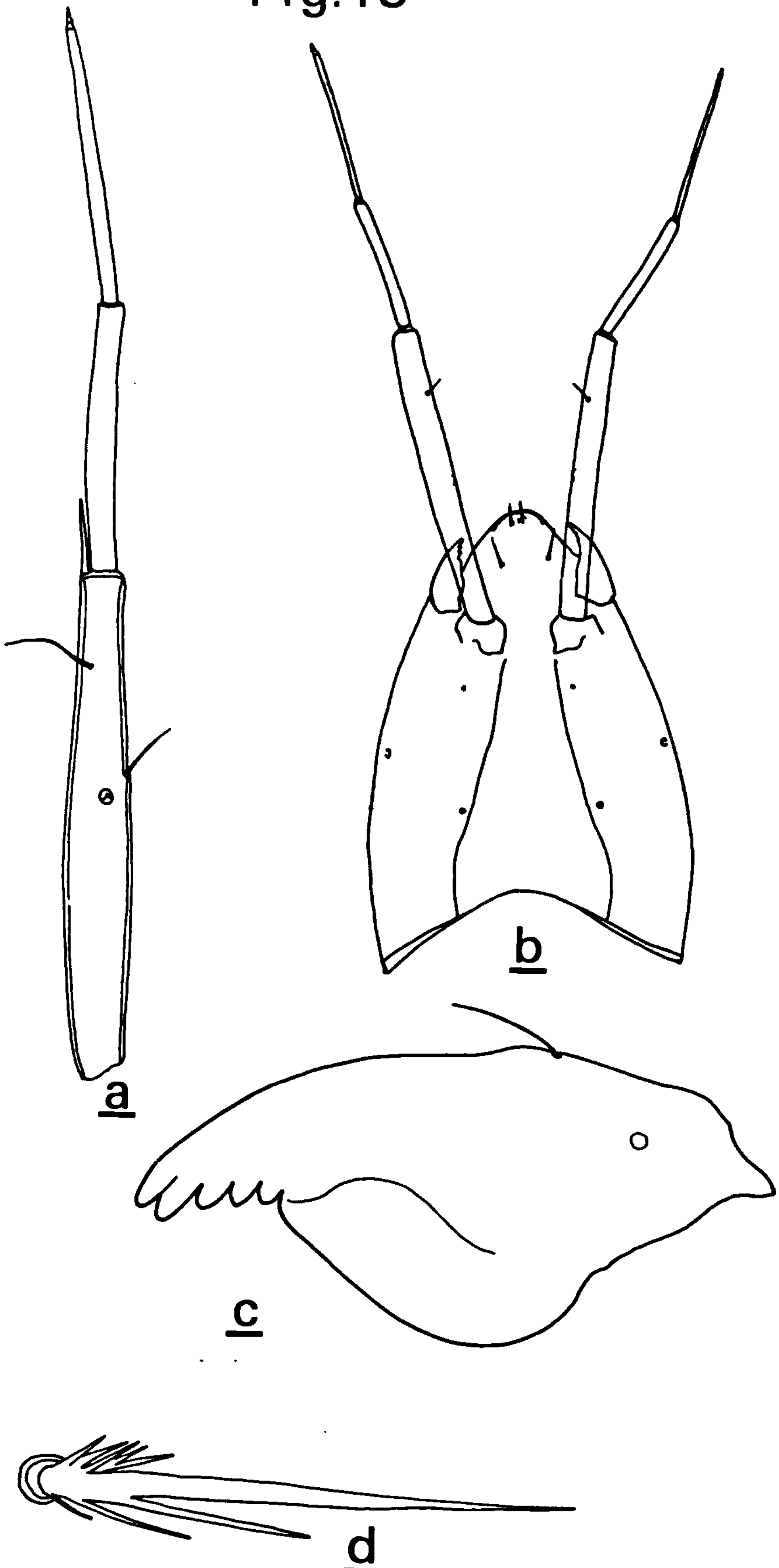


Figure 14

Corynoneura

a. - Labrum of *Corynoneura lacustris* Edwards (Oil)

b. - Palatum of *Corynoneura coronata* Edwards (Oil)

c. - Premandible of *Corynoneura lacustris* Edwards (flattened and partially rotated) (Oil)

d. - Dorsal head capsule sculpturing of *Corynoneura coronata* Edwards (Oil, ph se contrast)

e. - Dorsal head capsule sculpturing of *Corynoneura scutellata* Winnertz (Oil, phase contrast)

Fig. 14

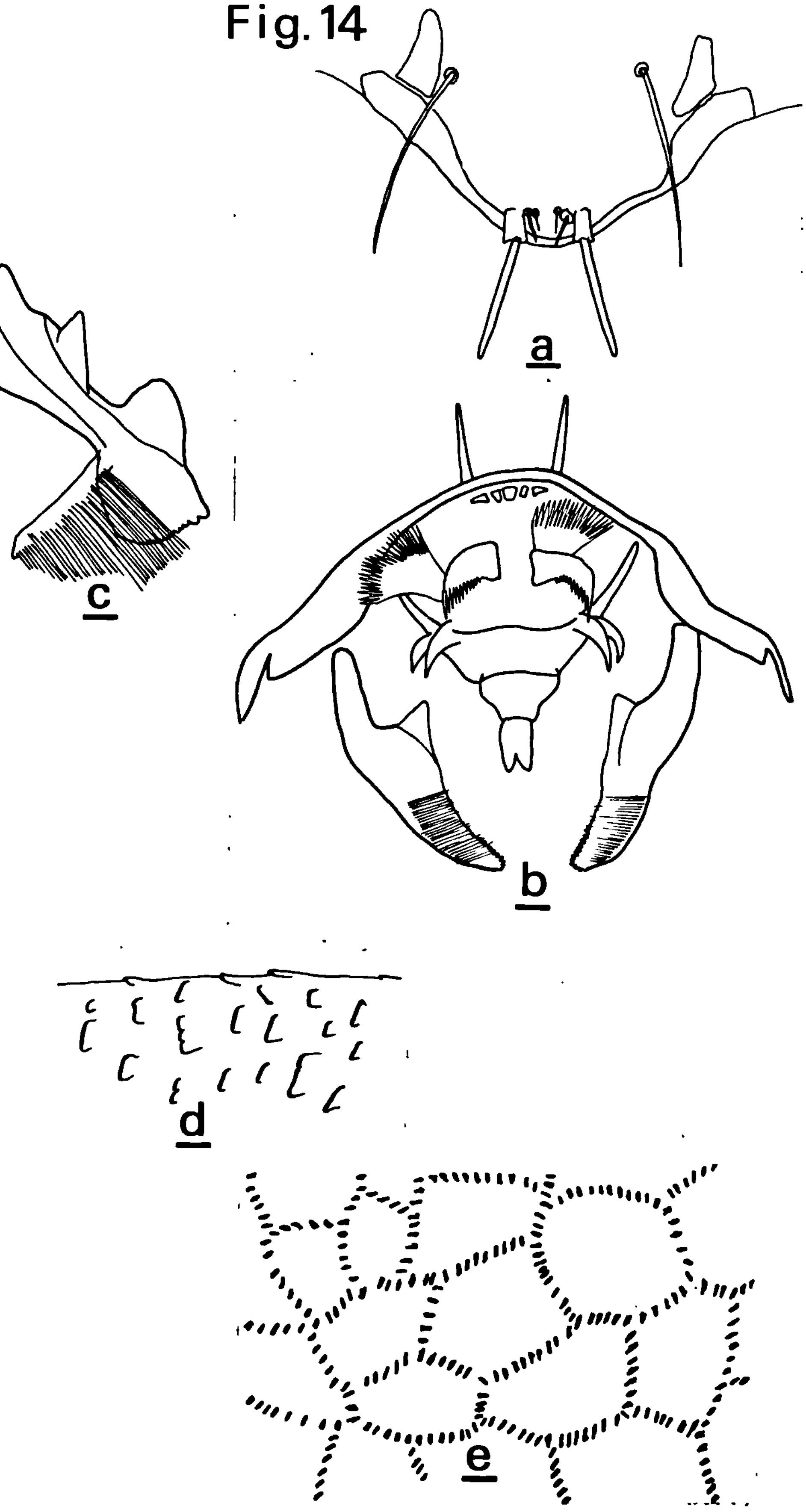


Figure 15

Corynoneura

a. - Mentum of Corynoneura coronata Edwards (011)

b. - Mentum of Corynoneura lacustris Edwards (011)

c. - Mentum of Corynoneura lobata Edwards (011)

d. - Mentum of Corynoneura scutellata Winnertz (011)

e. - Mentum of Corynoneura species A (011)

Fig. 15

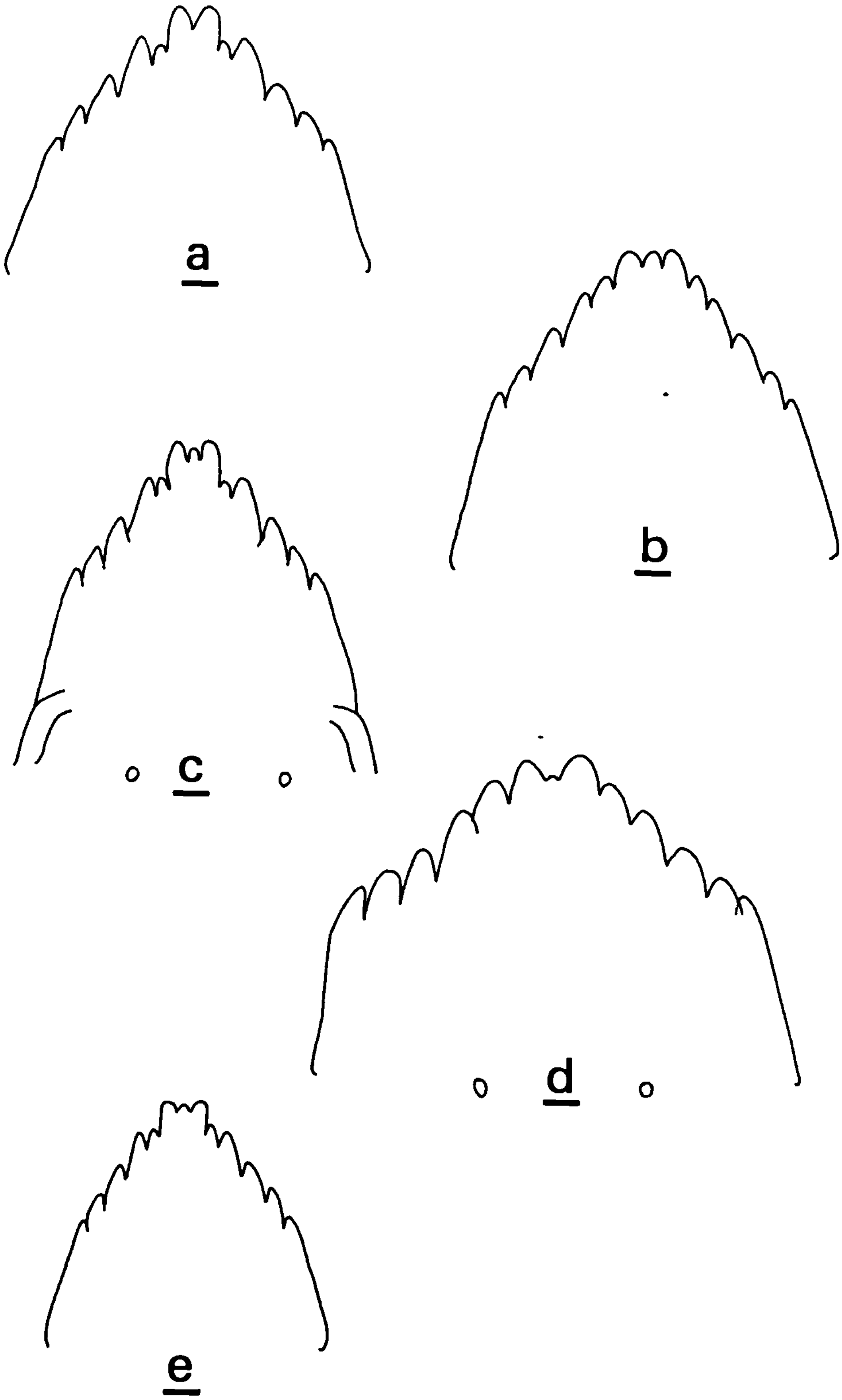


Figure 16

Cricotopus (Cricotopus)

a. - Antenna of C.(C.) albiforceps (Kieffer). (011)

b. - Mentum of C. (C.) albiforceps (Kieffer). (400)

c. - Mentum of C.(C.) annulator Goetghebuer. (400)

d. - Mandible of C.(C.) annulator Goetghebuer. (400)

e. - Antenna of C.(C.) annulator Goetghebuer. (011)

Fig. 16

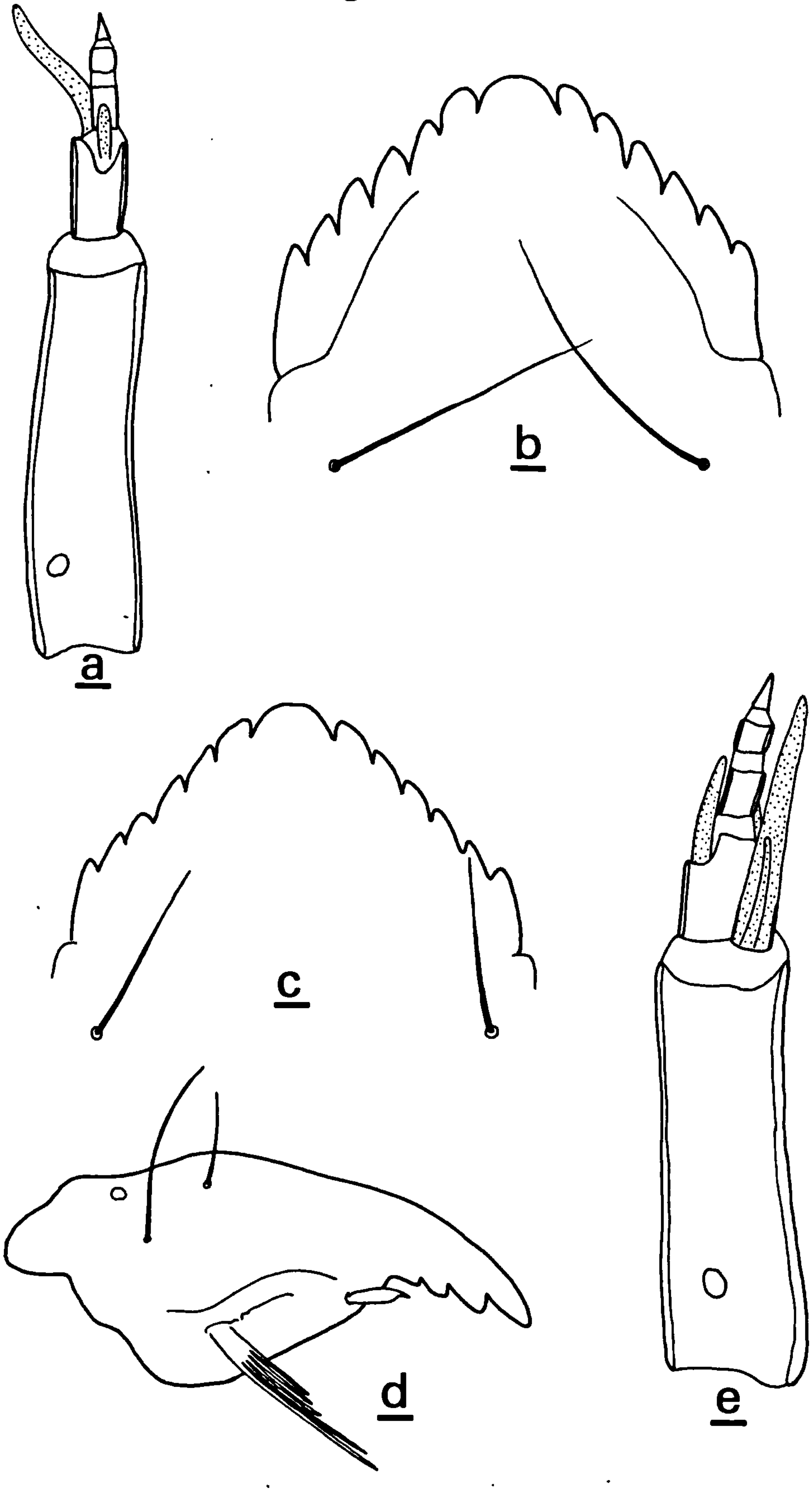


Figure 17

Cricotopus (Cricotopus) species A.

a. - Antenna (Oil)

b. - Labrum and palatum (400)

c. - Mandible (400)

d. - Mentum (400)

e. - Maxilla (Oil)

Fig.17

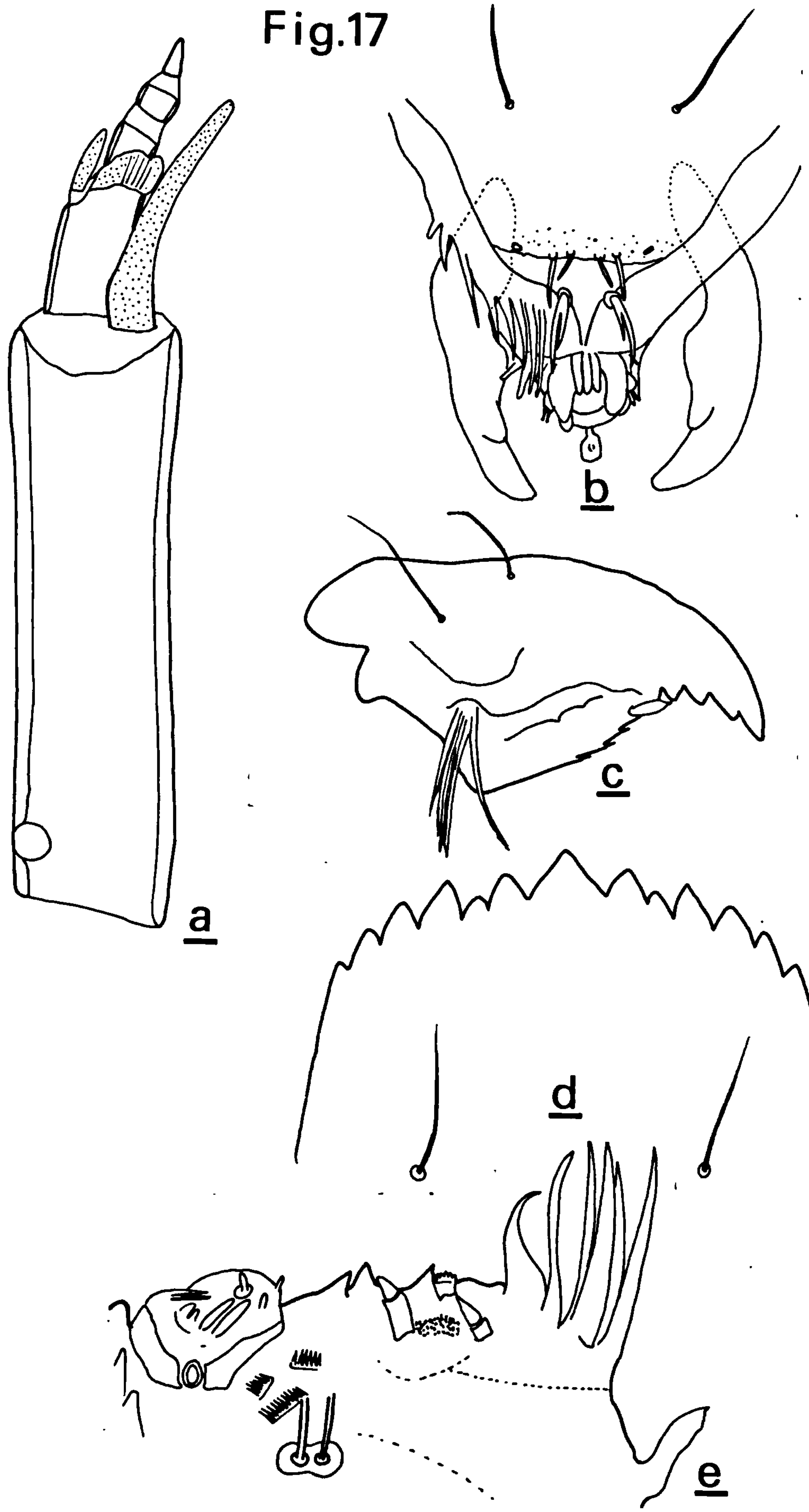


Figure 18

<u>Cricotopus</u> (<u>Cricotopus</u>)

a. - Antenna of <u>C</u>. (<u>C</u>.) <u>bicinctus</u> (Meigen). (011)

b. - Mentum of <u>C</u>. (<u>C</u>.) <u>bicinctus</u> (Meigen). (400)

c. - Mandible of <u>C</u>. (<u>C</u>.) <u>bicinctus</u> (Meigen). (400)

d. - Antenna of <u>C</u>. (<u>C</u>.) <u>fuscus</u> (Kieffer). (011)

e. - Mentum of <u>C</u>. (<u>C</u>.) <u>fuscus</u> (Kieffer). (400)

Fig.18

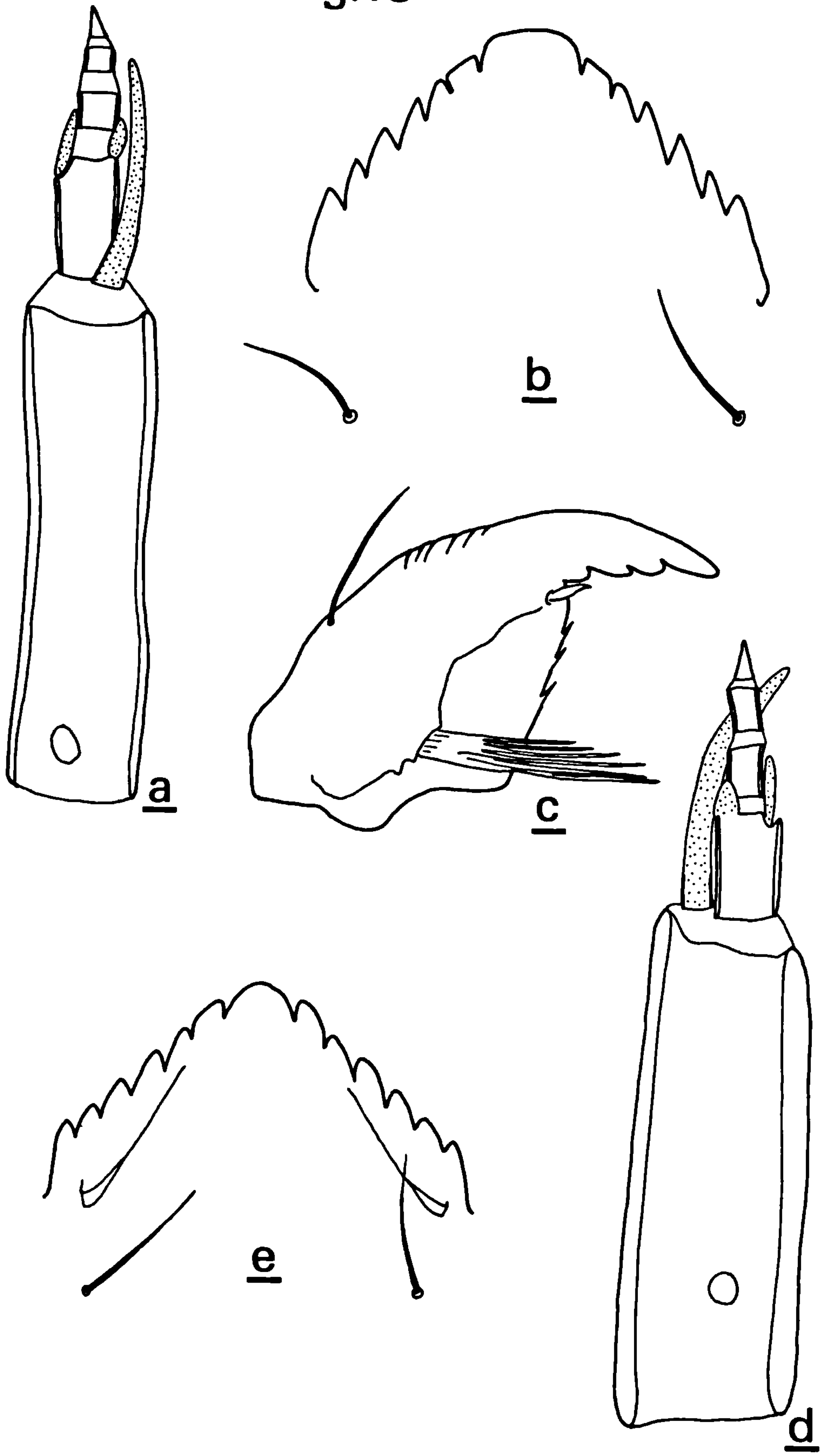


Figure 19

Cricotopus (*Cricotopus*) *pulchripes* Verrall

a. - Antenna (Oil)

b. - Labrum and palatum (without ungula and left premandible). (Oil)

c. - Mentum (400)

d. - Mandible (400)

e. - Maxilla (Oil)

f. - l_4 setal brush on abdominal segment IV

Fig.19

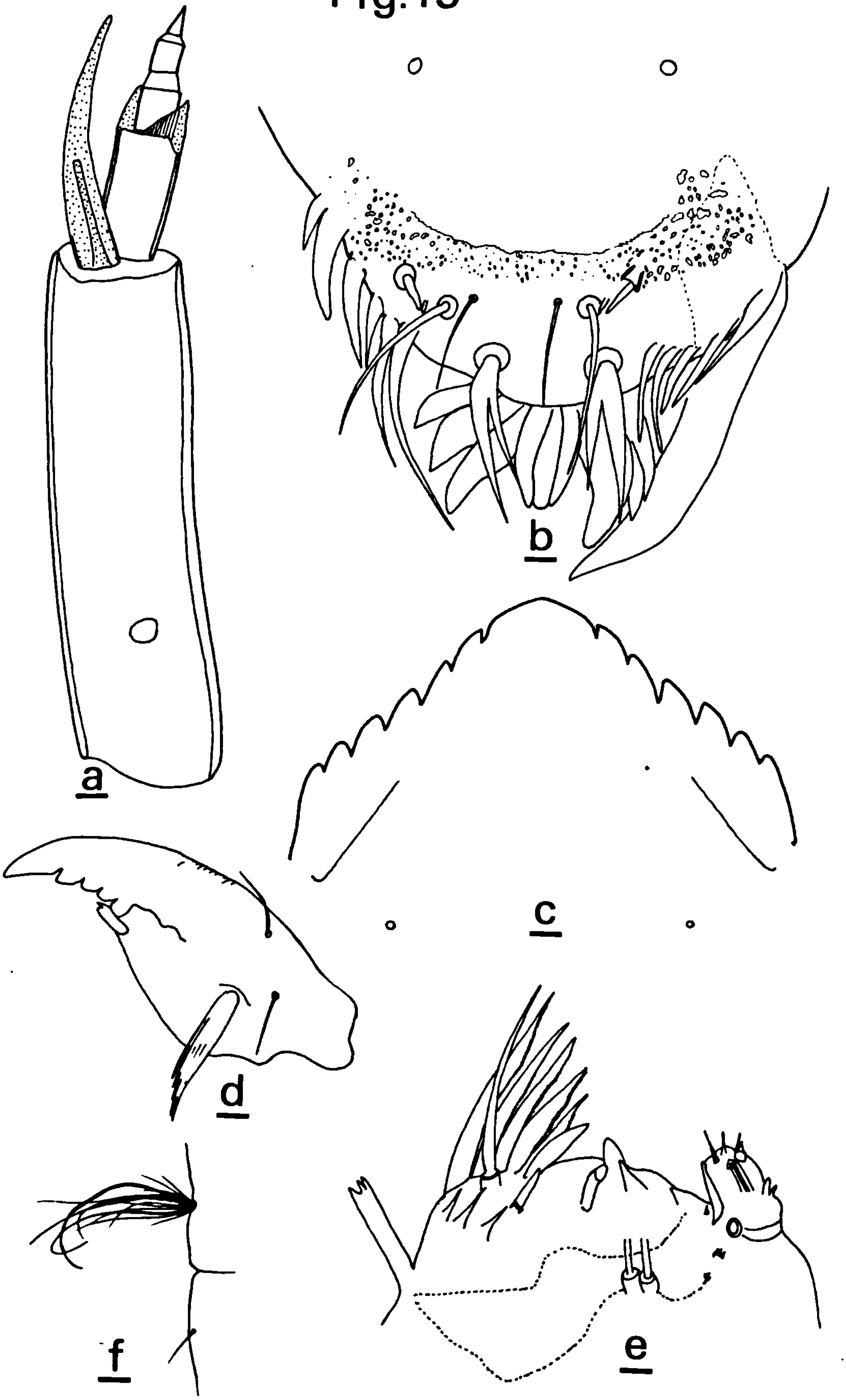


Figure 20

Cricotopus (Cricotopus)

a. - Antenna of C. (C.) triannulatus (Macquart). (Oil)

b. - Mentum of C. (C.) triannulatus. (400)

c. - Claws on anterior parapod of C. (C.) triannulatus. (Oil)

d. - Antenna of C. (C.) trifascia Edwards. (Oil, not same scale as Fig. 20a)

e. - Mentum of C. (C.) trifascia (400)

f. - Claws on anterior parapod of C. (C.) trifascia. (400)

Fig. 20

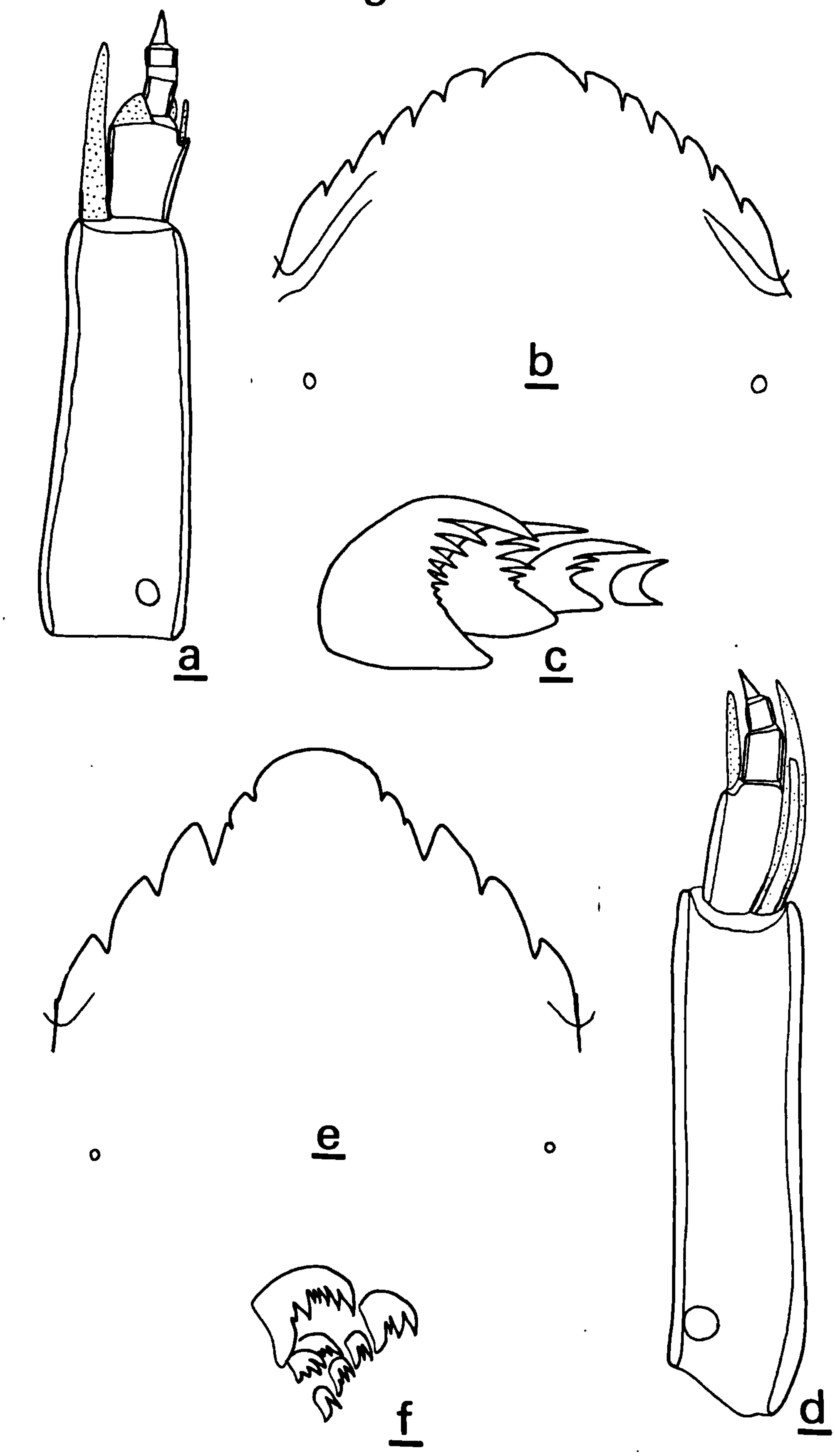


Figure 21

Cricotopus (*Isocladius*)

a. - Antenna of *Cricotopus* (*I.*) *brevipalpis* (Kieffer). (011)

b. - Mentum of *Cricotopus* (*I.*) *brevipalpis*. (400)

c. - Mandible of *Cricotopus* (*I.*) *brevipalpis*. (400)

d. - Mentum of *Cricotopus* (*I.*) *intersectus* (Staeger). (400)

e. - Mandible of *Cricotopus* (*I.*) *intersectus*. (400)

f. - Antenna of *Cricotopus* (*I.*) *intersectus*. (011)

Fig. 21

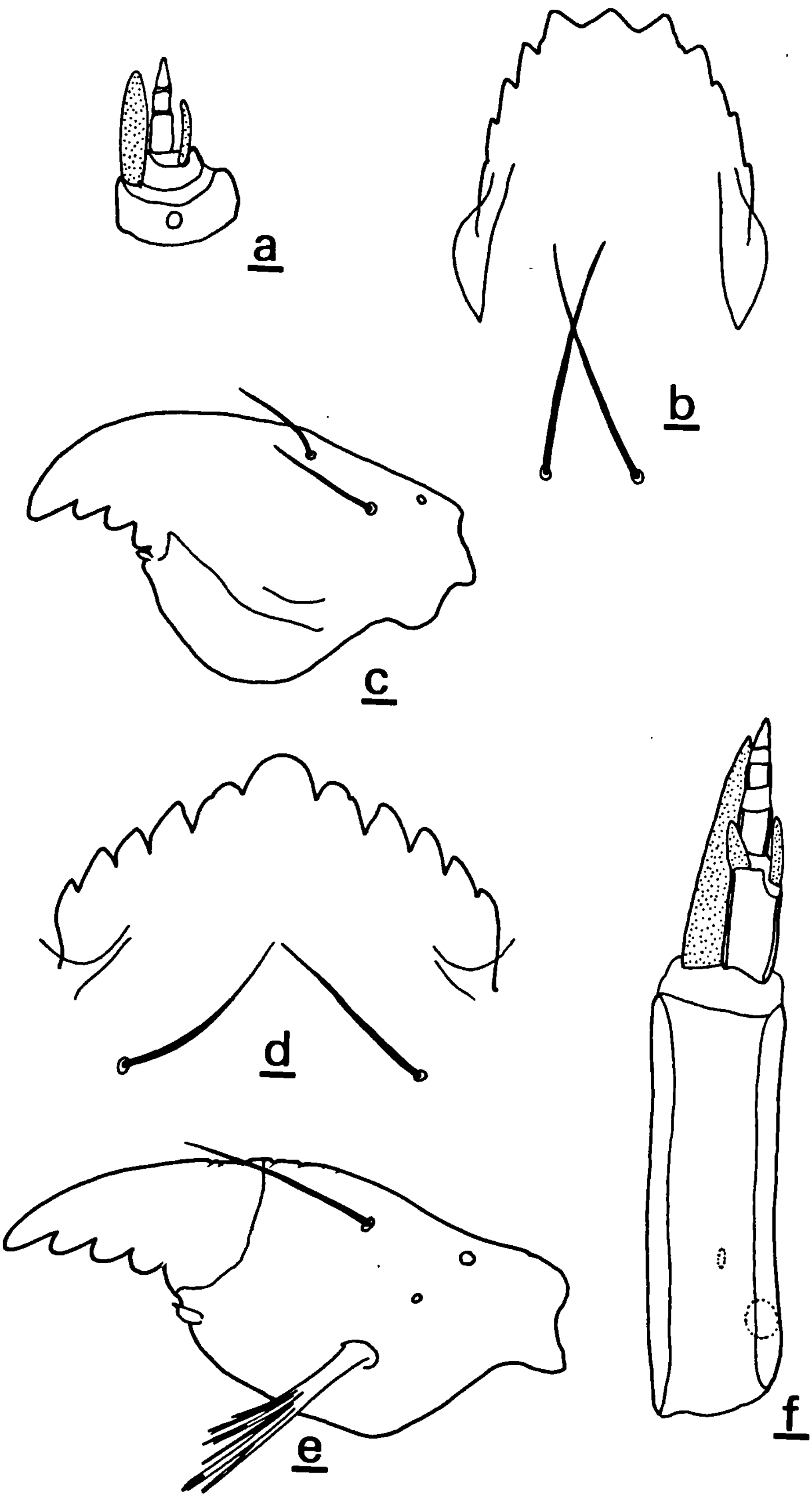


Figure 22

Cricotopus (*Isocladius*) *sylvestris* (Fabricius)

a. - Antenna of *C.* (*I.*) *sylvestris*. (011).

b. - Two views of premandible of *C.* (*I.*) *sylvestris*. (011)

c. - Mentum of *C.* (*I.*) *sylvestris*.(400)

d. - Mandible of *C.* (*I.*) *sylvestris*. (400)

e. - Claws of anterior parapod of *C.* (*I.*) *sylvestris*. (011).

Fig. 22

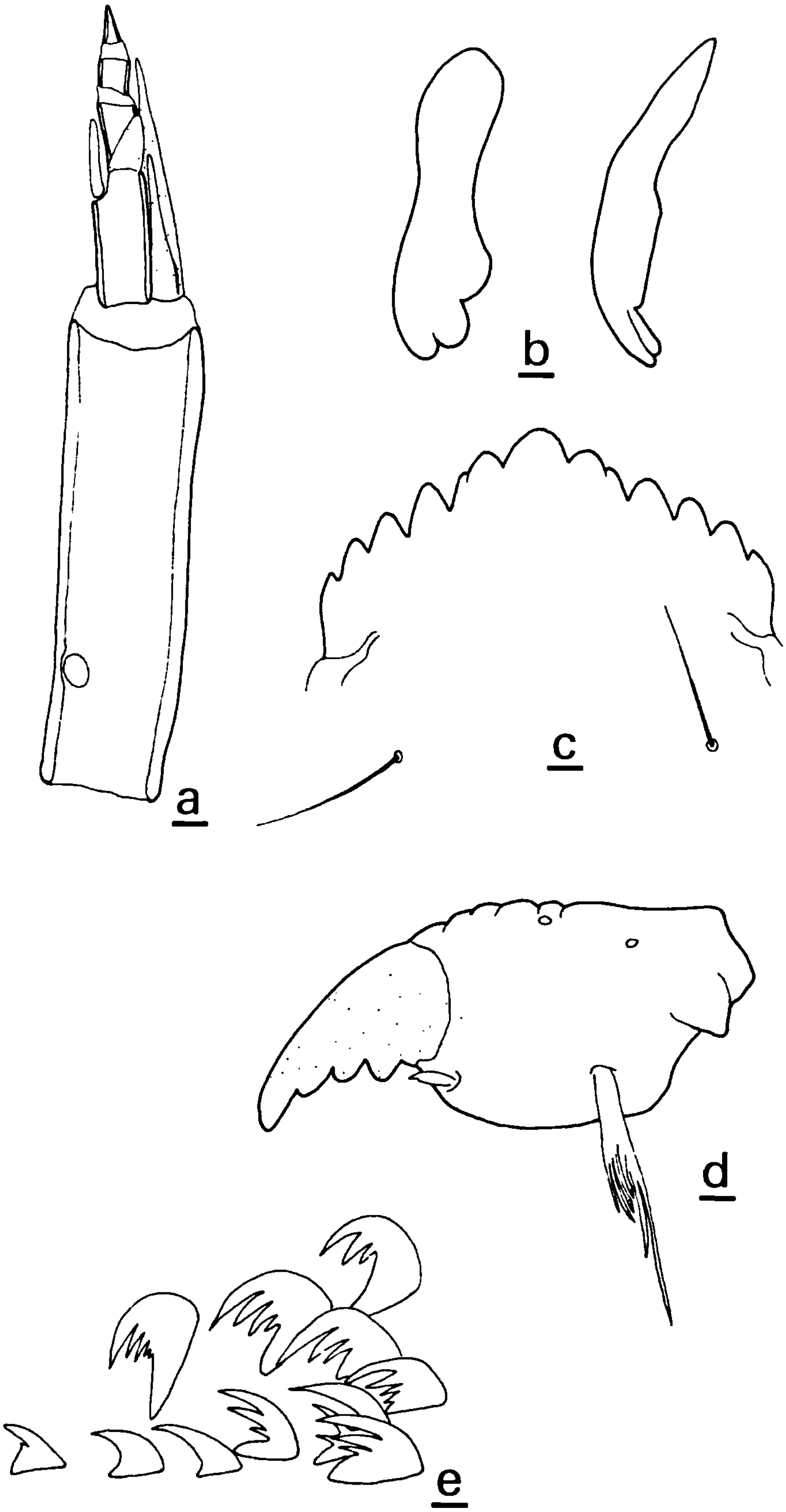


Figure 23

Cricotopus (*Isocladius*) *trifasciatus* Meigen

a. - Antenna. (011)

b. - Labrum and palatum. (011)

c. - Premandible, flattened lateral view. (011)

d. - Mentum. (400)

e. - Claw on anterior parapod. (011)

Fig. 23

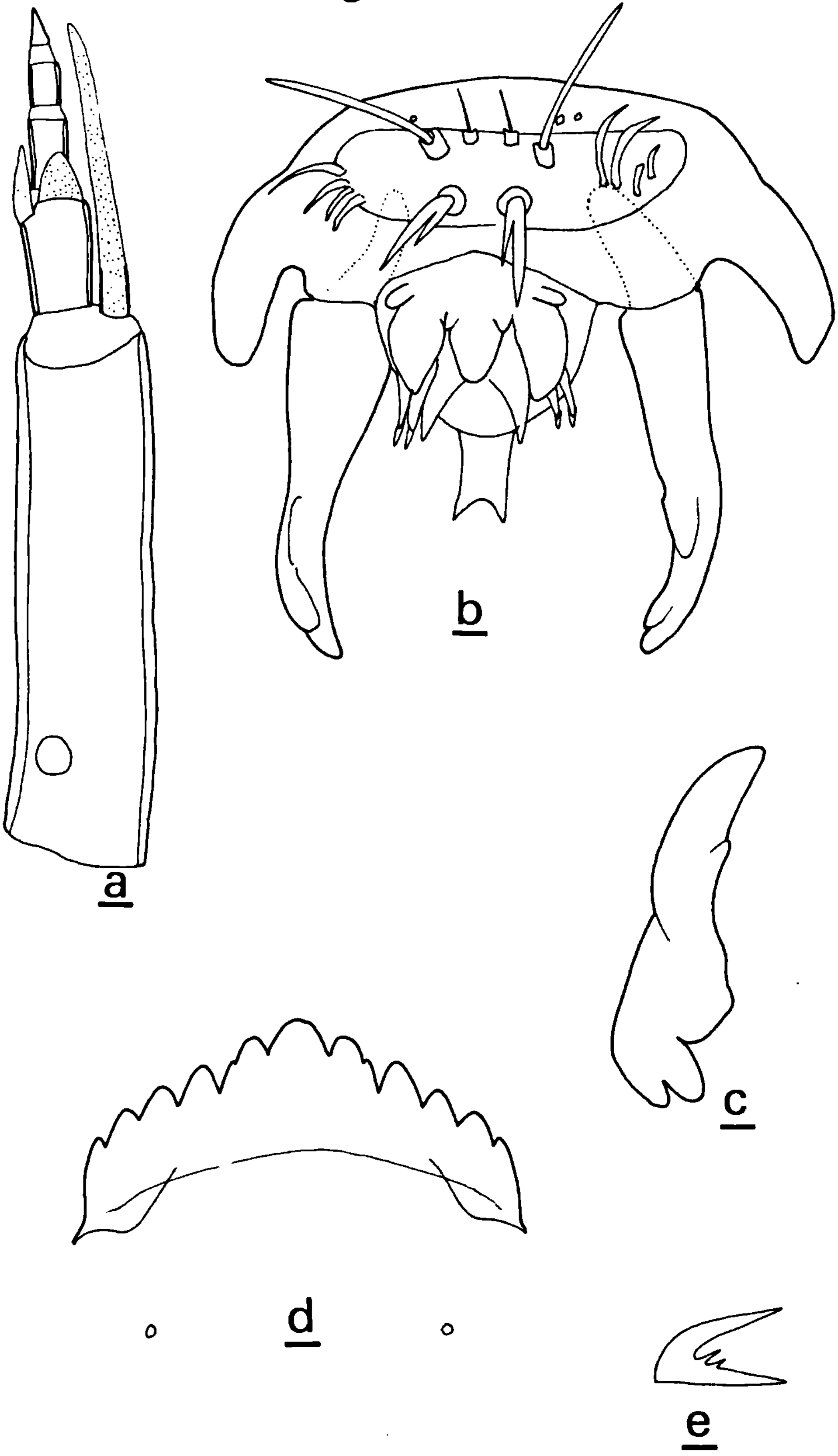


Figure 24

Epoicocladius flavens Malloch

a. - Antenna (011)

b. - Labrum (011)

c. - Mandible (011)

d. - Left half of flattened mentum (011)

e. - Mentum (unflattened) (011)

f. - Posterior segments of abdomen (100)

Fig. 24

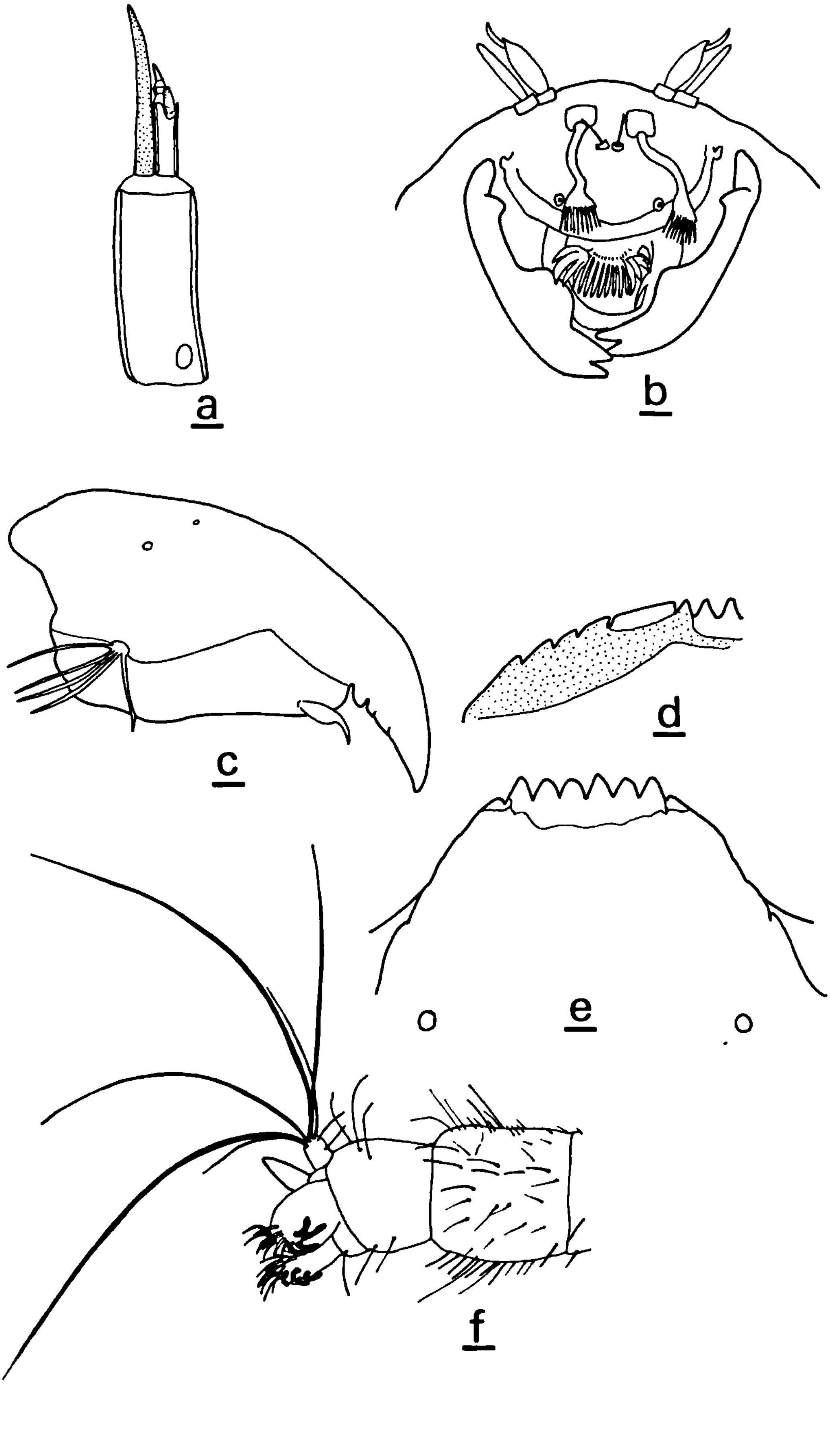


Figure 25

Eukiefferiella brevicalcar (Kieffer)

a. - Antenna (011)

b. - Mentum (011)

c. - Mandible (011)

d. - Maxilla (011)

e. - Procercus (400)

Fig. 25

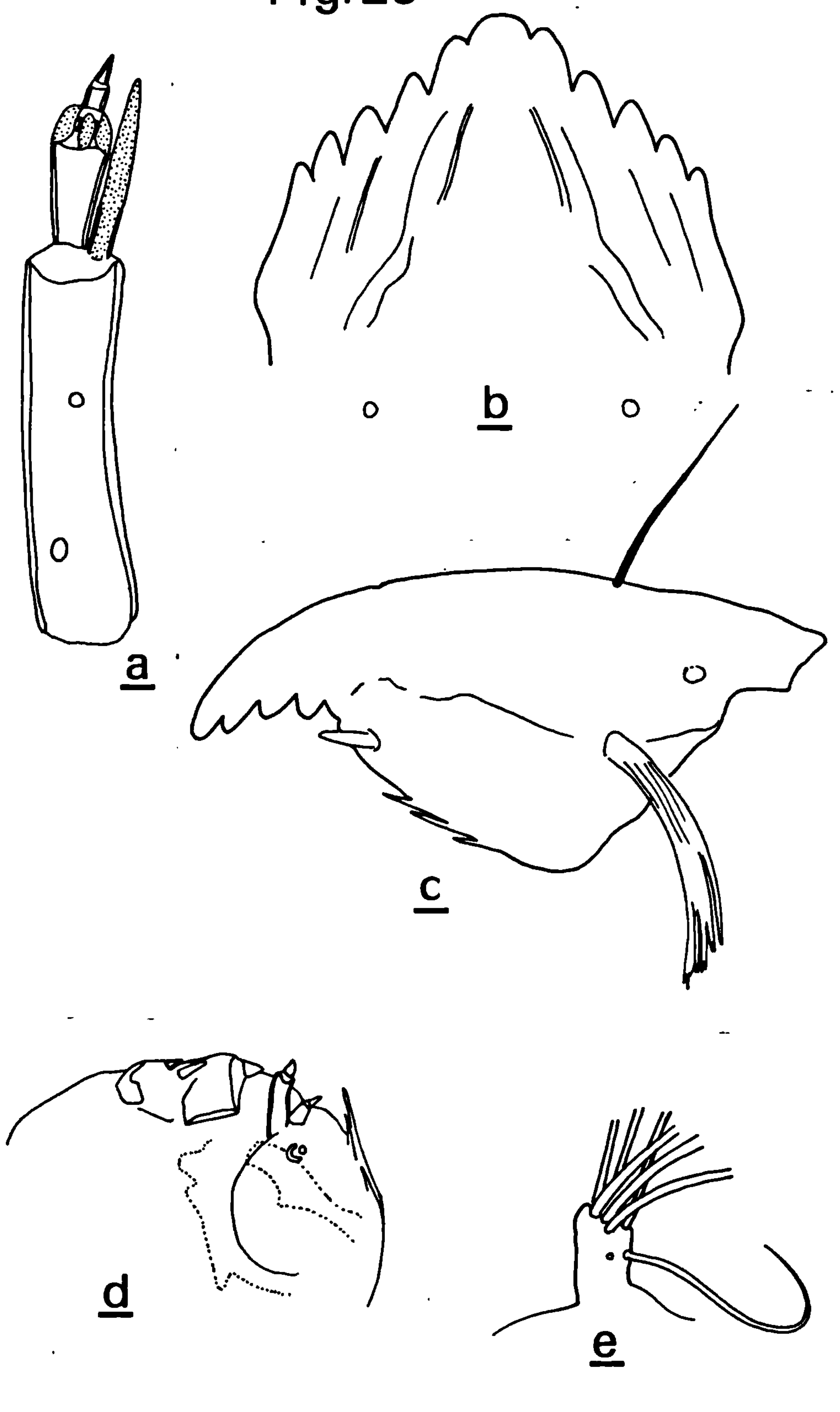


Figure 26

Eukiefferiella calvescens

a. - Antenna (011)

b. - Mandible (400)

c. - Mentum (400)

d. - Maxilla (400)

Eukiefferiella claripennis

e. - Mandible (400)

f. - Mentum (400)

g. - Antenna (011)

Fig. 26

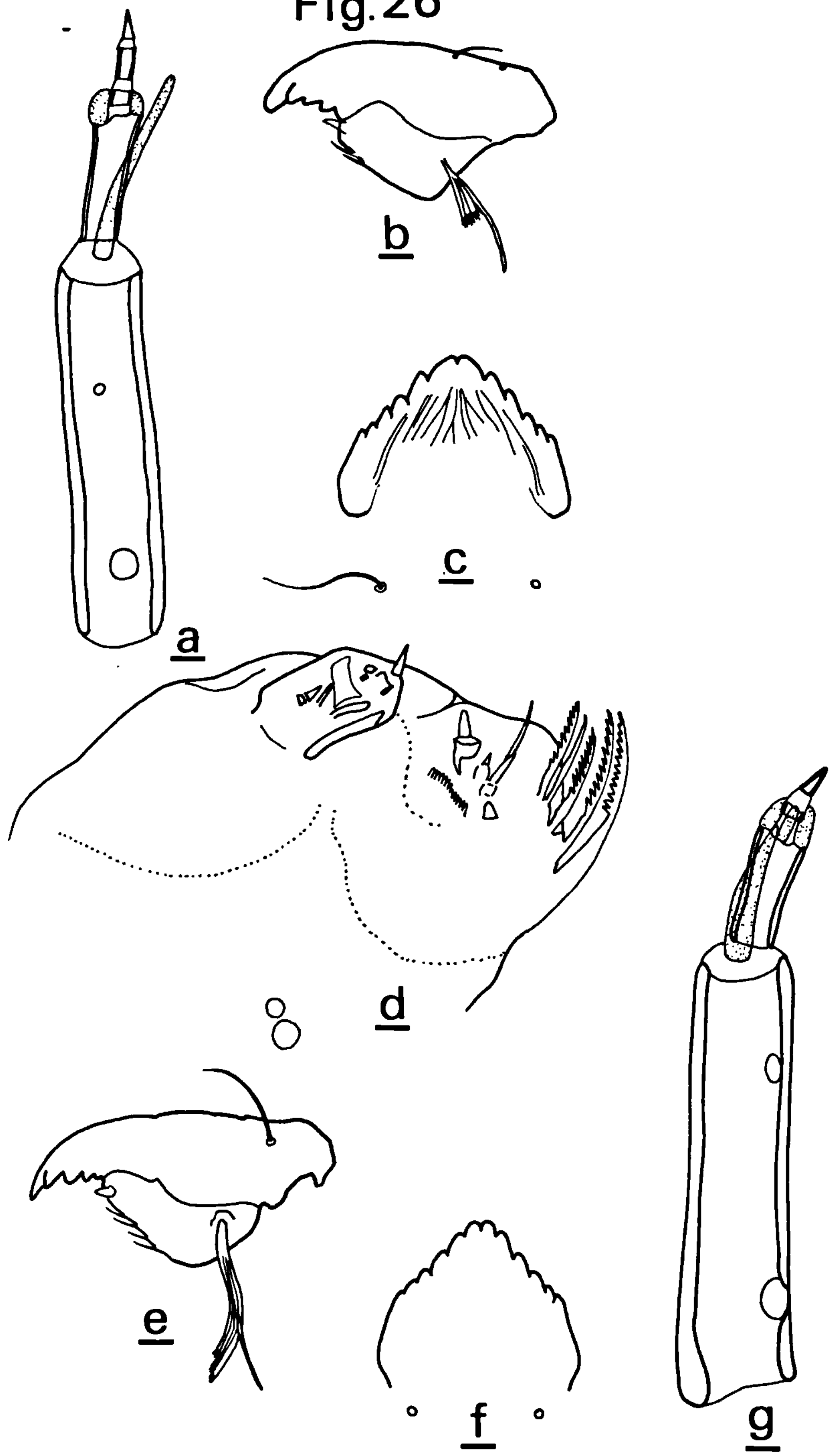


Figure 27

Eukiefferiella clypeata

a. - Antenna (011)

b. - Labrum (011)

c. - Mandible (011)

d. - Mentum (011)

Fig.27

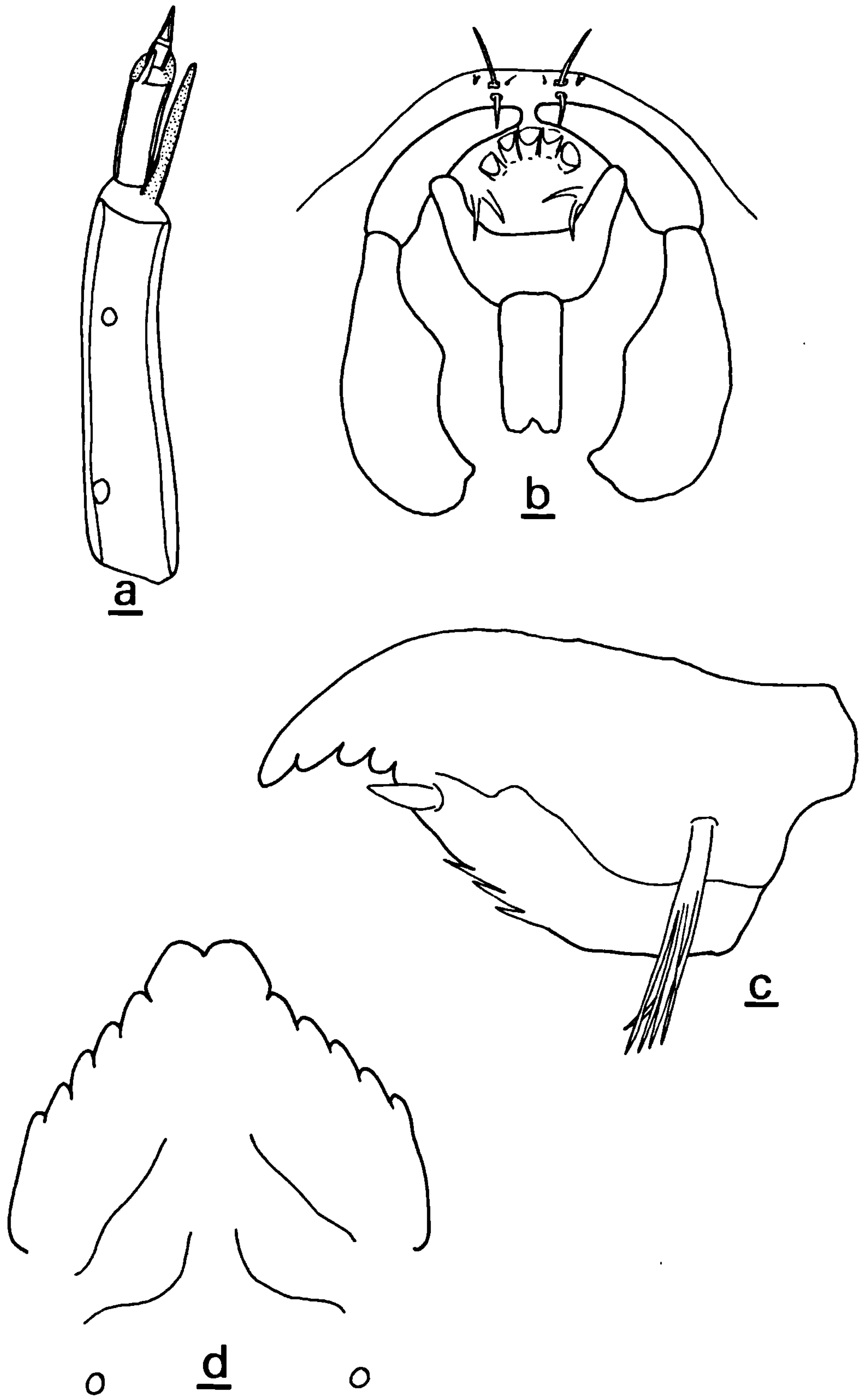


Figure 28

Eukiefferiella discoloripes

a. - Antenna (011)

b. - Mandible (400)

c. - Mentum (400)

Eukiefferiella verralli

d. - Antenna (011)

e. - Mandible (400)

f. - Mentum (400)

g. - SI, SII and SIII of labrum (011)

Fig. 28

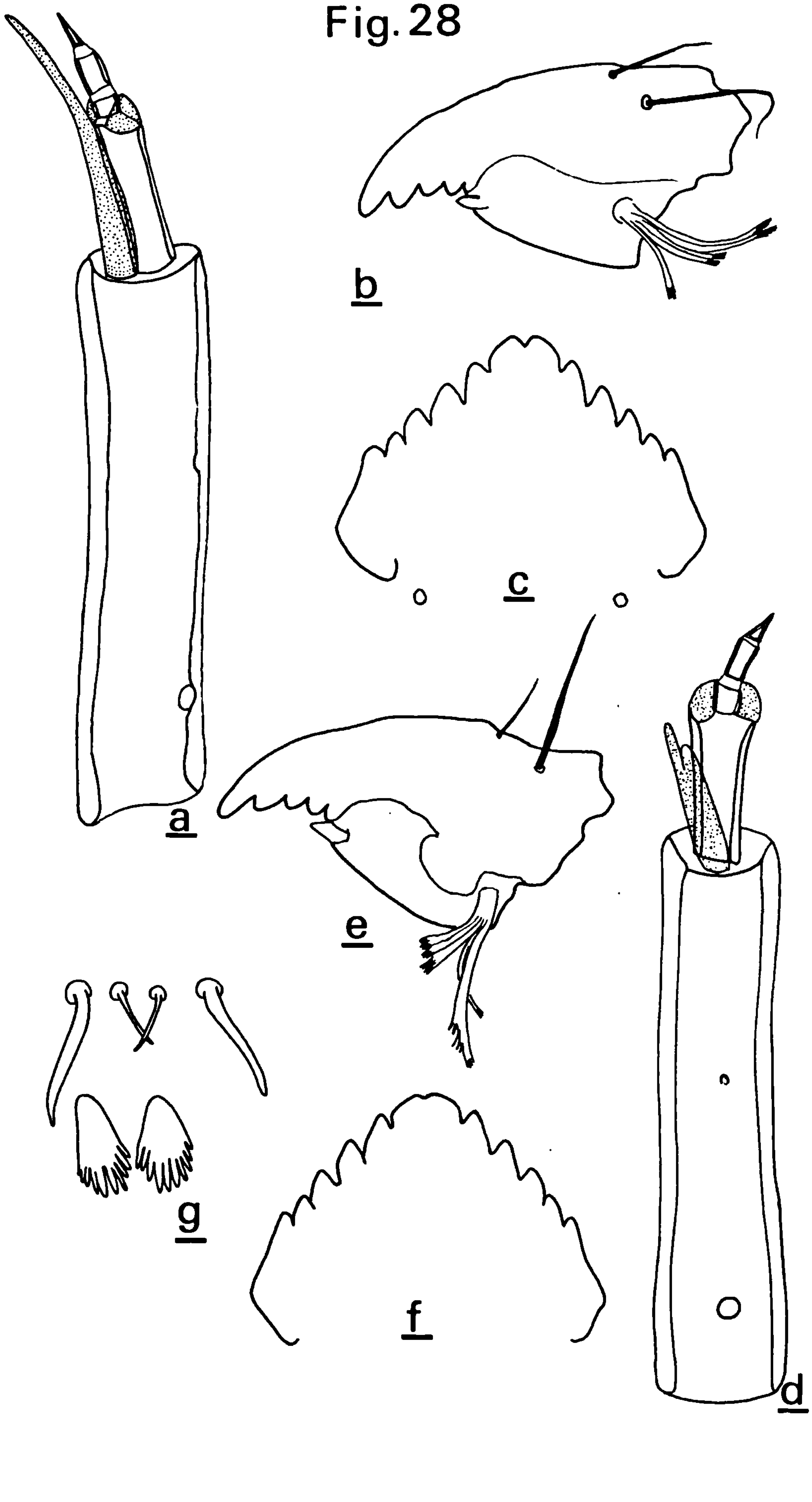


Figure 29

Eukiefferiella gracei

a. - Antenna (Oil)

b. - Mandible (400)

c. - Mentum (400)

d. - Anterior parapod claws (Oil)

Eukiefferiella minor

e. - Mandible (400)

f. - Mentum (400)

Fig.29

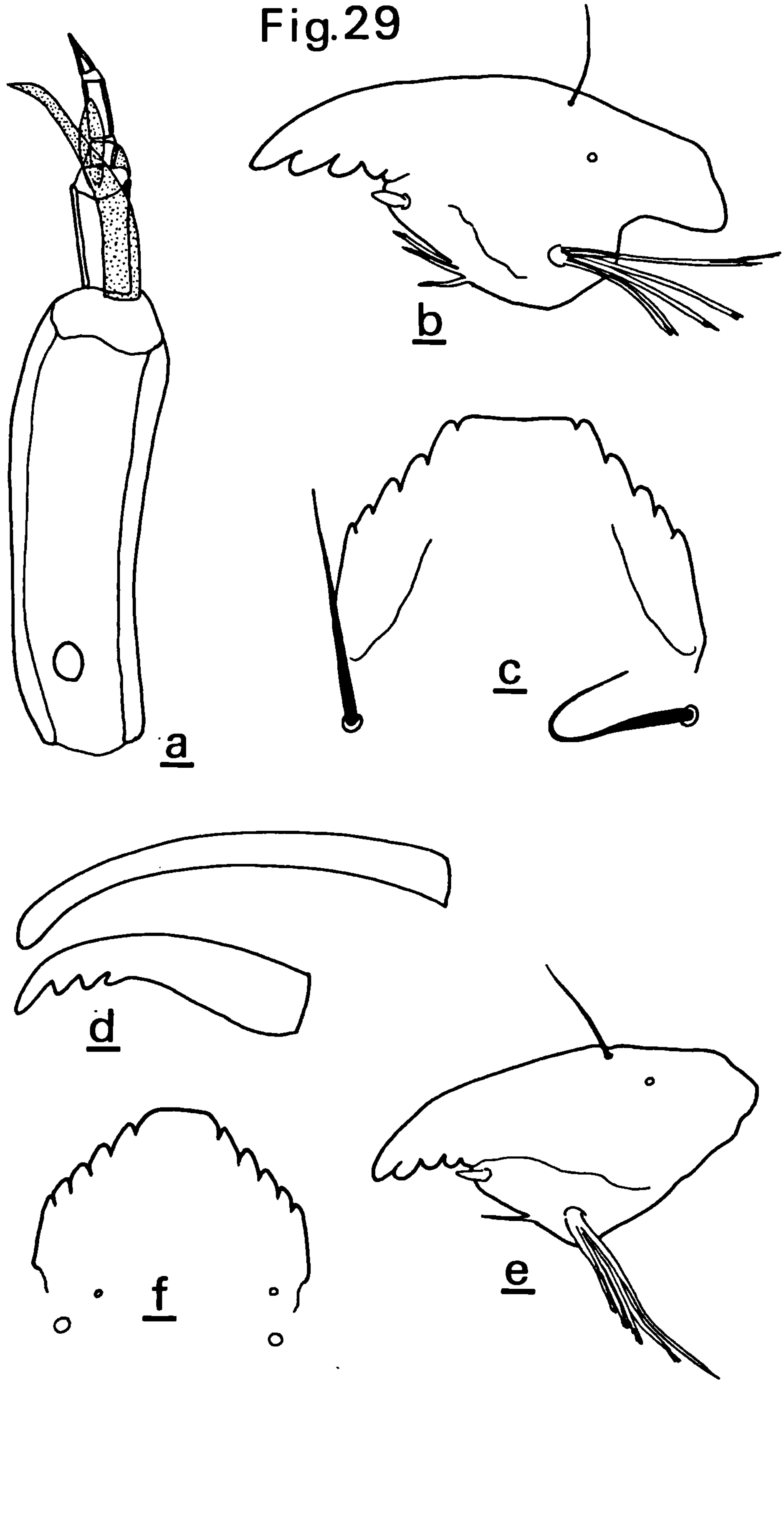


Figure 30

Eukiefferiella ilkleyensis (Edwards)

a. - Antenna (O11)

b. - Labrum (O11)

c. - Mandible (O11)

d. - Mentum (O11)

Eukiefferiella species A.

e. - Antenna (O11)

f. - Mentum (O11)

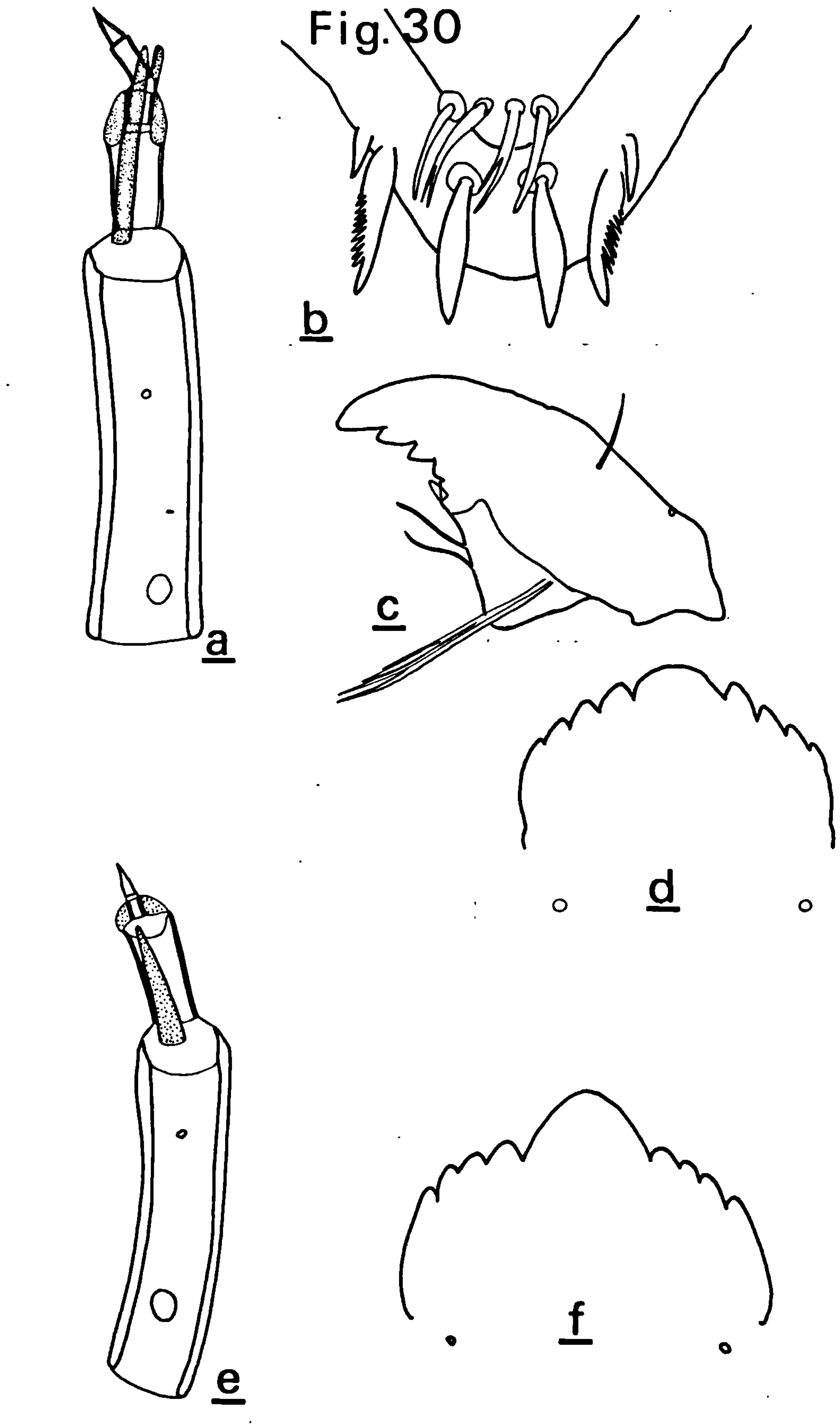


Fig. 30

Figure 31

Eukiefferiella species C

a. - Antenna (011)

b. - Labrum (011)

c. - Mentum (400)

d. - Mandible (400)

Fig.31

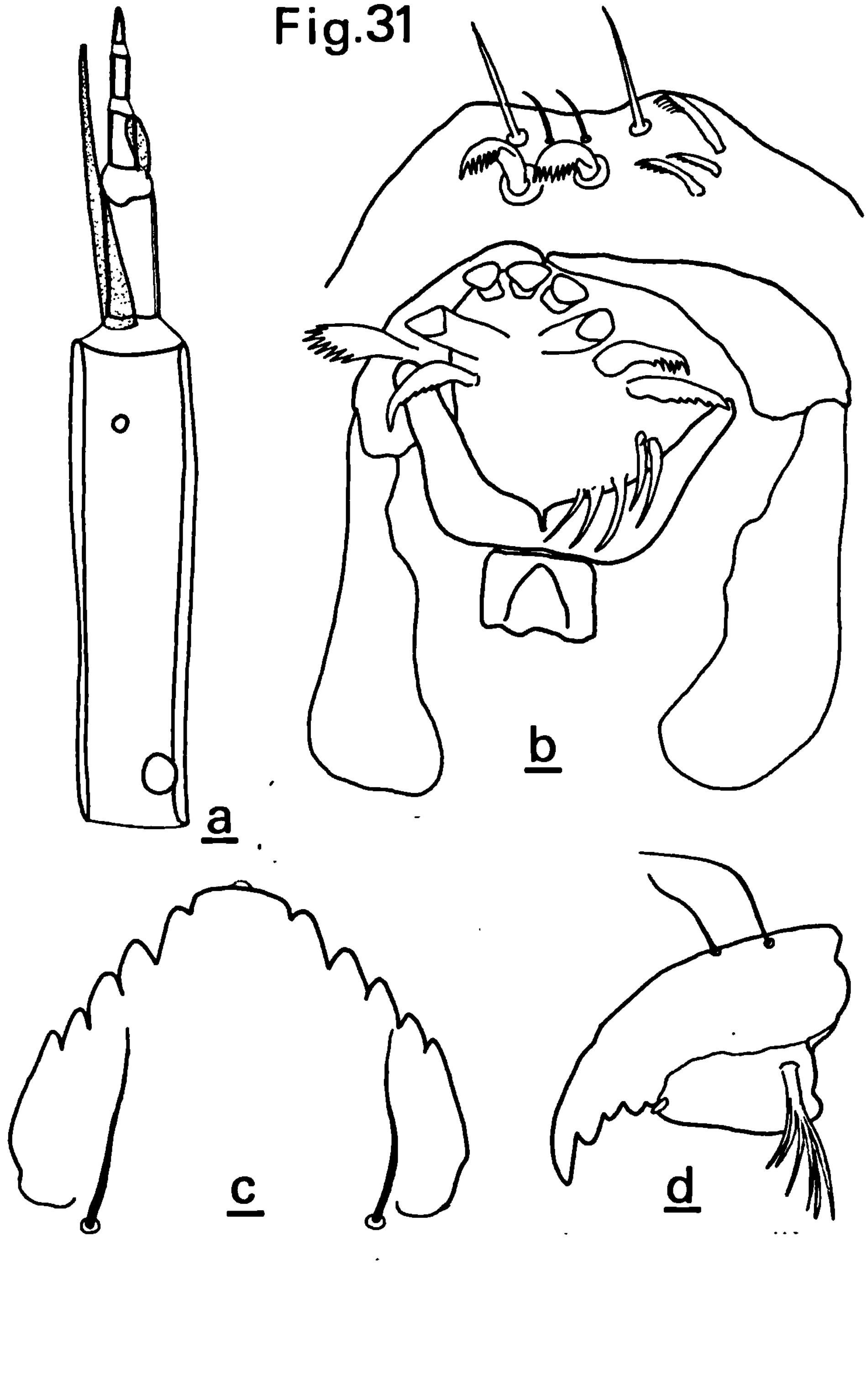


Figure 32

Eukiefferiella species D

a. - Antenna (Oil)

b. - Mentum (Oil) above are two worn specimens

c. - Mandible (Oil)

d. - Claws of anterior parapod (Oil).
Showing four different sizes of claws with characteristic shapes.

Fig.32

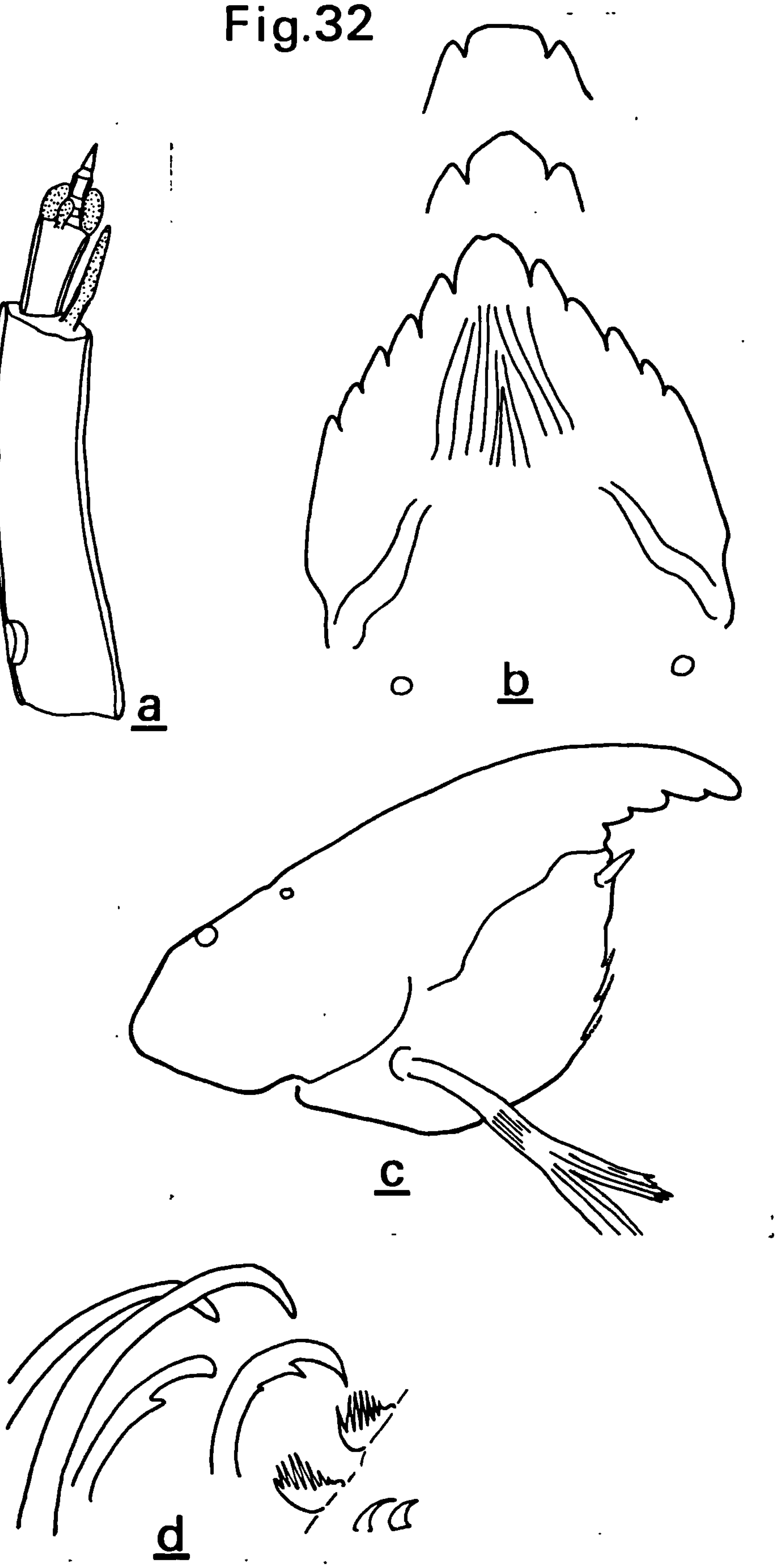


Figure 33

Cymnometriocnemus ? brumalis (Edwards)

a. - Antenna (Oil)

b. - Labrum and palatum (Oil). Drawn from a compressed specimen - the relationship of the parts of the palatum is not accurate.

c. - Mentum (400)

d. - Anterior parapod (100)

e. - Posterior segments (100)

Fig. 33

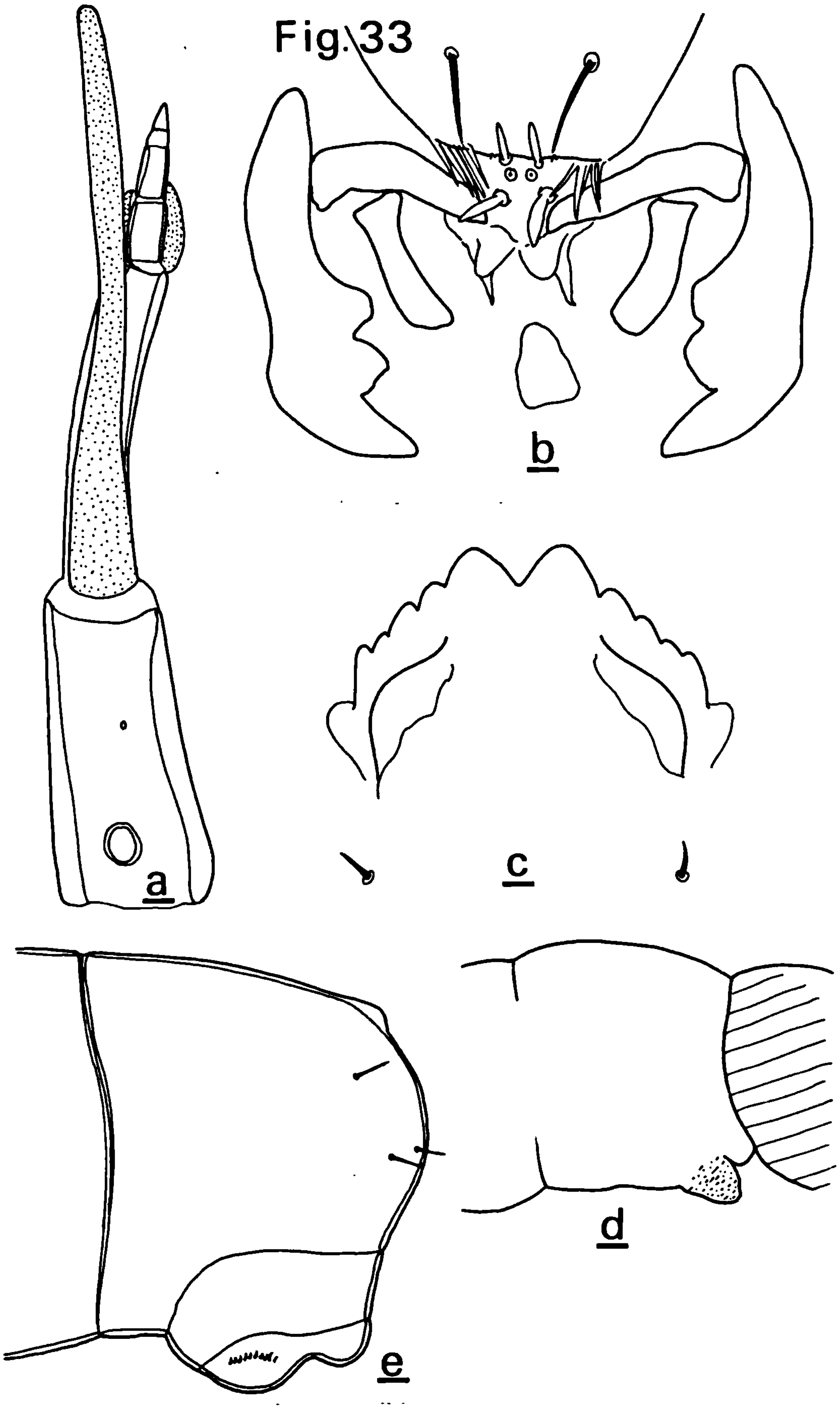


Figure 34

Halocladius

a. - Antenna of *H. fucicola* (Edwards) (011)

b. - Premandible of H. fucicola (Edw.) (011)

c. - Premandible of *H. variabilis* (Staeger) (011)

d. - Mentum of *H. fucicola* (Edw.) (400)

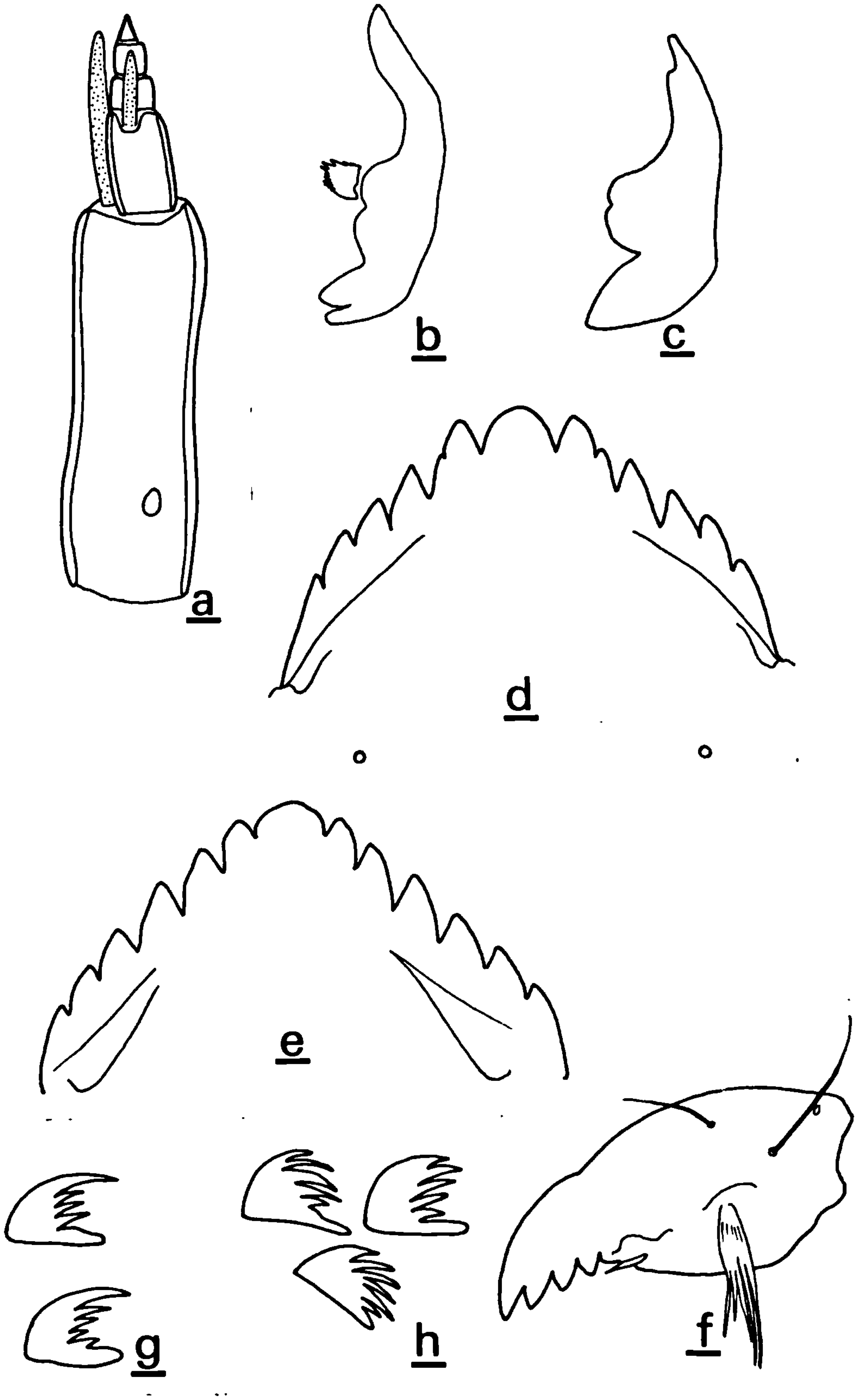
e. - Mentum of *H. variabilis* (Staeger) (400)

f. - Mandible of *H. variabilis* (Staeger) (400)

g. - Smallest anterior parapod claws with multiple teeth on *H. varians* (Staeger)

h. - Smallest anterior parapod claws with multiple teeth on *H. variabilis* (Staeger)

Fig.34



/

<u>Figure 35</u>

<u>Heleniella ornaticollis</u> (Edwards)

a. - Antenna (011)

b. - Labrum and palatum (011)

c. - Mentum (400)

d. - Mandible (400)

Fig.35

Figure 36

Heterotanytarsus apicalis (Kieffer)

a. - Dorsal view of whole head (400)

b. - Mandible (400)

c. - Mentum (400)

d. - Palatum and SI setae of labrum (011)

e. - Anterior parapod (100)

Fig. 36

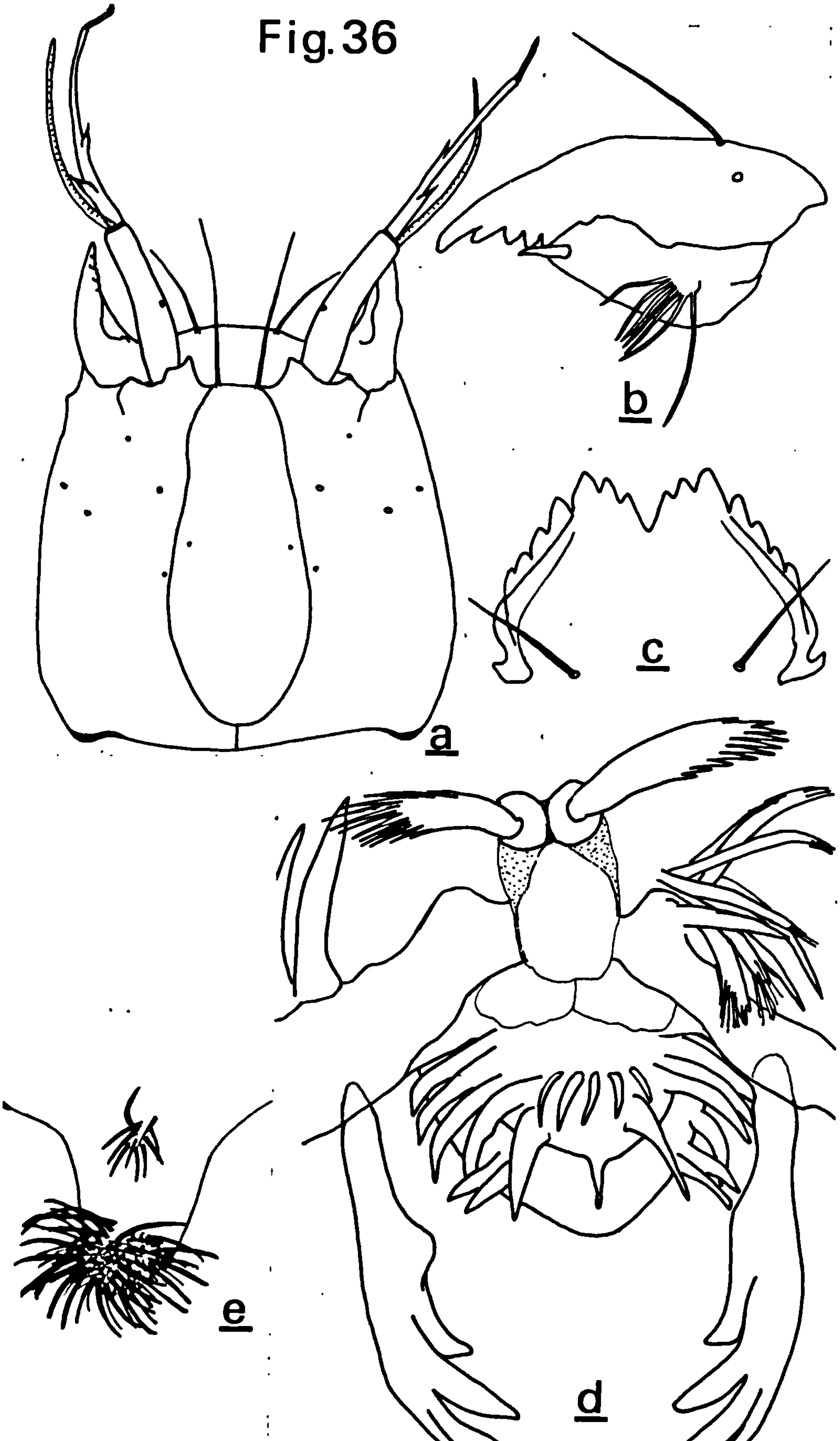


Figure 37

* *Heterotrissocladius marcidus* (Walker)

a. - Antenna (011)

b. - Labrum and palatum (011)

c. - Mandible (400)

d. - Mentum and postmentum, stippled to show extent of dark colouration (400)

e. - Maxilla (011)

Fig.37

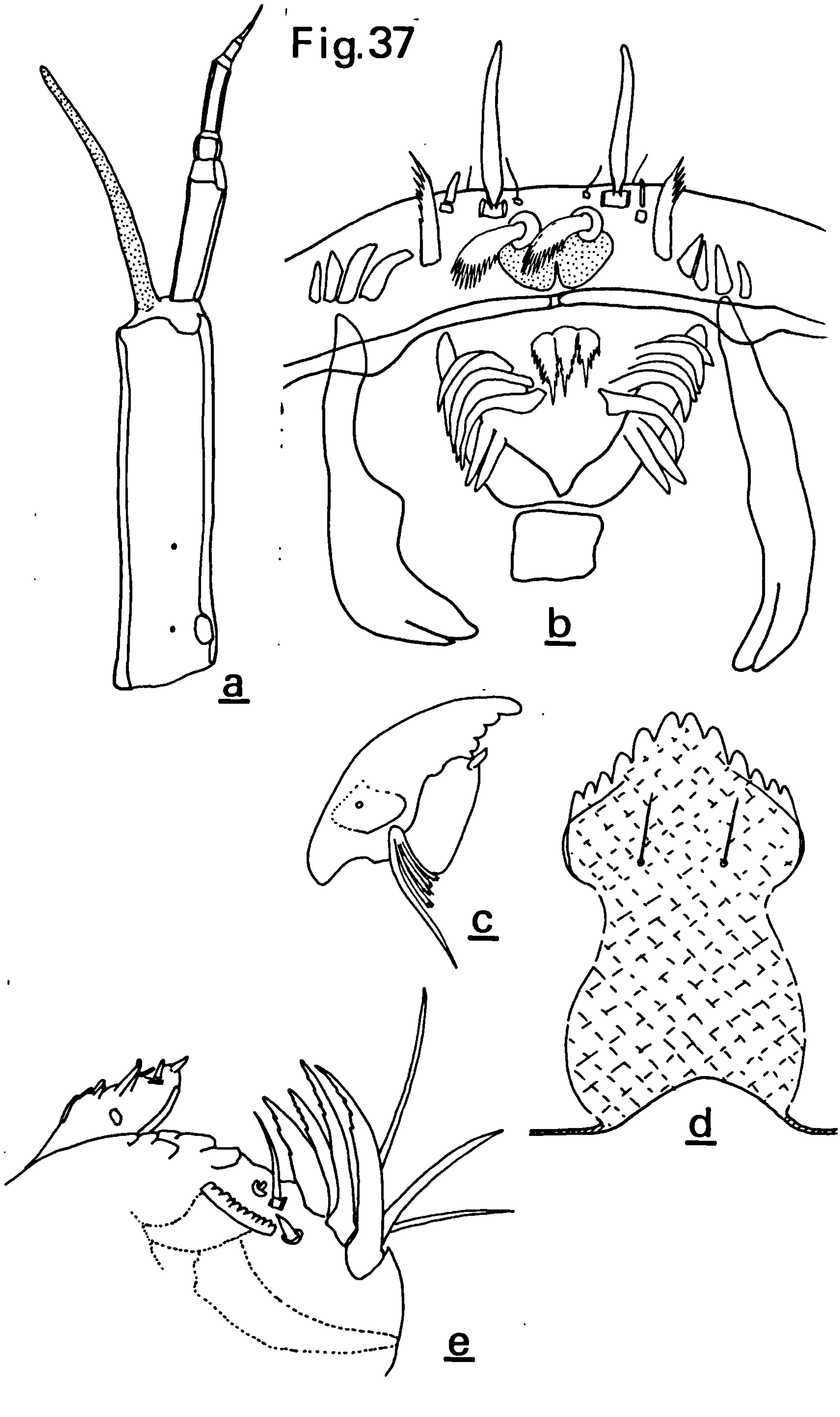


Figure 38

Krenosmittia camptophleps (Edwards)

a. - Antenna (Oil)

b. - Labrum (Oil) detached premandible below, palatum not drawn

c. - Mandible (Oil)

d. - Palpiger of maxilla (Oil)

e. - Mentum (Oil)

f. - Posterior segments of the body (100)

Fig. 38

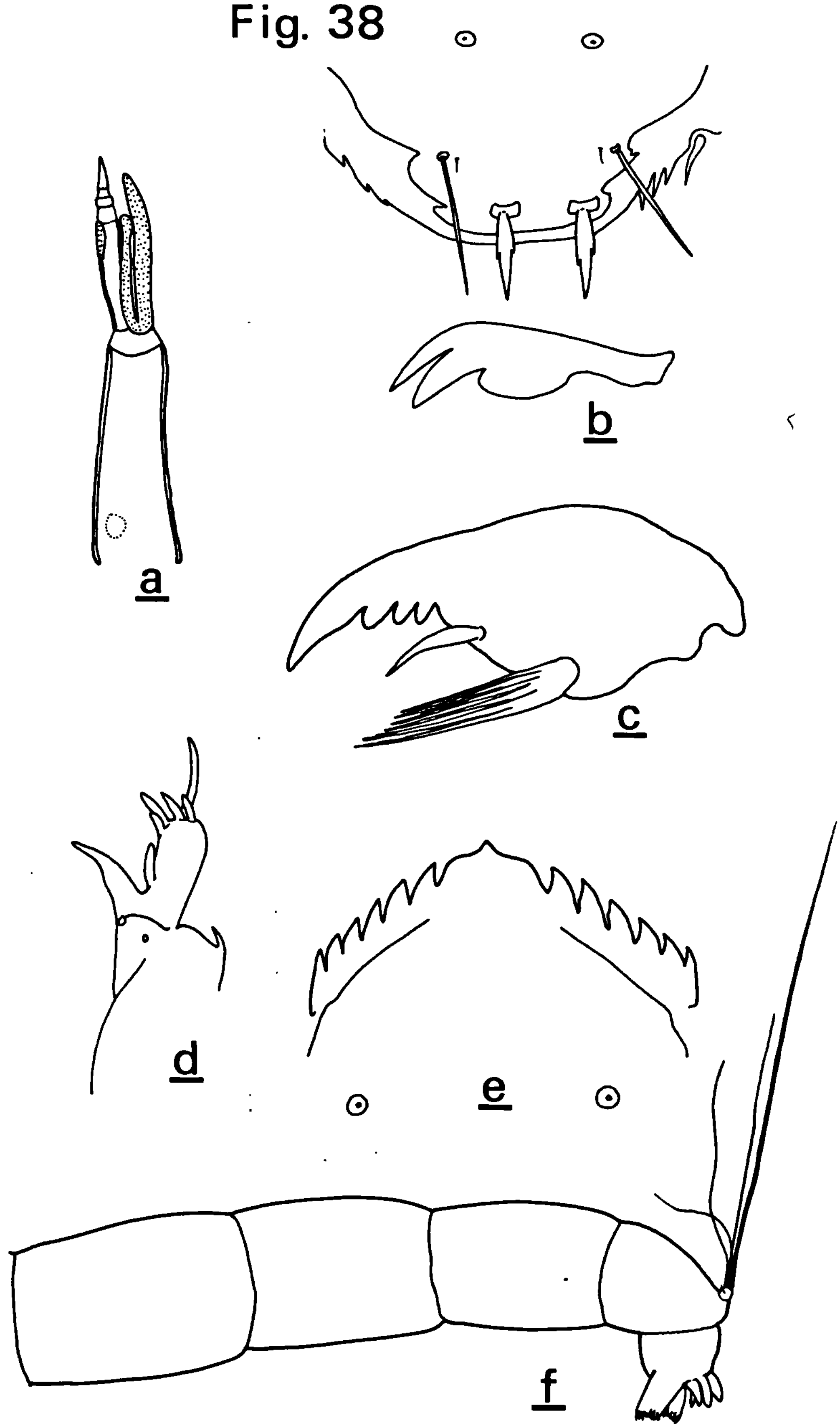


Figure 39

Limnophyes globifer (Lundström)

a. - Antenna (011)

b. - Labrum and palatum (011)

c. - Premandible (011)

d. - Mentum (400)

e. - Mandible (011)

f. - Maxilla (011)

g. - Posterior segments (400)

Fig. 39

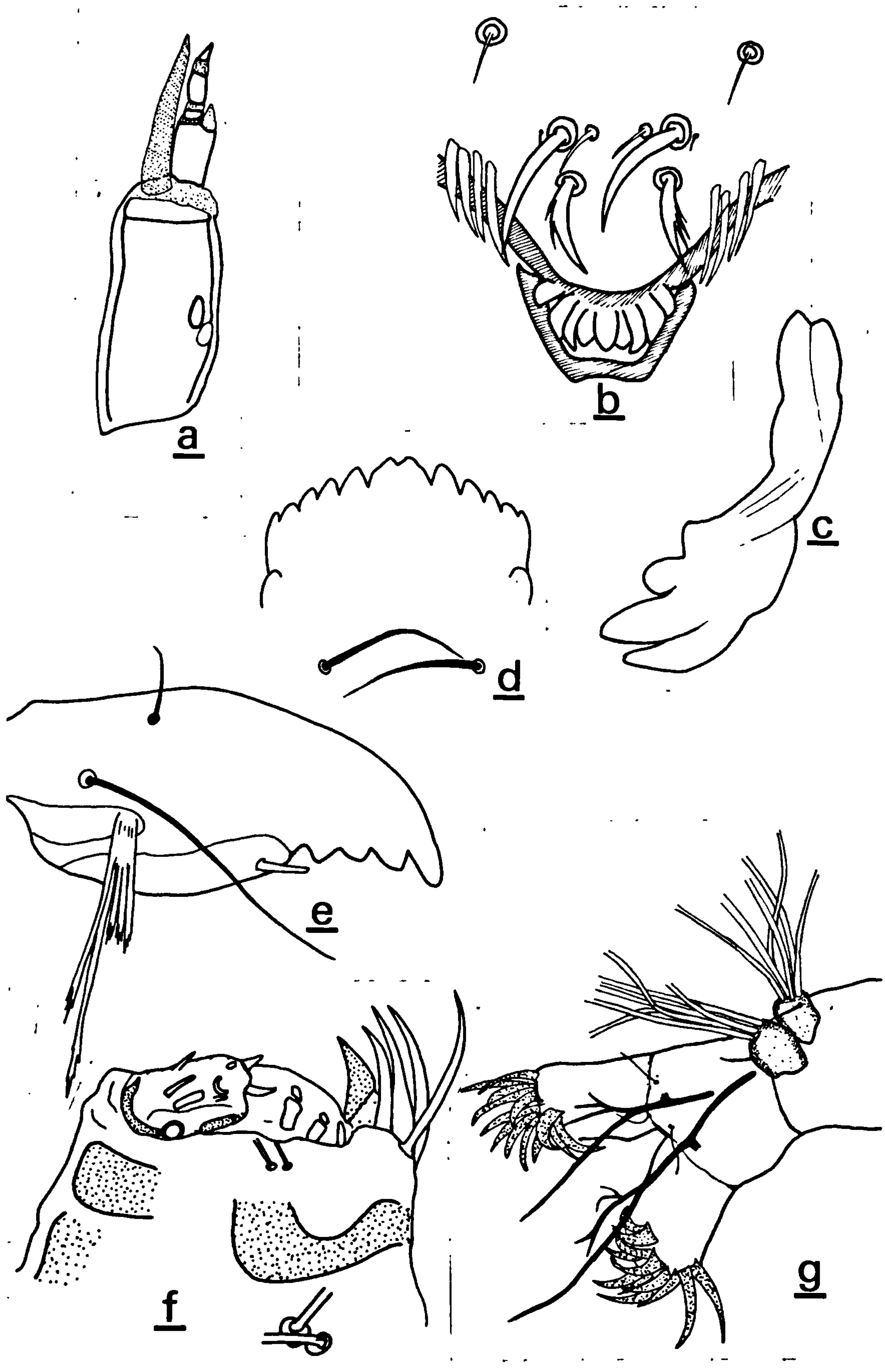


Figure 42

Limnophyes species A

a. - Antenna (011)

b. - Premandible (011)

c. - Mentum (011)

d. - Mandible (400)

e. - Maxilla (011)

Fig.40

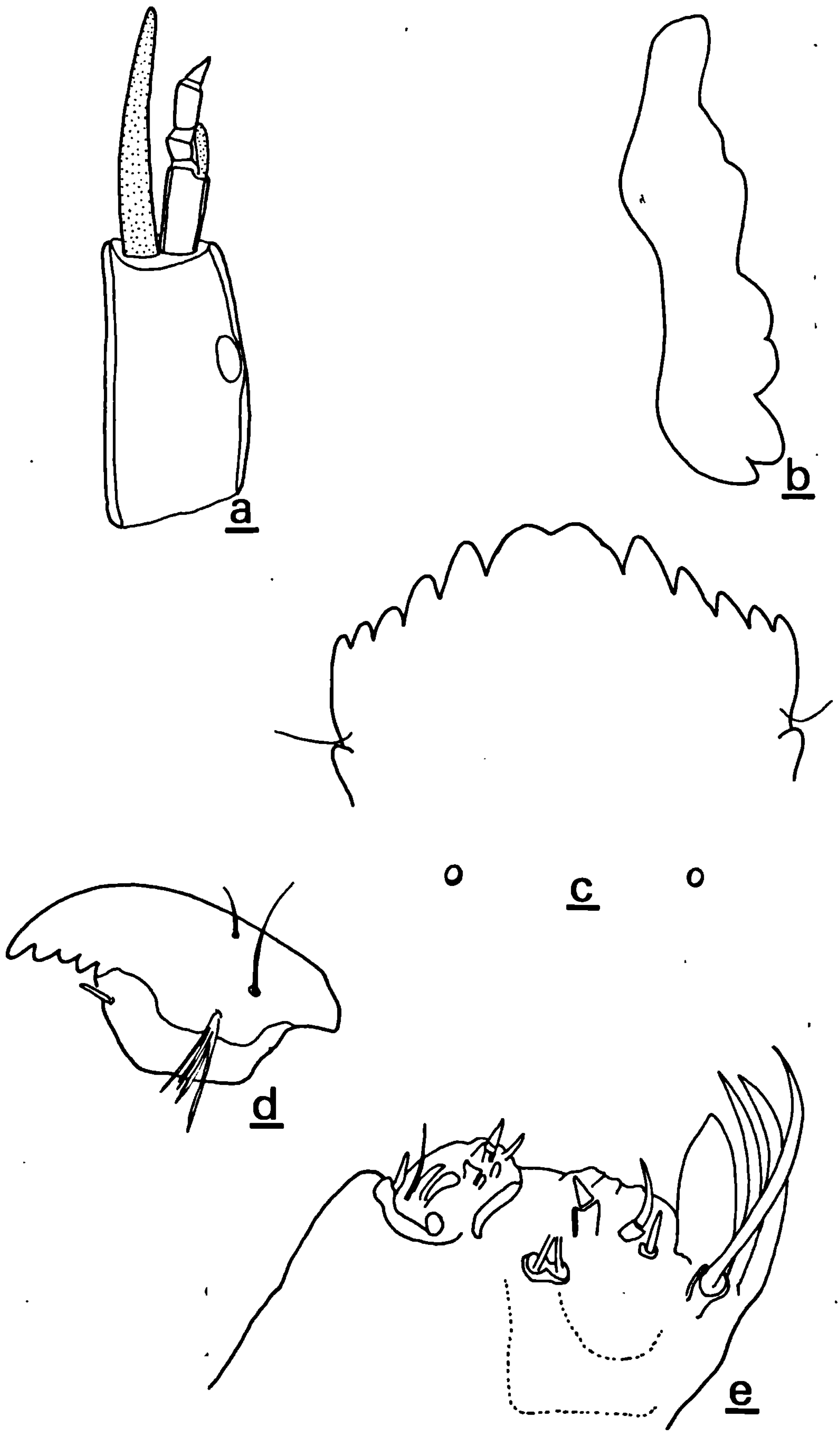


Figure 41

Metriocnemus ? hygropetricus Kieffer

a. - Antenna (011)

b. - Labrum (011)

c. - Premandible (011)

d. - Mandible (400)

e. - Mentum (011)

f. - Maxilla (011)

Fig. 41

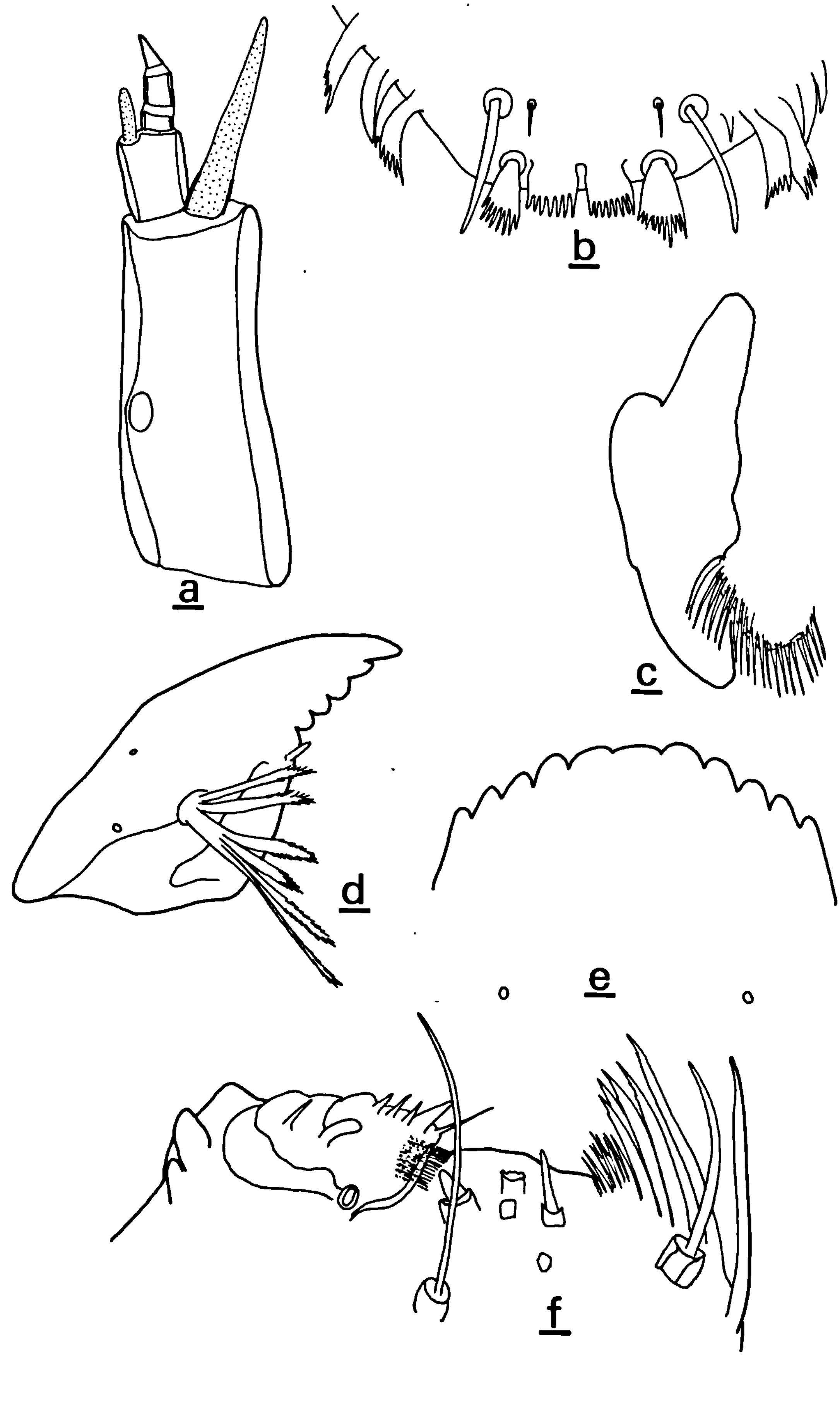


Figure 42

Metriocnemus martinii Thienemann

a. - Antenna (011)

b. - Labrum and anterior palatum (011)

c. - Premandible (011)

d. - Mandible (400)

e. - Mentum (400)

f. - Posterior segments to show proc rci and procercal setae (200)

Fig. 42

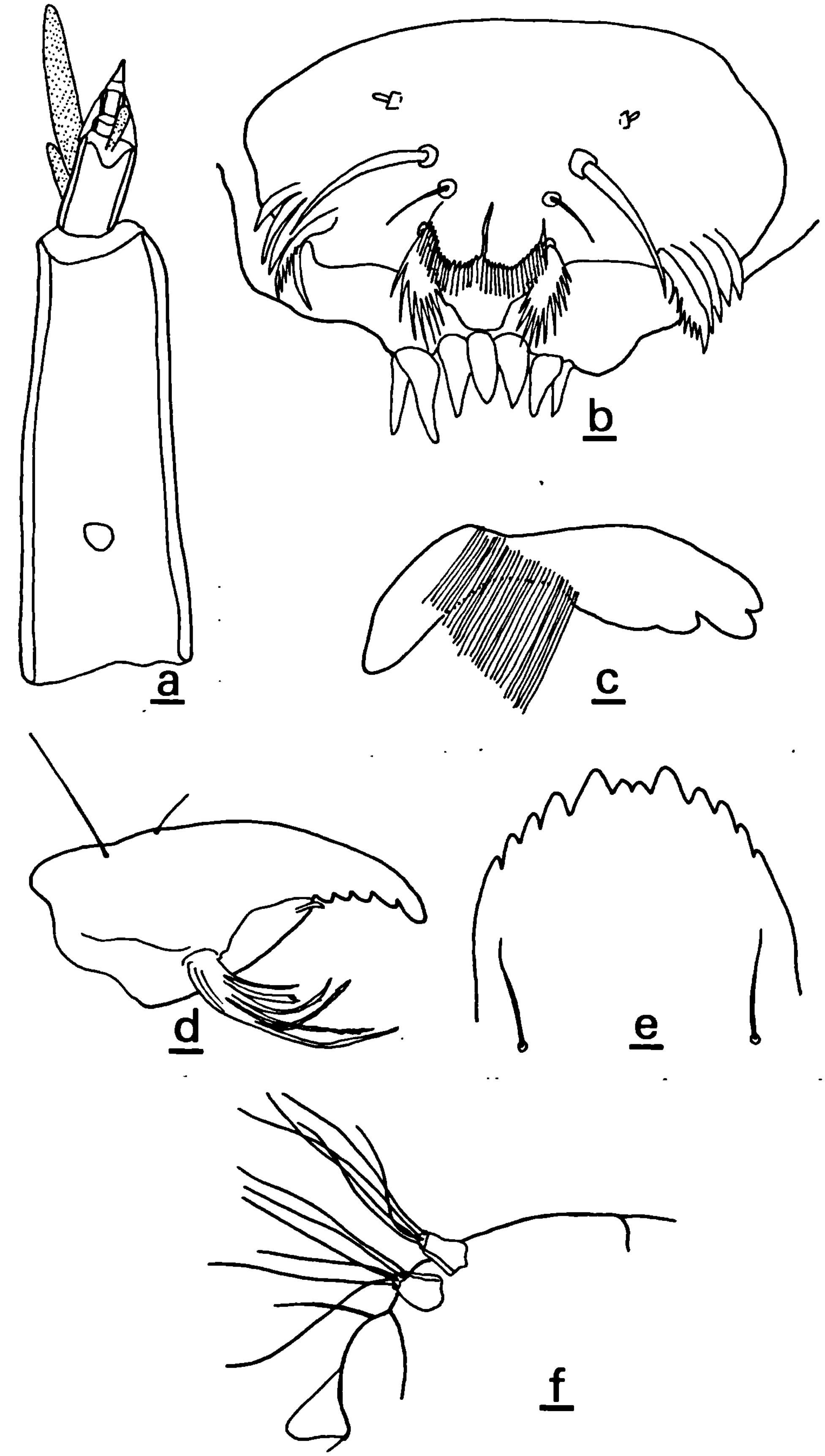


Figure 43

Nanocladius

a. - Antenna of *Nanocladius rectinervis* (Kieffer) (011)

b. - Labrum and palatum of *N. rectinervis* (011)

c. - Mentum of *N. rectinervis* (011)

d. - Mandible of *N. rectinervis* (400)

e. - Claw of anterior parapod of *N. rectinervis* (011)

f. - Antenna of *Nanocladius bicolor* (Zetterstedt) (011)

Fig. 43

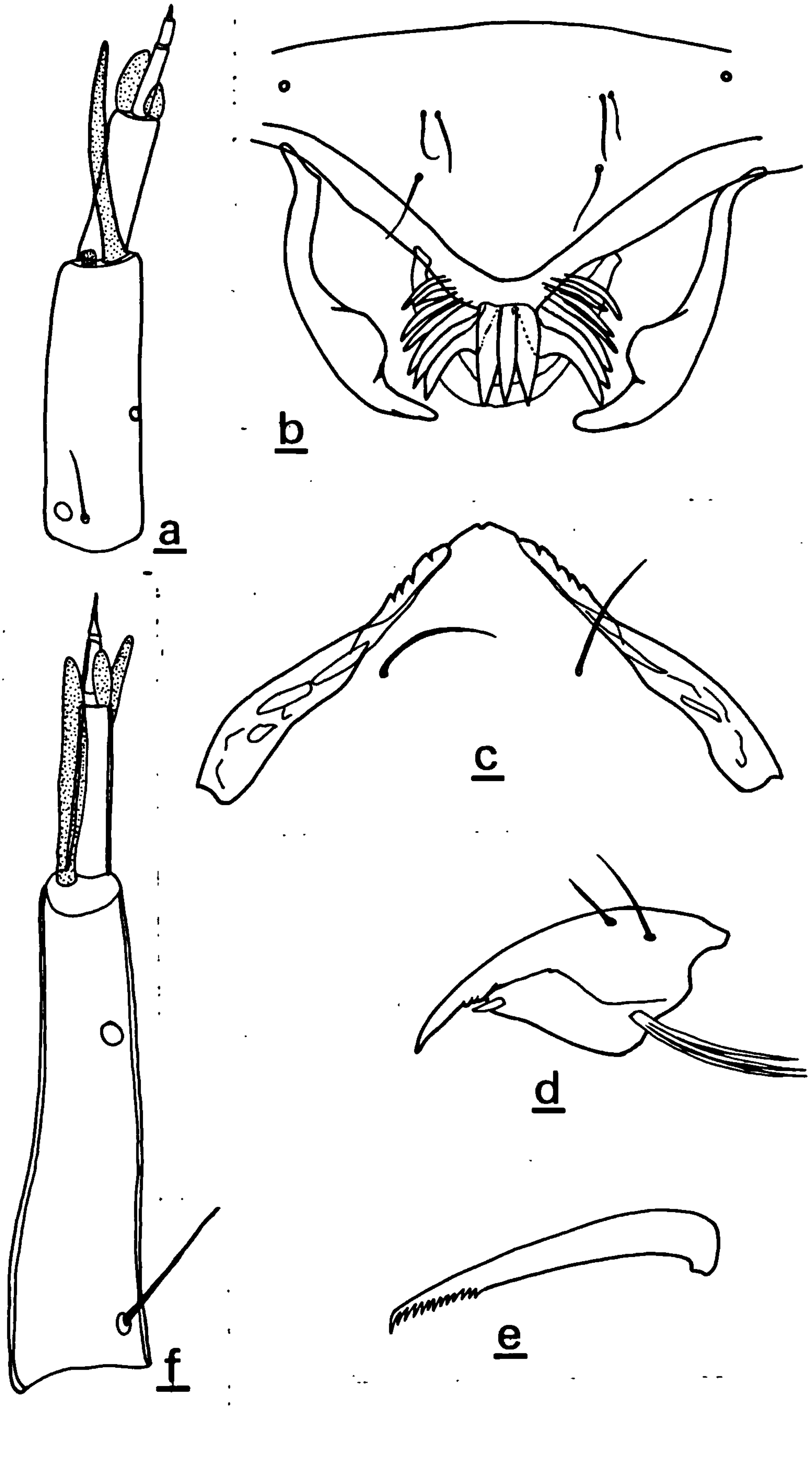


Figure 44

Orthocladius (Eudactylocladius) mixtus (Holmgren)

a. - Antenna (C11)

b. - Labrum, palatum and left premandible (011)

c. - Mentum (somewhat worn) (400)

d. - Mandible (400)

e. - Maxilla (011)

Fig. 44

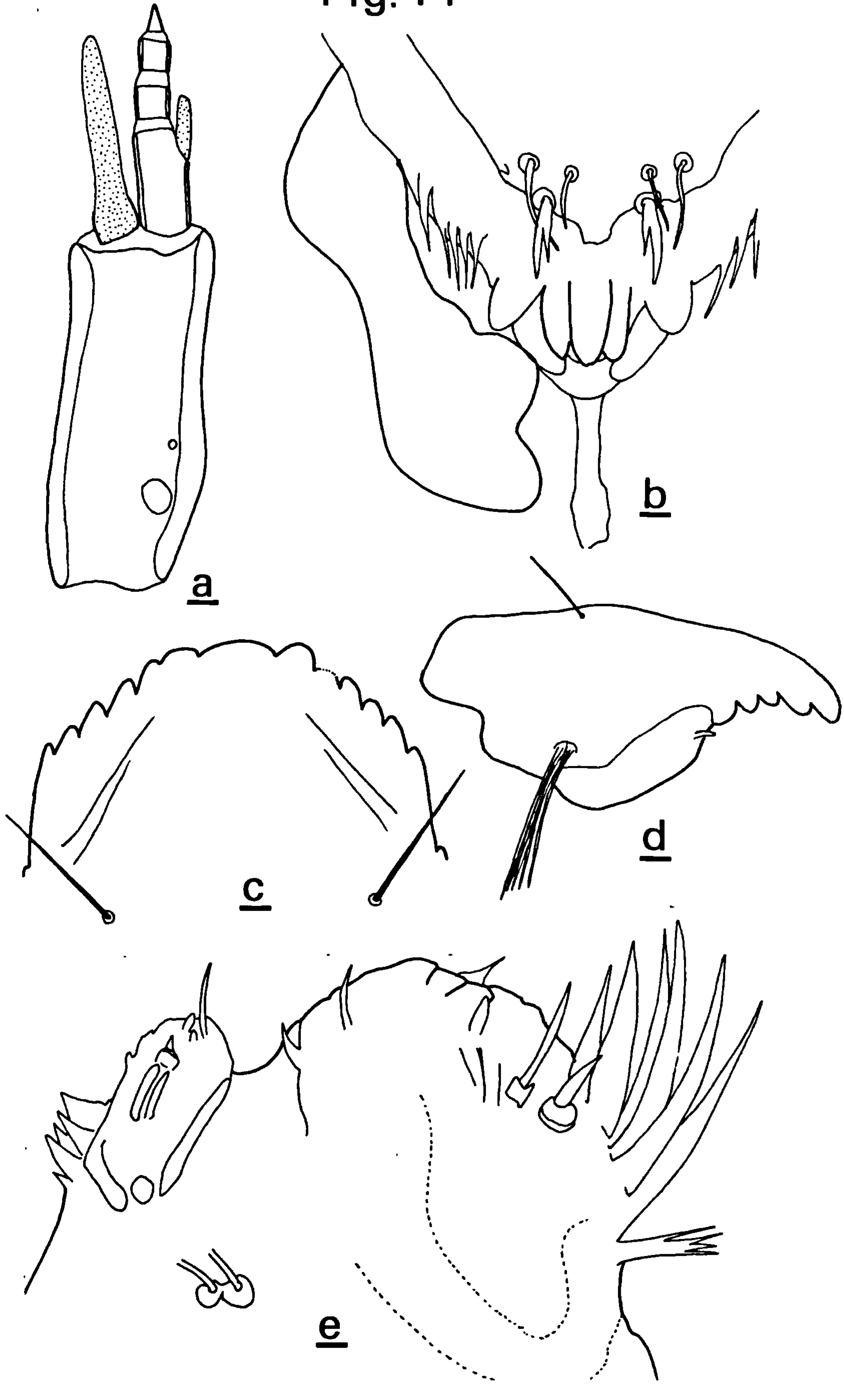


Figure 45

Orthocladius (*Eudactylocladius*) species A

a. - Antenna (011)

b. - Mandible (400)

c. - Mentum (400)

d. - Mandible (011)

Fig.45

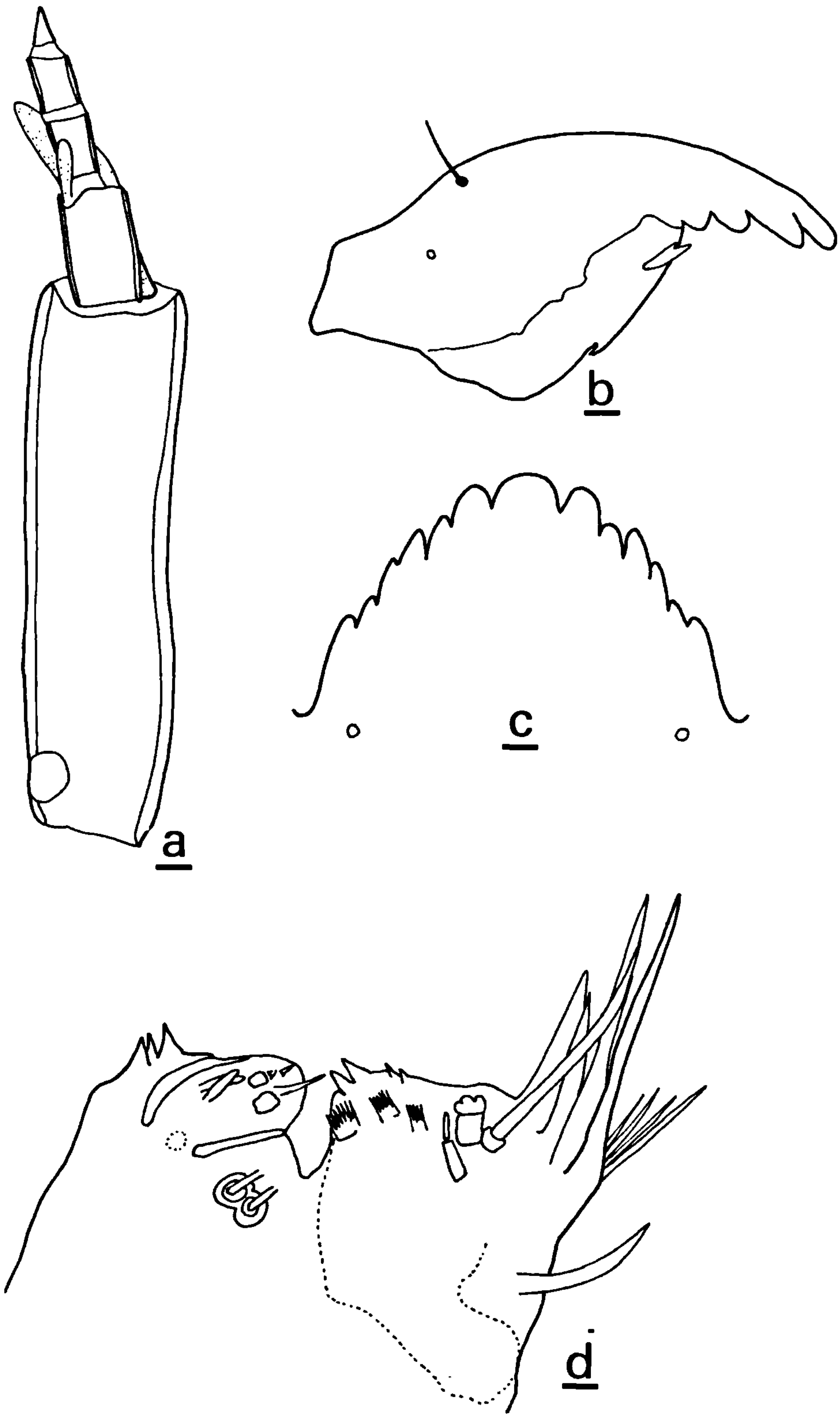


Figure 46

Orthocladius (*Eudactylocladius*) species B

a. - Labrum and palatum (011)

b. - Antenna (011)

c. - Mentum (400)

d. - Mandible (400)

Fig.46

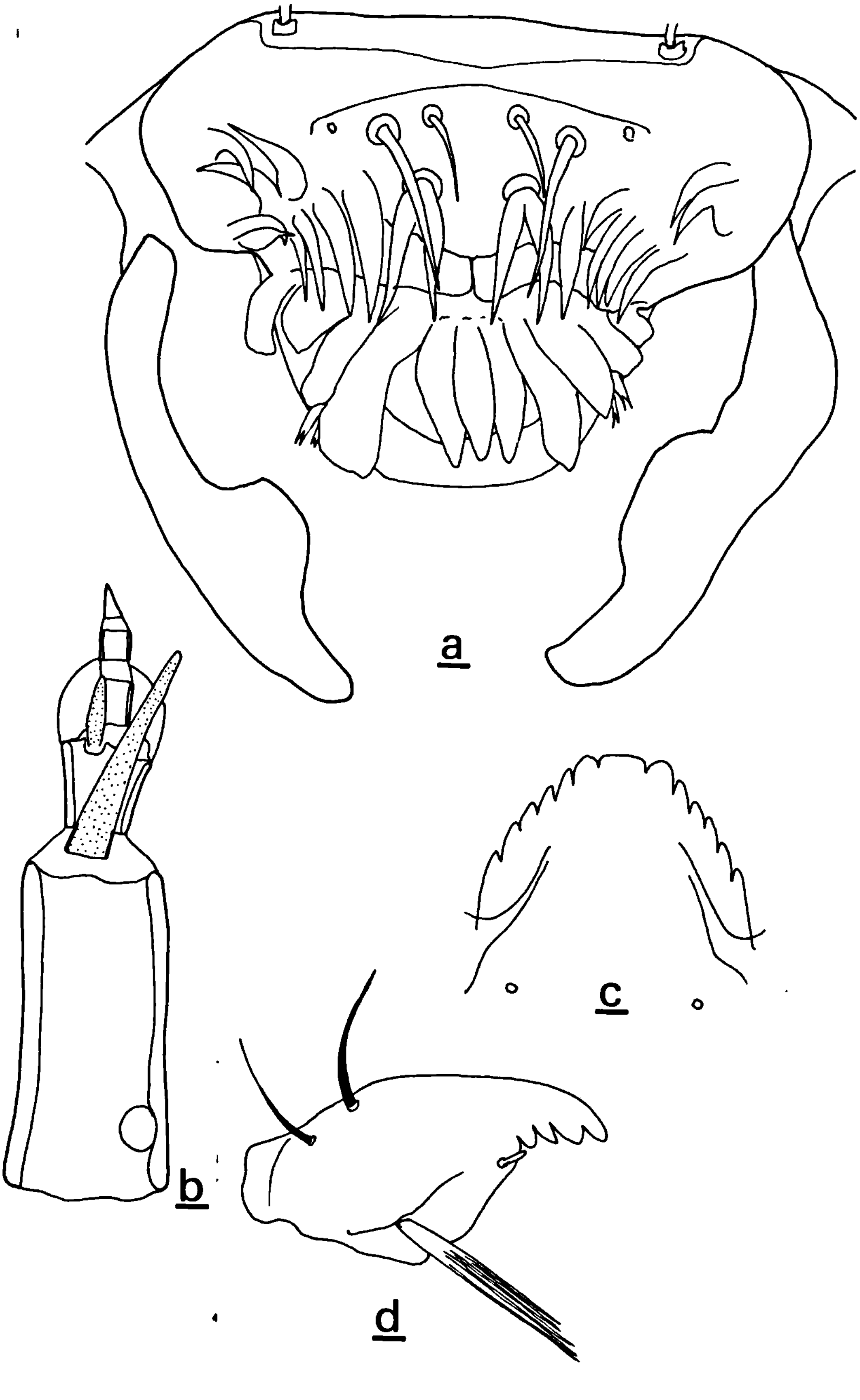


Figure 47

Orthocladius (*Euorthocladius*) *frigidus* (Zetterstedt)

a. - Antenna (611)

b. - Labrum and palatum (400)

c. - Mandible (400)

d. - Mentum (400)

e. - Maxilla (611)

Fig. 47

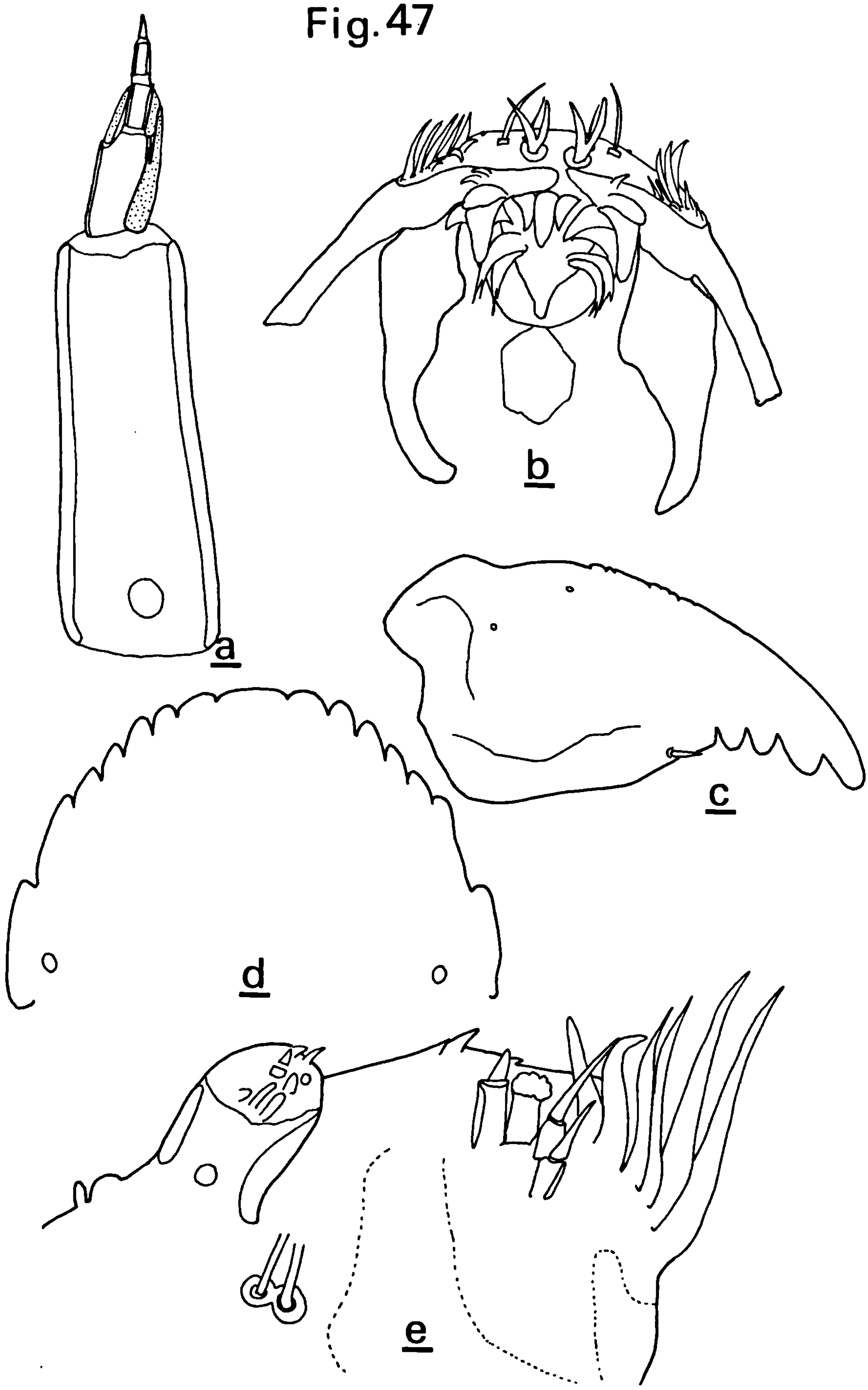


Figure 8

Orthocladius (Euorthocladius) rivulorum Kieffer

a. - Antenna (011)

b. - Labrum and palatum (400)

c. - Mentum (400)

d. - Mandible (400)

e. - Maxilla (011)

Fig. 48

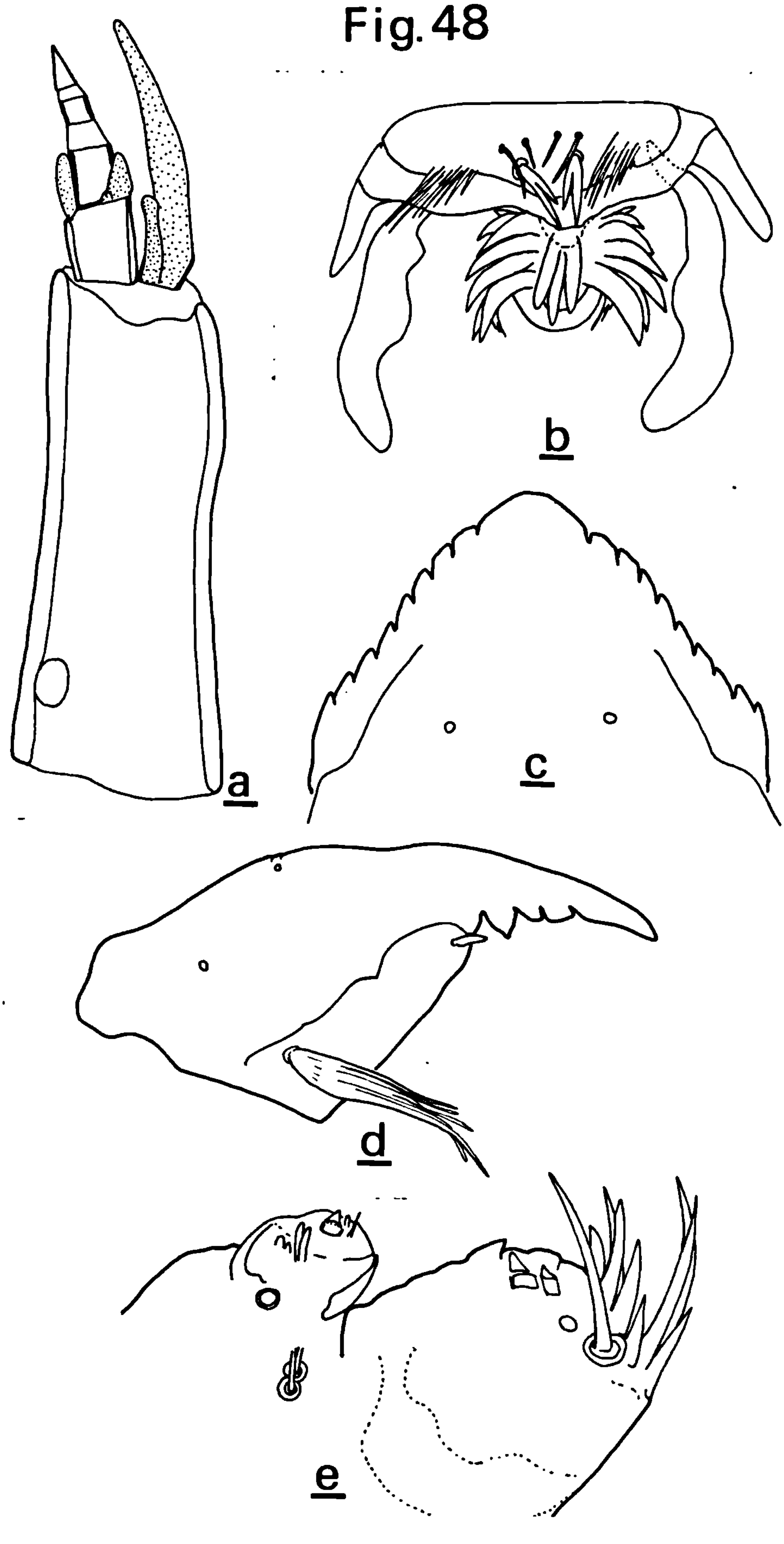


Figure 49

Orthocladius (*Euorthocladius*) *thienemanni* Kieffer

a. - Antenna (011)

b. - Labrum and palatum (400)

c. - Mentum (400)

d. - Mandible (400)

e. - Maxilla (011)

Fig. 49

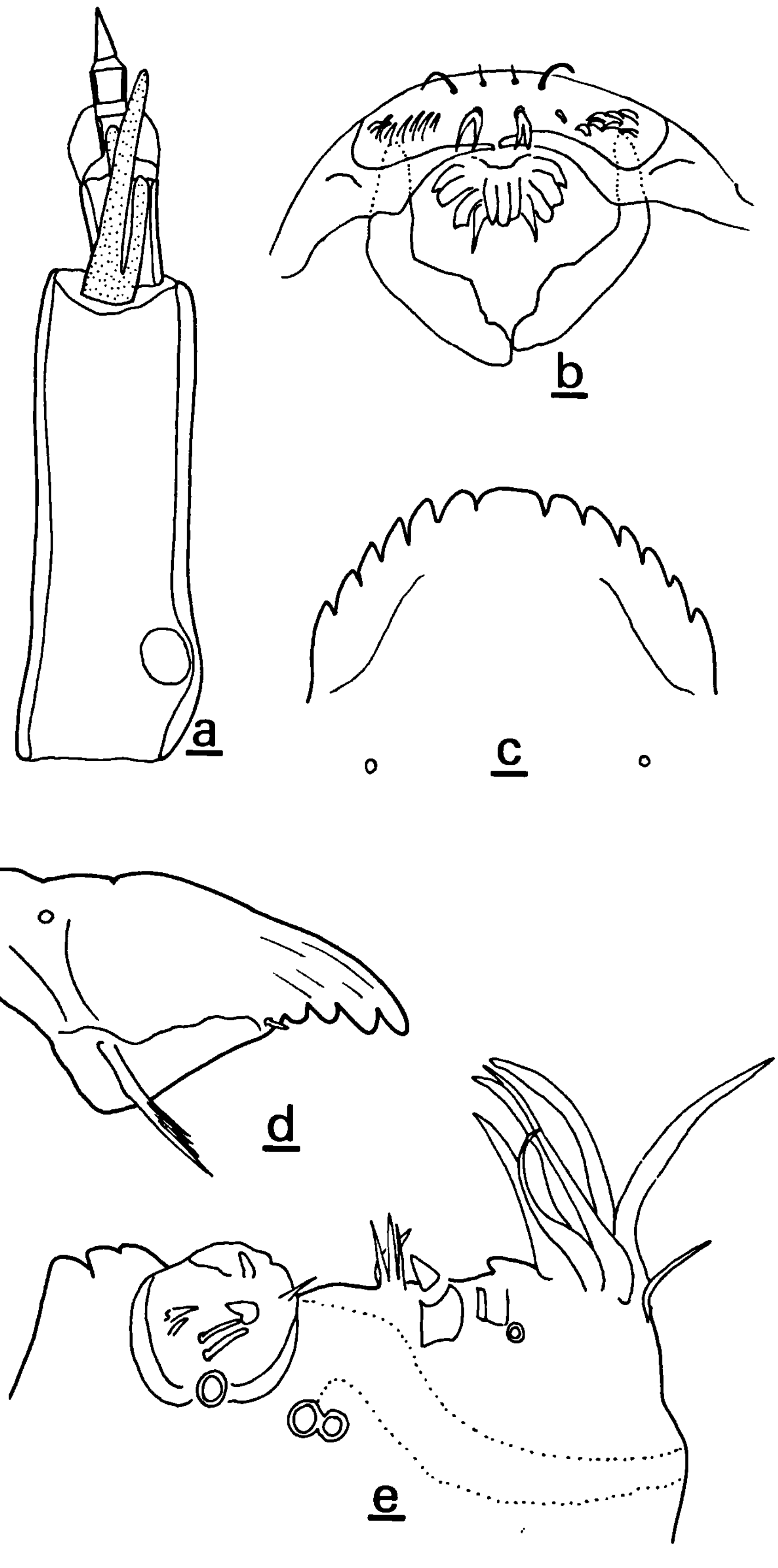


Figure 50

Orthocladius (*Orthocladius*) *rhyacobius* Kieffer

a. - Antenna (011)

b. - Labrum (011)

c. - Mentum (400)

d. - Mandible (400)

e. - Claws of anterior parapod (011)

Fig.50

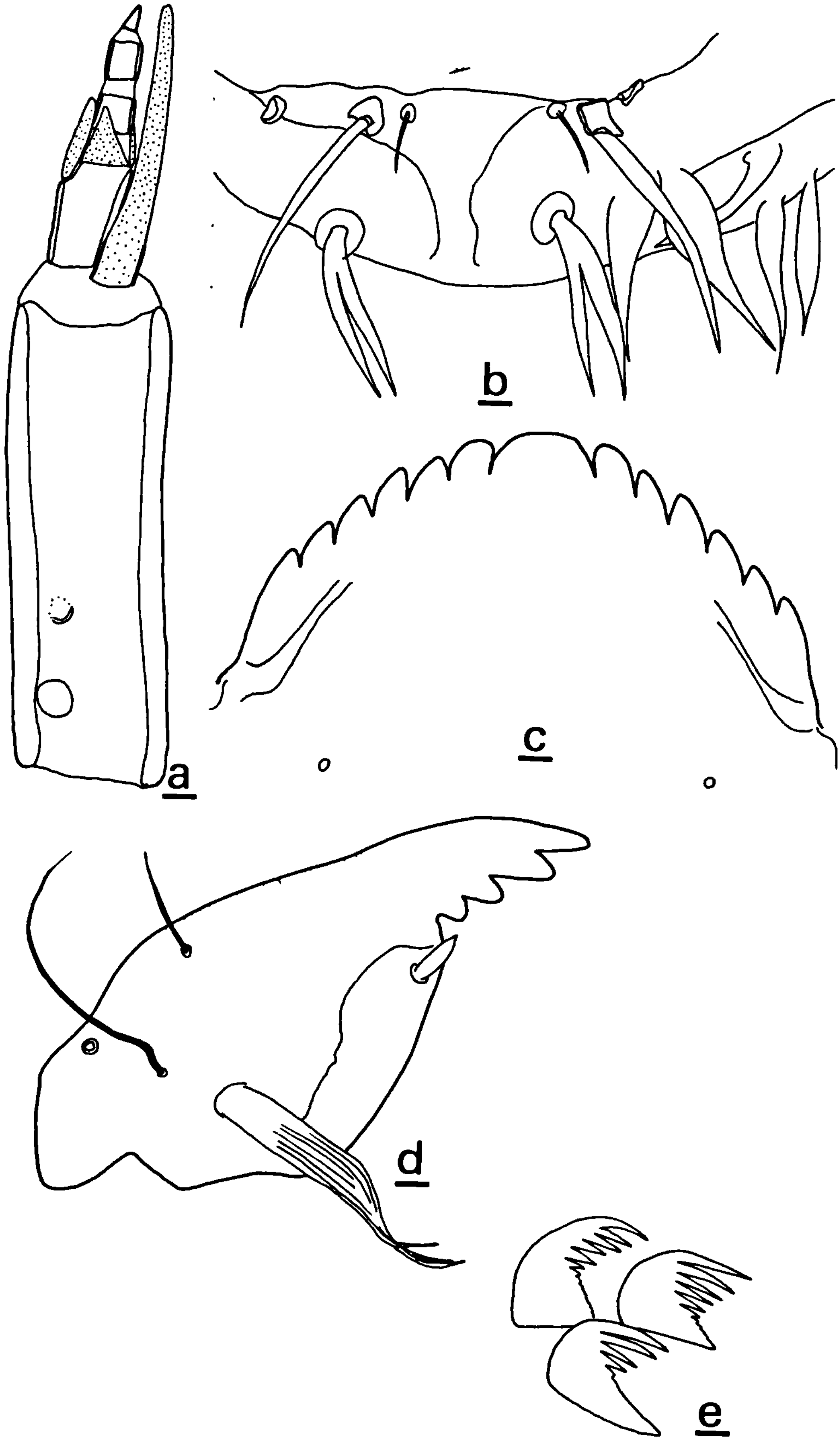


Figure 51

Orthocladius (*Orthocladius*) *rubicundus* (Meigen)

a. - Antenna (Oil)

b. - Labrum and palatum (Oil)

c. - Mentum (400)

d. - Mandible (400)

e. - Maxilla (Oil)

Fig. 51

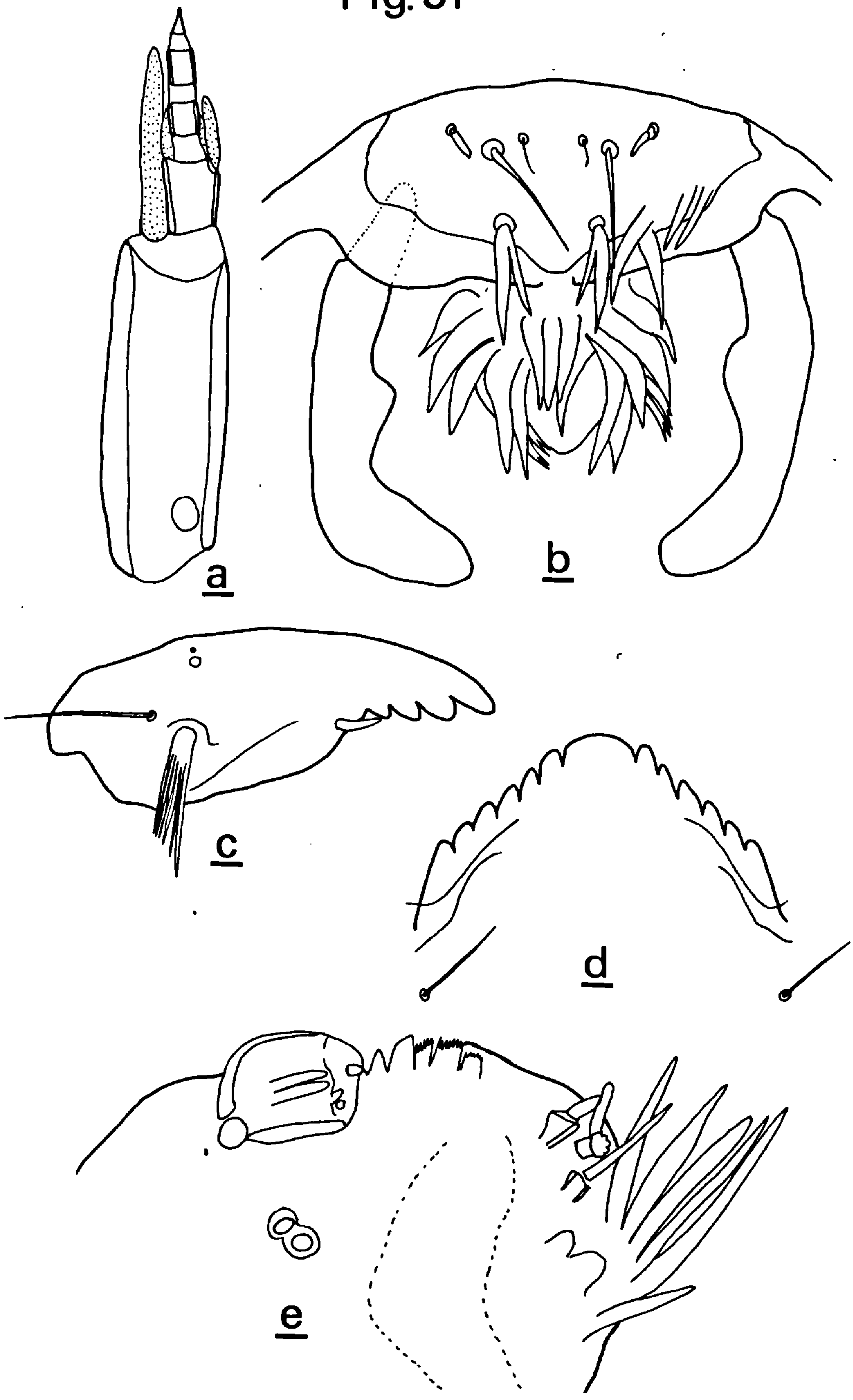


Figure 52

Orthocladius (O.) vetterensis Brundin

a. - Antenna (Oil)

b. - Labrum and premandible. Reconstructed from damaged specimen, positions not accurate. Palatum too badly prepared for a figure (400)

c. - Mentum (Right half fully flattened, left half not). Reconstructed from two halves of the mentum (400).

d. - Mandible (400)

e. - Claws of anterior parapod.

Fig. 52

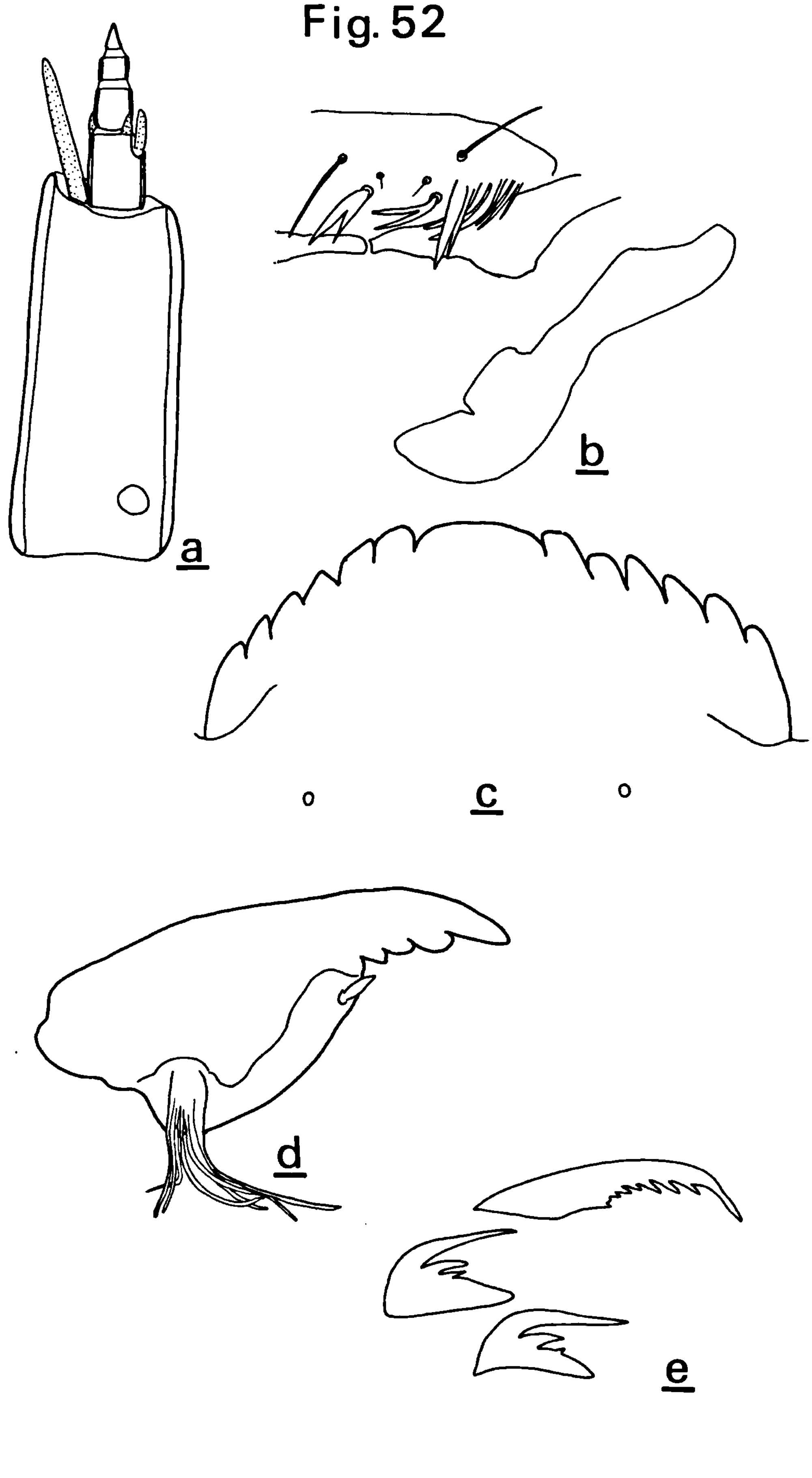


Figure 53

Orthocladius (*Orthocladius*) *species A* of Pinder

a. - Antenna (Oil)

b. - Mentum (400)

c. - Mandible (400)

d. - Maxilla (Oil)

Fig.53

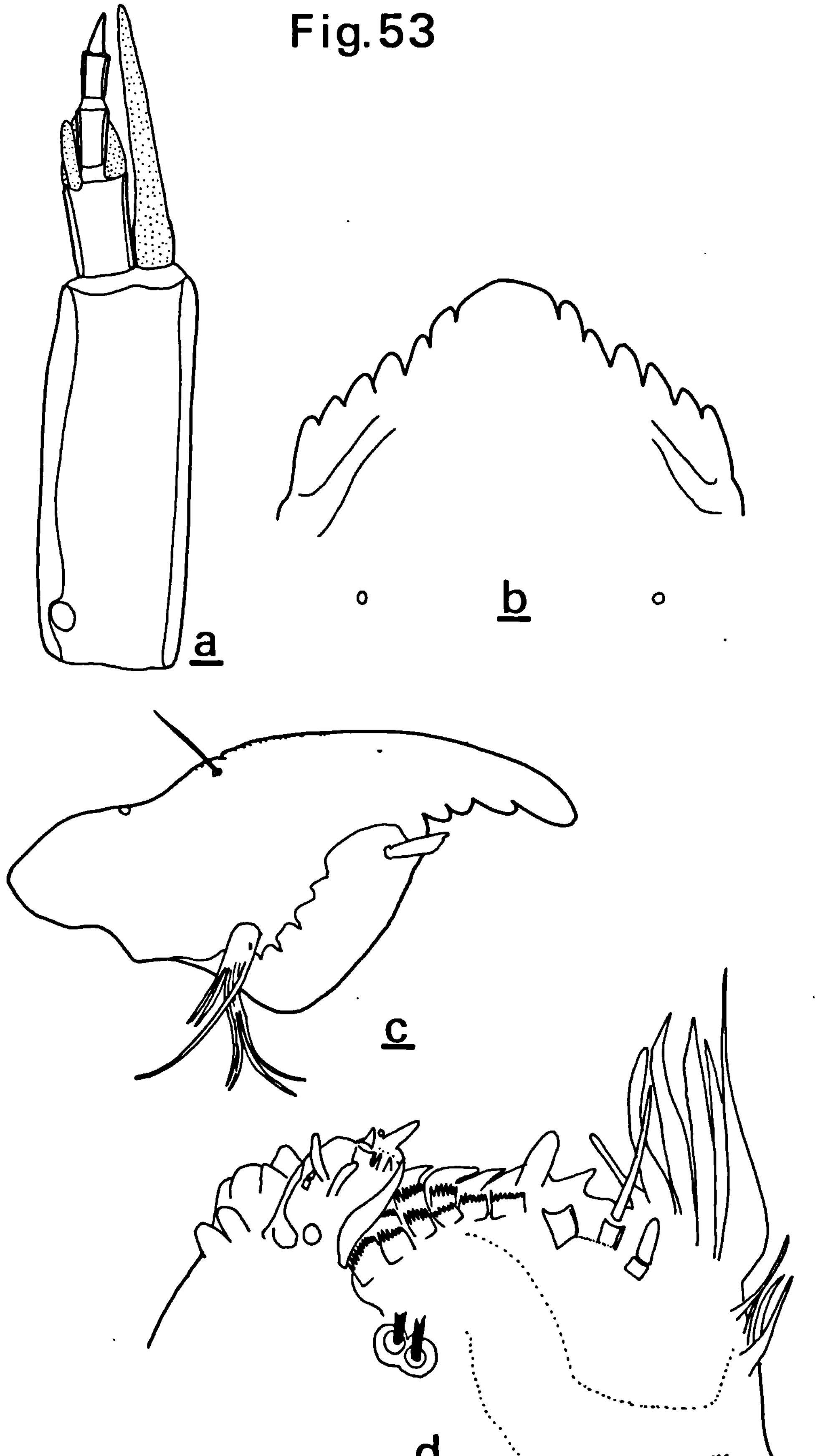


Figure 54

Orthocladius (Orthocladius) ? oblidens (Walker)

a. - Antenna (Oil)

b. - Mentum (400)

c. - Mandible (400)

d. - Maxilla (Oil)

Fig.54

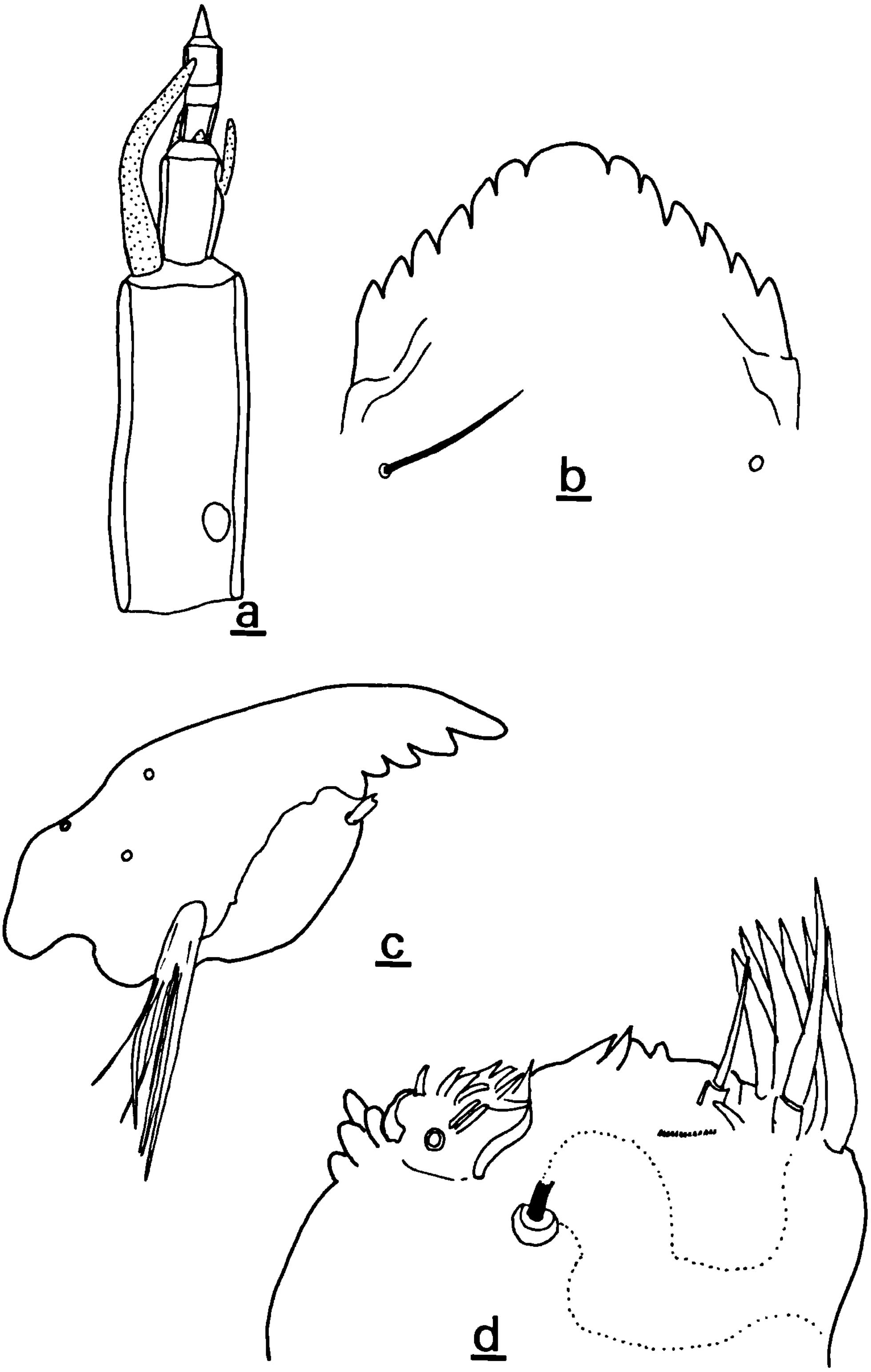


Figure 55

Orthocladius (*Pogonocladius*) *consobrinus* (Holmgren)

a. - Antenna (011)

b. - Labrum and palatum (400)

c. - Mentum (400)

d. - Mandible (400)

e. - Maxilla (011)

Fig.55

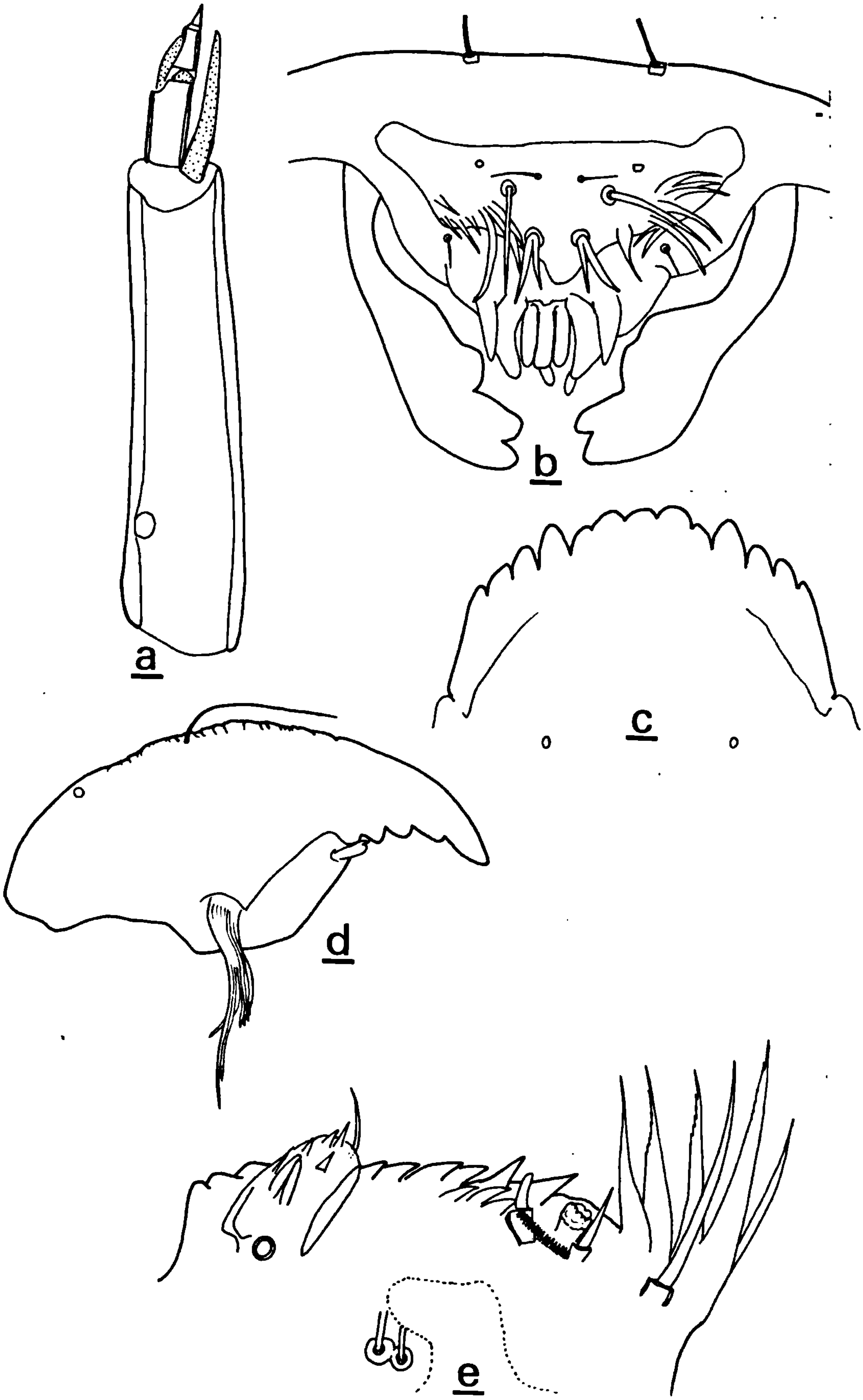


Figure 56

Paracladius conversus Walker

a. - Antenna (Oil)

b. - Labrum (Oil)

c. - Mandible (400)

d. - Mentum (400)

e. - Maxilla (Oil)

f. - Procercus (400)

Fig.56

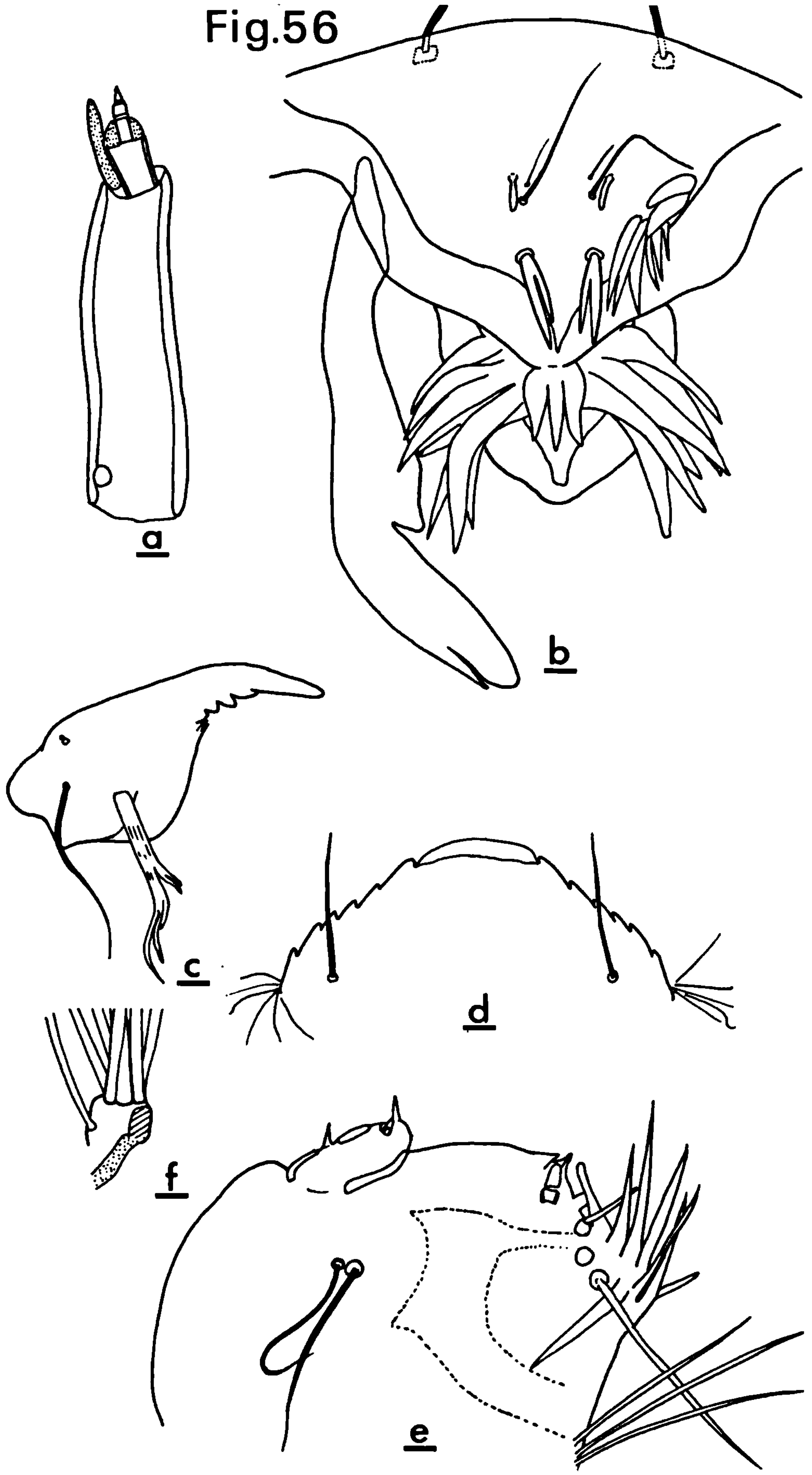


Figure 57

Parakiefferiella bathophila Kieffer

a. - Antenna (Oil)

b. - Labrum (Oil)

c. - Mandible (Oil)

d. - Mentum (Oil)

e. - Maxilla (Oil)

Fig.57

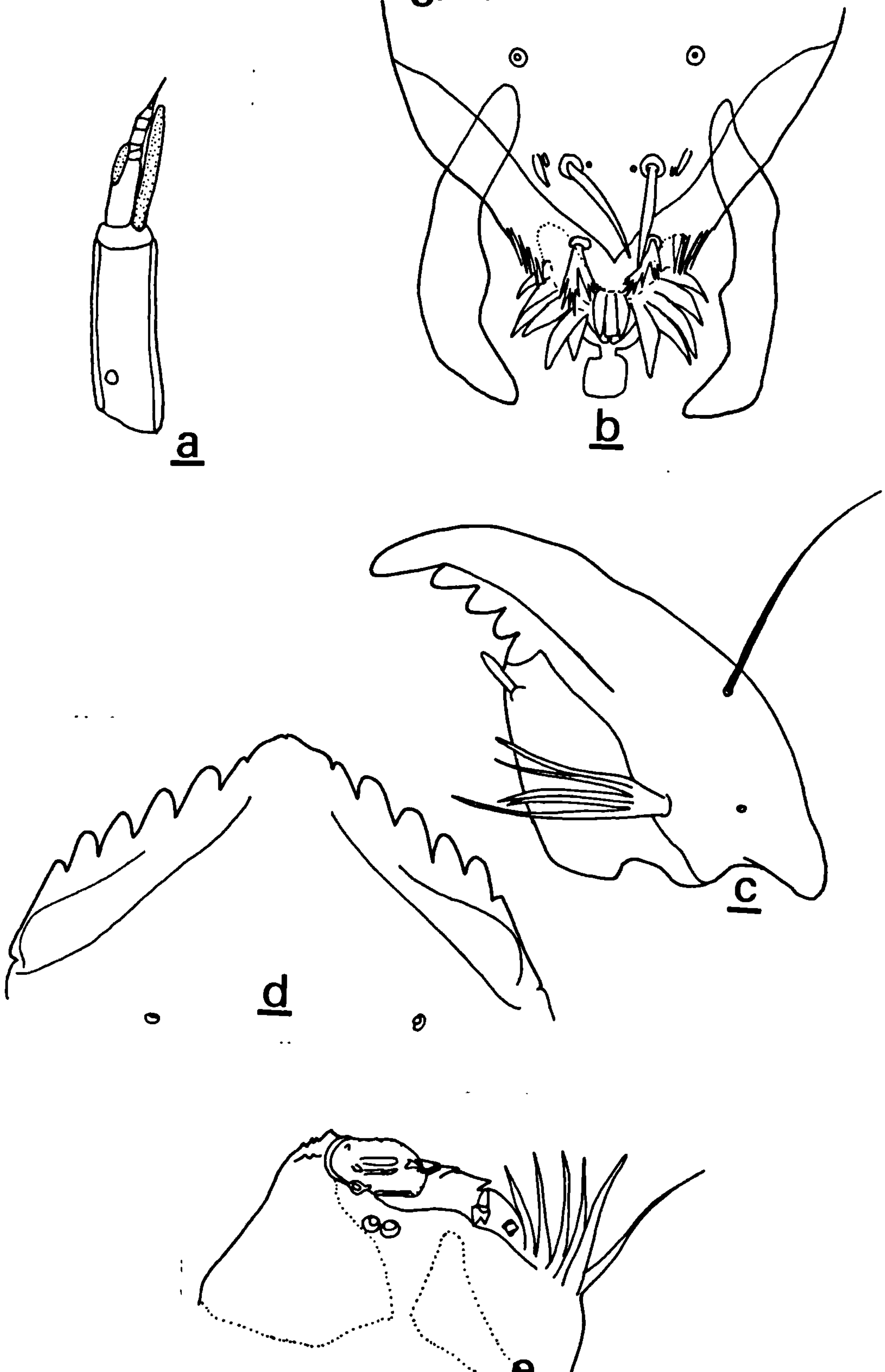


Figure 58

Paralimnophyes hydrophilus (Goetghebuer)

a. - Antenna (Oil)

b. - Mentum (400)

c. - Maxilla (Oil)

d. - Mandible (400)

e. - Terminal segments of the abdomen (100)

Fig. 58

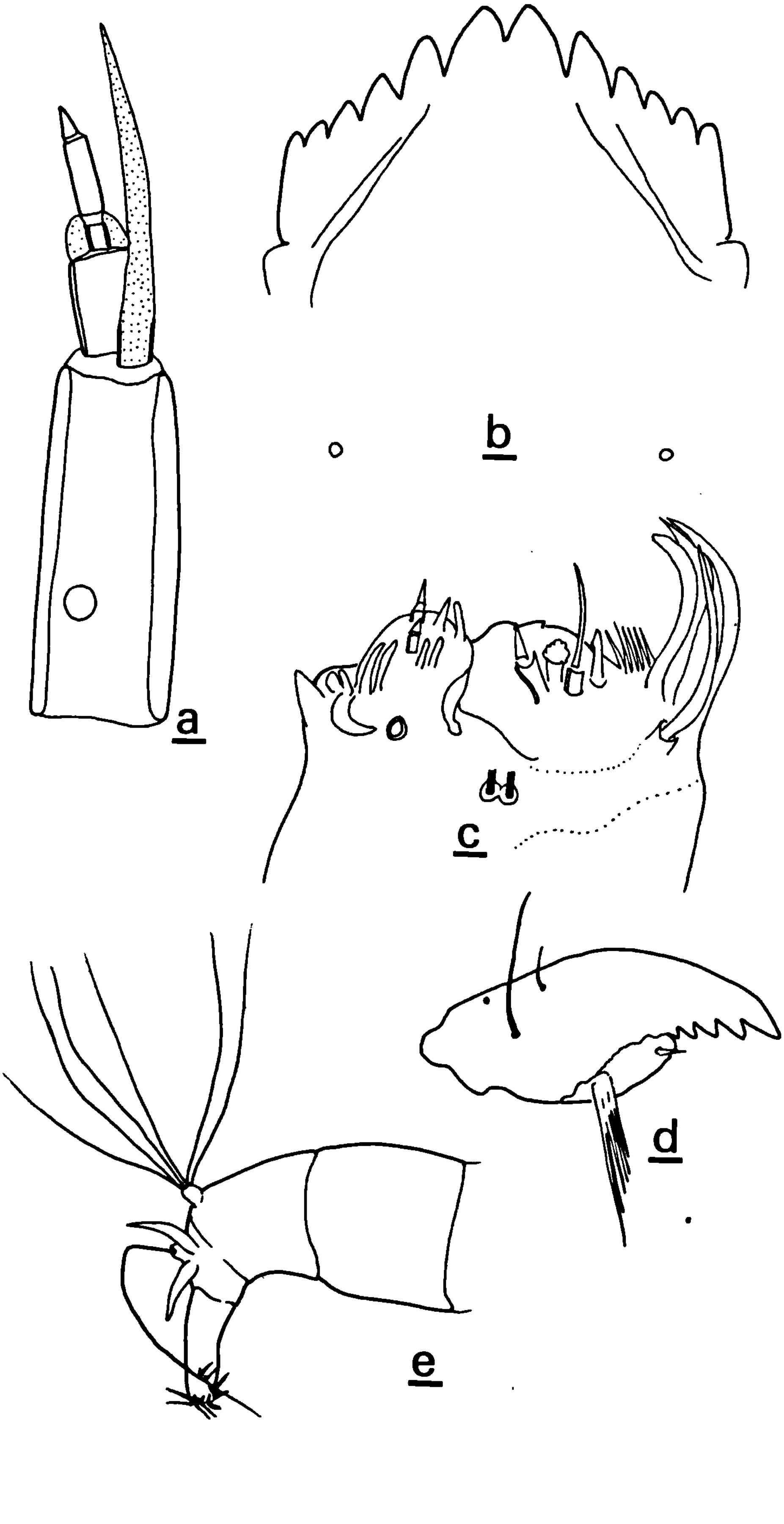


Figure 59

Parametriocnemus stylatus Kieffer

a. - Antenna (Oil)

b. - Part of the labrum and palatum (slightly twisted such that the pecten epipharynx cannot be seen) (Oil)

c. - Mandible (400 +)

d. - Mentum (Oil)

e. - Maxilla (Oil)

Fig.59

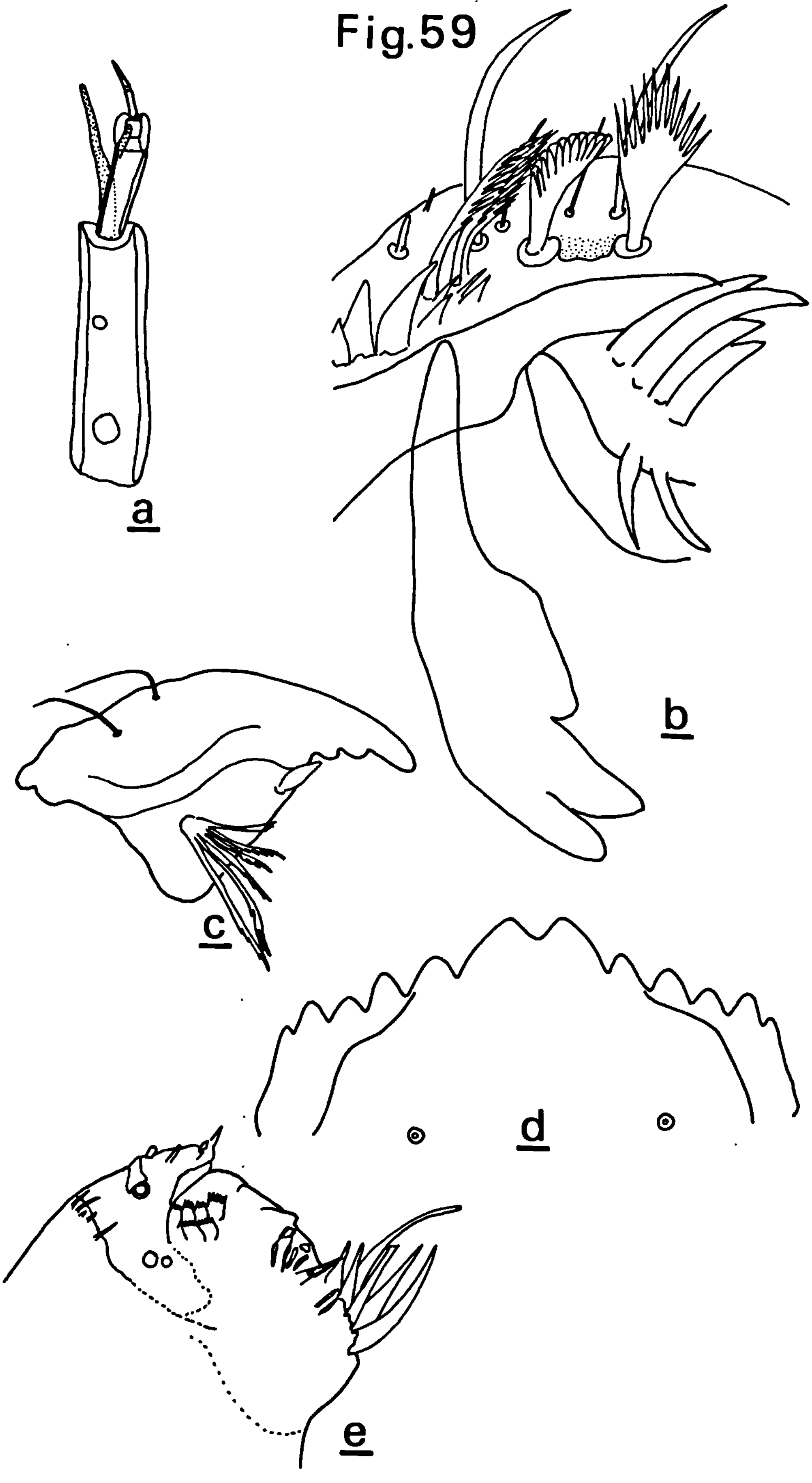


Figure 62

Paraphaenocladius sp. A.

a. - Antenna (011)

b. - Premandible (011)

c. - S. setae (011)

d. - Mentum (011)

e. - Mandible (011)

f. - Maxilla (011)

g. - Abdomen (100)

Fig.60

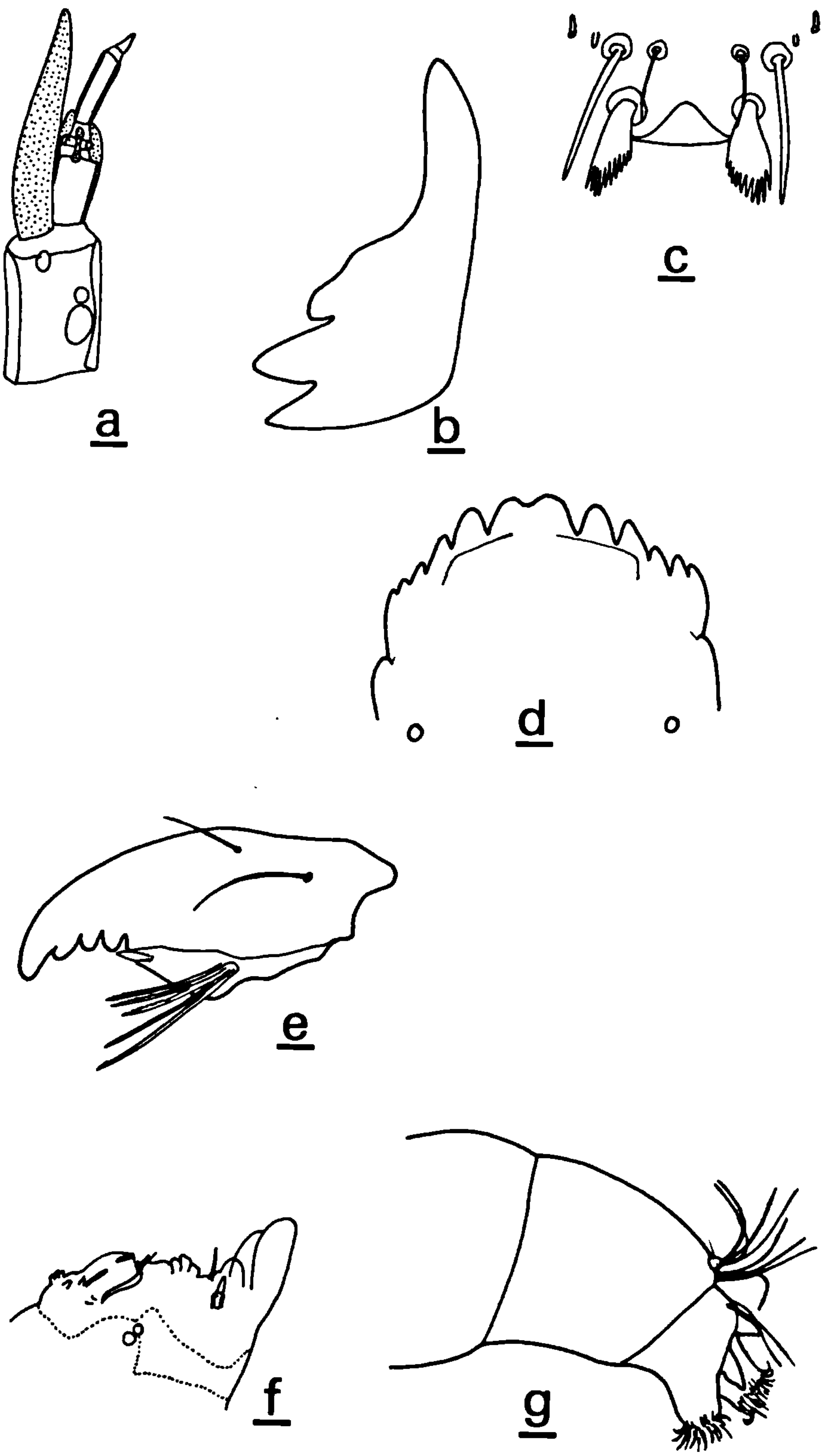


Figure 61

Paratrichocladius

a. - *rufiventris* (Meigen) antenna (Oil)

b. - *rufiventris* mentum (Oil)

c. - *rufiventris* mandible (400)

d. - *skirwithensis* (Edwards) mandible (400)

e. - Dorsal view of clypeus *skirwithensis* (100)

f. - *skirwithensis* antenna (Oil)

g. - *skirwithensis* mentum (Oil)

Fig.61

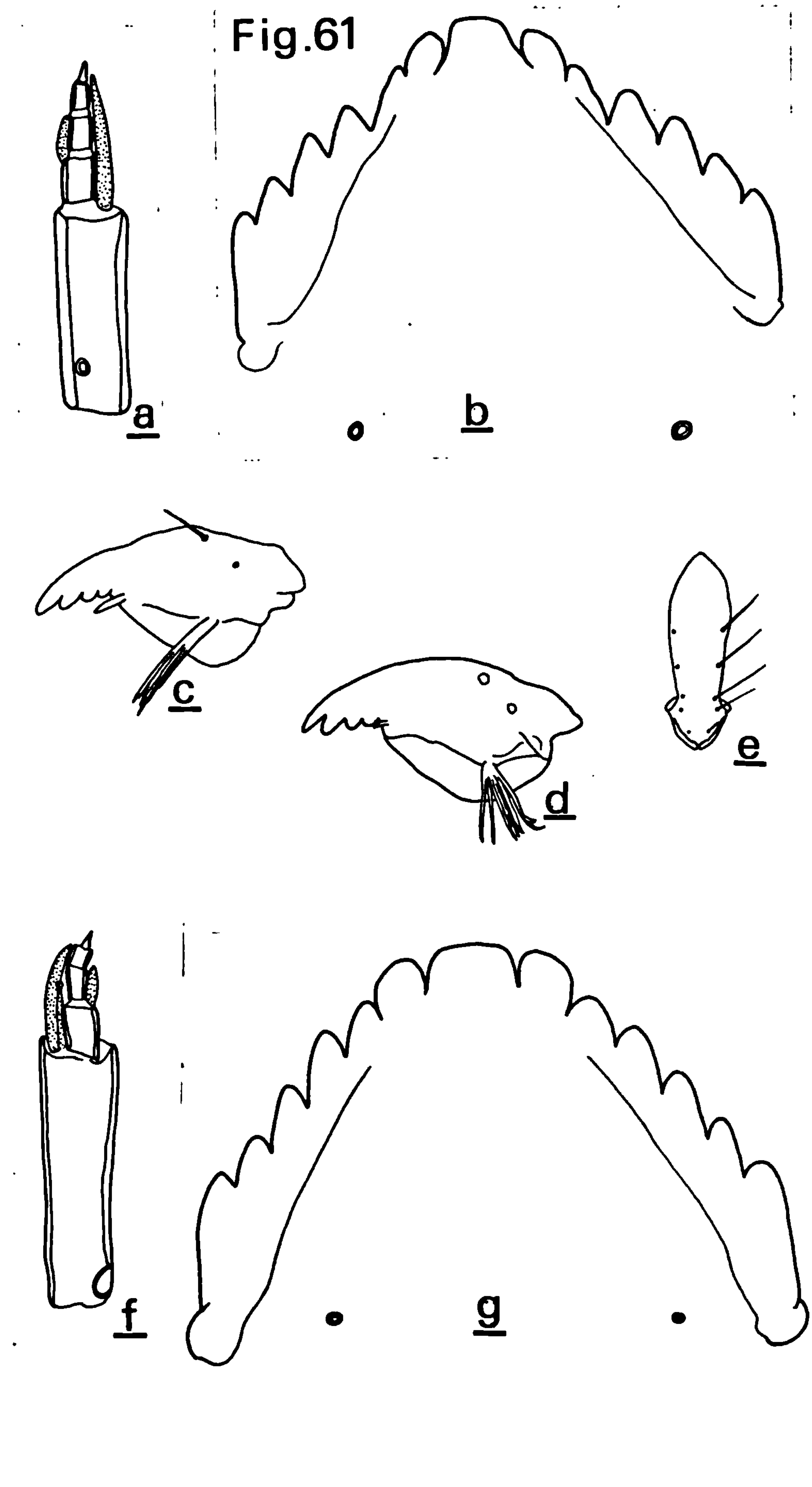


Figure 62

Paratrissocladius excerptus (Walker)

a. - Antenna (400)

b. - Labrum and palatum (011)

c. - Mandible (400)

d. - Mentum (400)

Fig.62

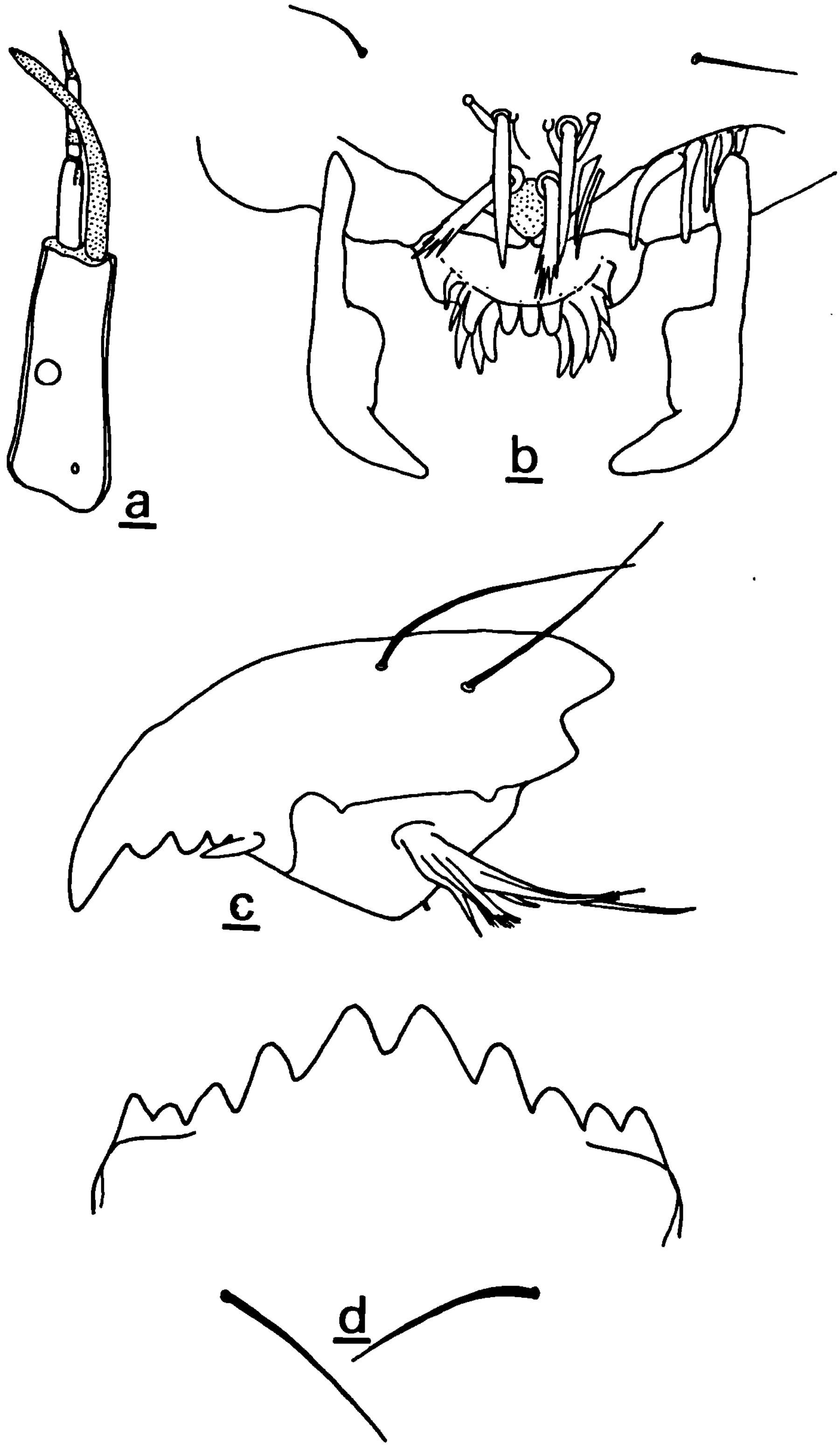


Figure 63

Psectrocladius (Allopsectrocladius) obvius

a. - Antenna (400)

b. - Labrum and palatum (400)

c. - Mentum (400)

d. - Maxilla (400)

e. - Mandible (400)

f. - Procercus (100)

Fig. 63

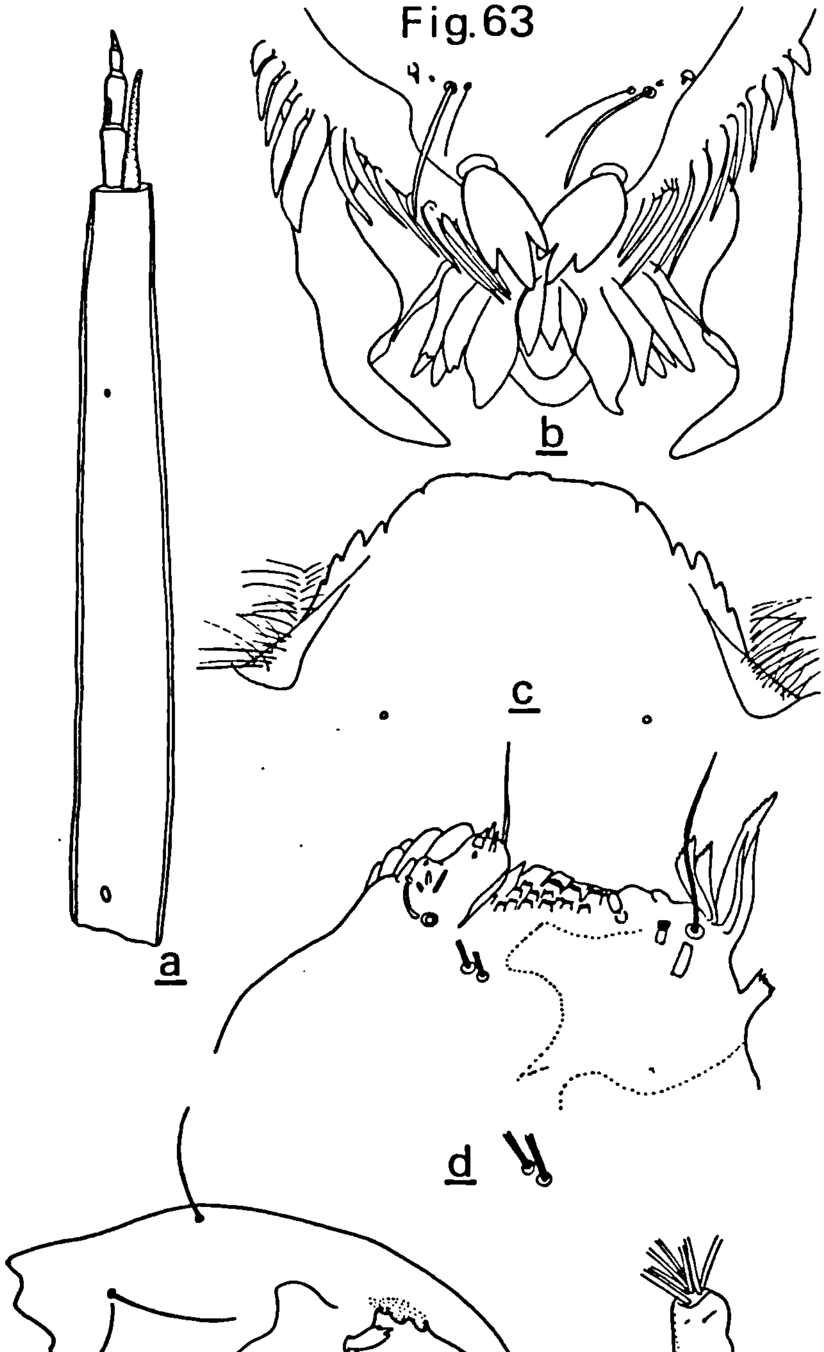


Figure 64

Psectrocladius barbimanus Edwards

a. - Antenna (400)

b. - Labrum and palatum (011)

c. - Mentum (400)

d. - Mandible (400)

e. - Maxilla (011)

Fig. 64

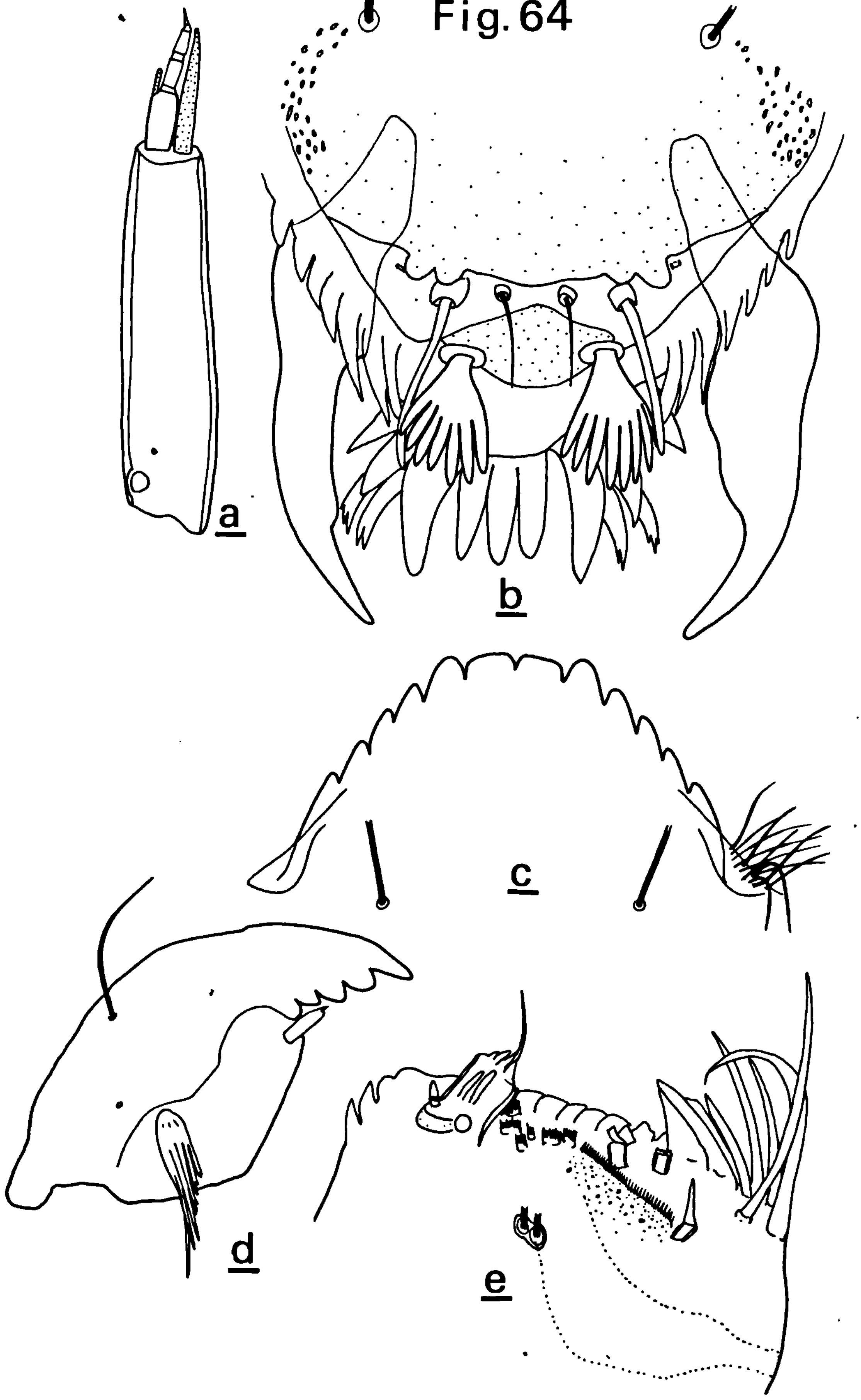


Figure 65

Psectrocladius edwardsi Brundin

a. - Antenna (011)

b. - Mentum (400)

c. - Mandible (400)

d. - Maxilla (011)

Fig. 65

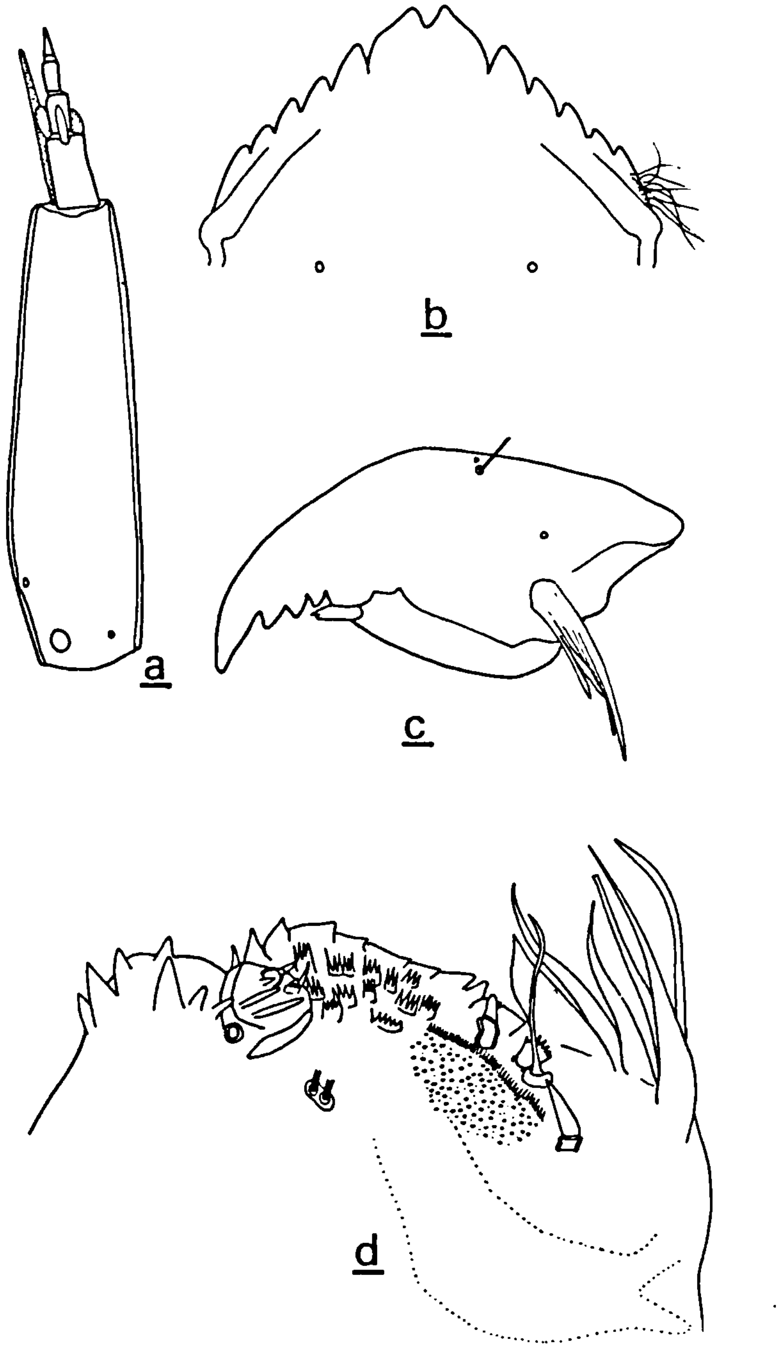


Figure 66

Psectrocladius limbatellus (Holmgren)

a. - Antenna (011)

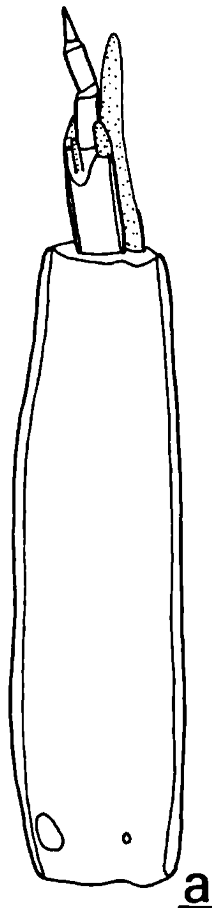
b. - Labrum and palatum (400)

c. - Mentum (400)

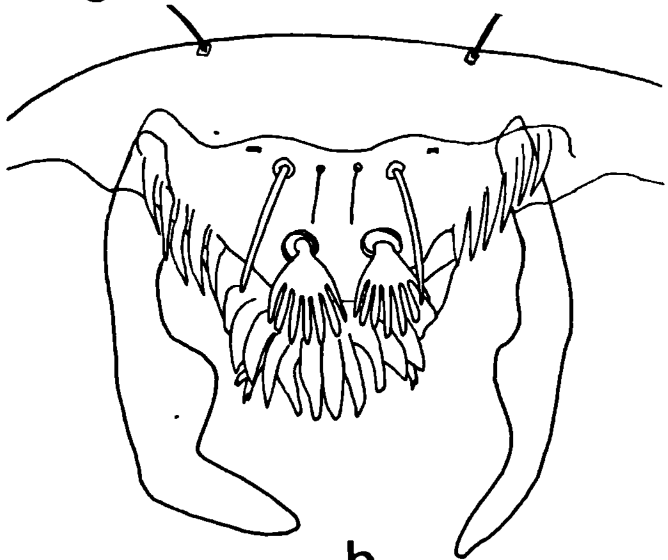
d. - Mandible (400)

e. - Procercus (400)

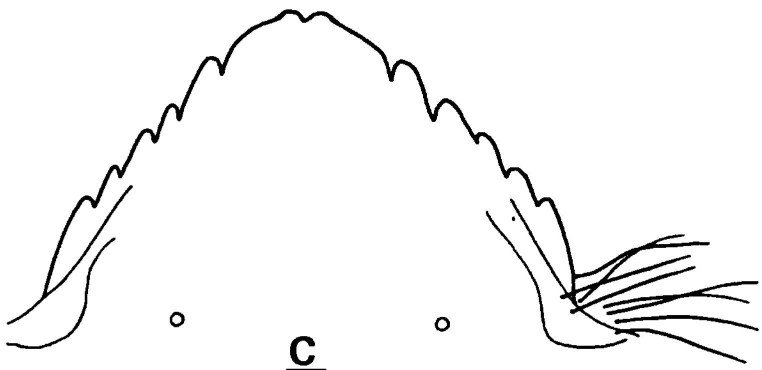
Fig.66



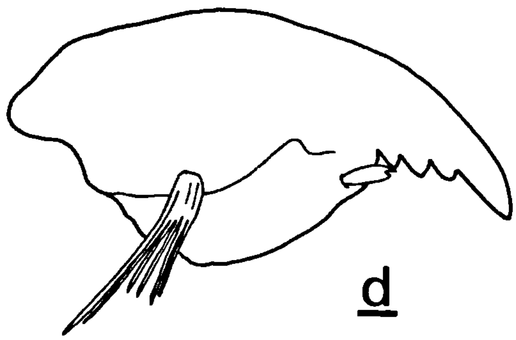
a



b



c



d

e

Figure 67

Psectrocladius octomaculatus Wulker

a. - Antenna (011)

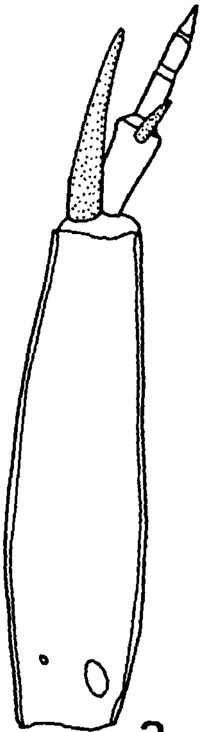
b. - Labrum and palatum (011)

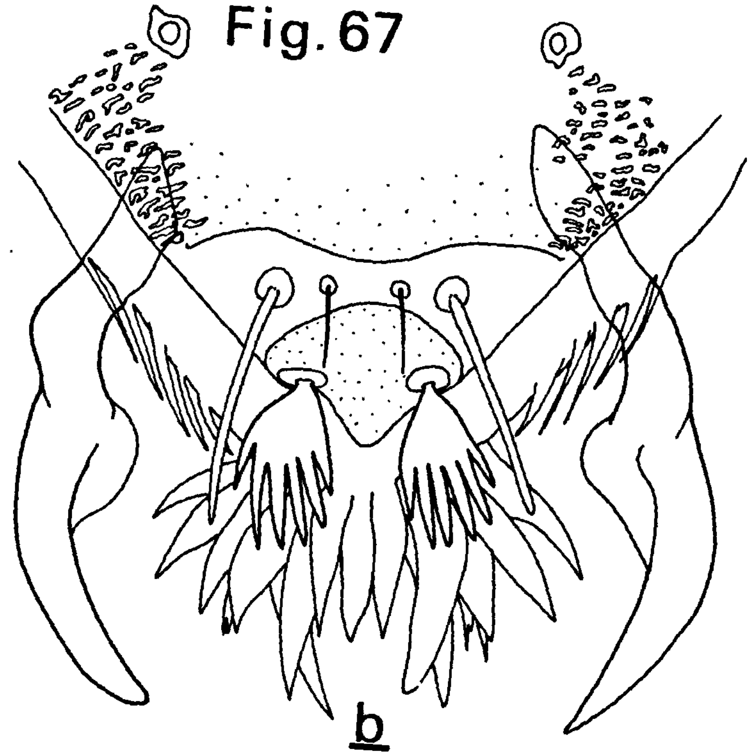
c. - Mentum (400)

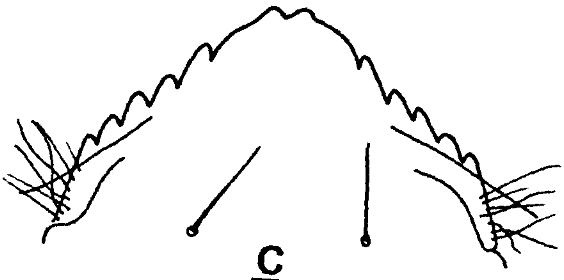
d. - Mandible (400)

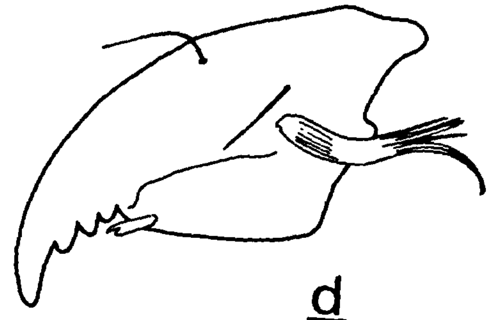
e. - Maxilla (011)

Fig. 67


a


b


c


d

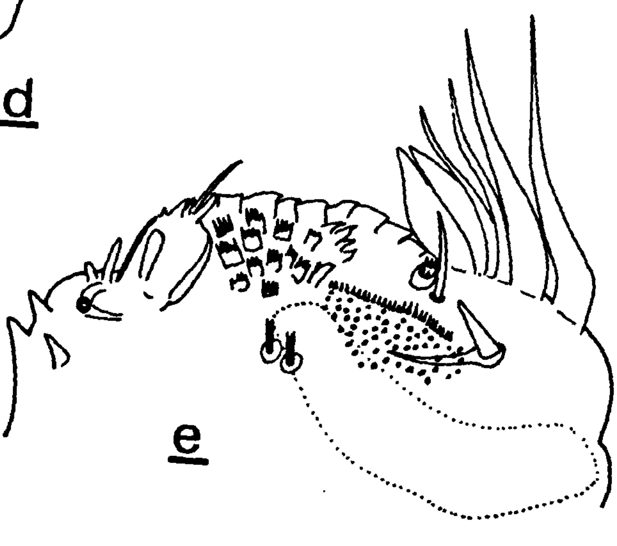

e

Figure 63

Psectrocladius psilopterus Kieffer

a. - Antenna (011)

b. - Labrum and palatum (011)

c. - Mandible (400)

d. - Mentum (400)

e. - Maxilla (011)

Fig.68

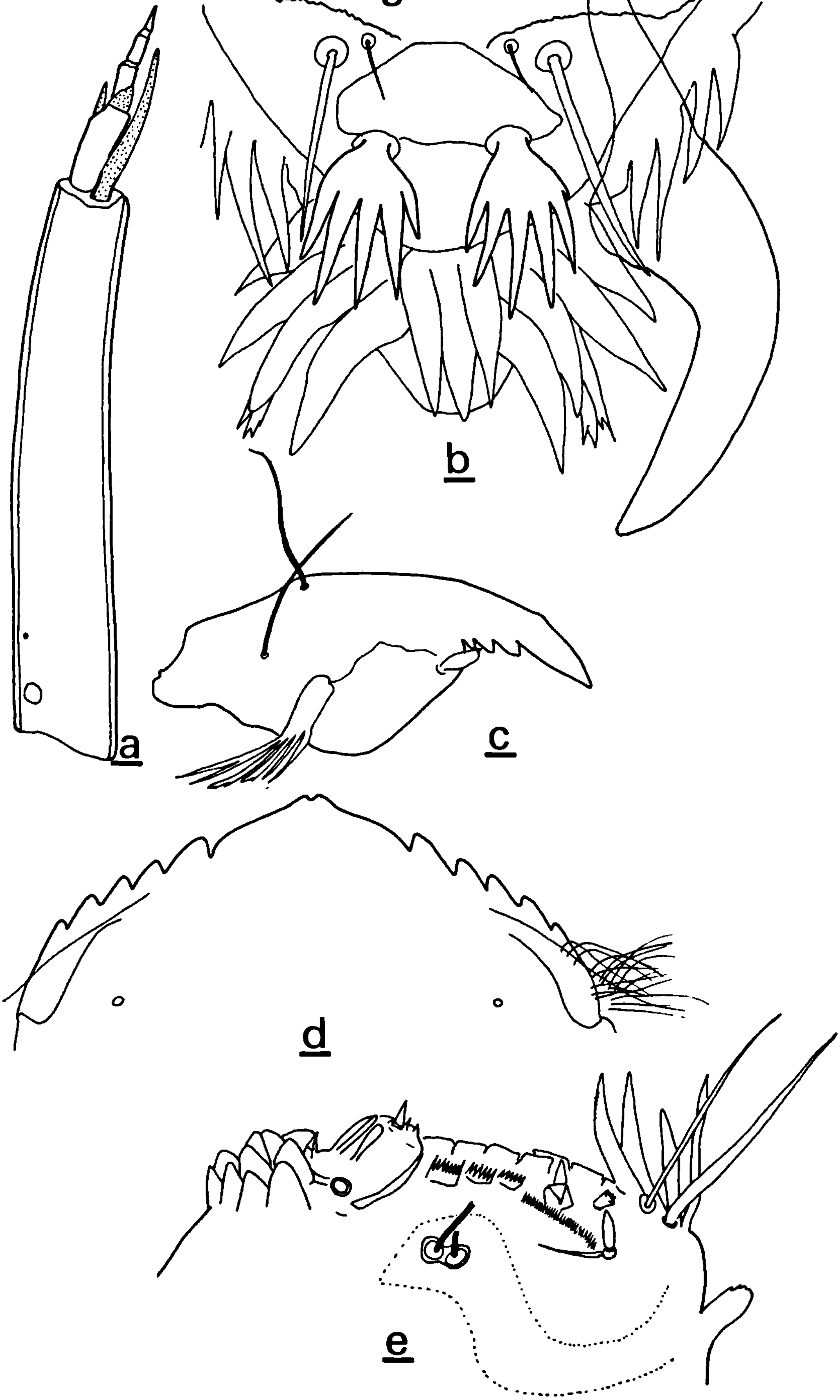


Figure 69

Psectrocladius sordidellus (Zetterstedt)

a. - Antenna (011)

b. - Labrum and palatum (011)

c. - Mandible (400)

d. - Mentum (400)

Fig.69

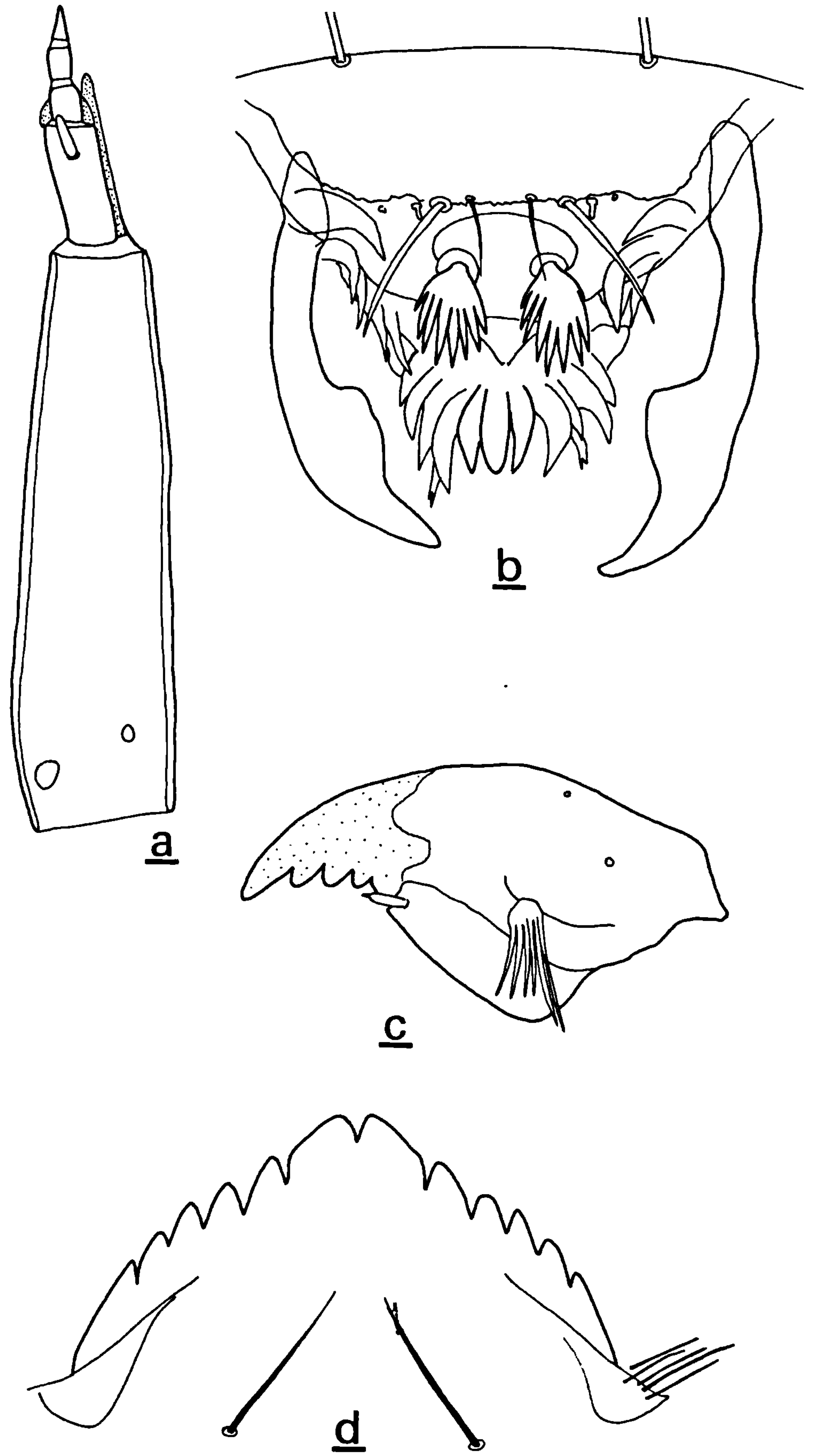


Figure 70

Pseudorthocladius cfr *curtistylus*

a. - Antenna (Oil)

b. - Labrum and palatum (Oil)

c. - Mandible (Oil)

d. - Mentum (400)

e. - Posterior segments (100)

Fig.70

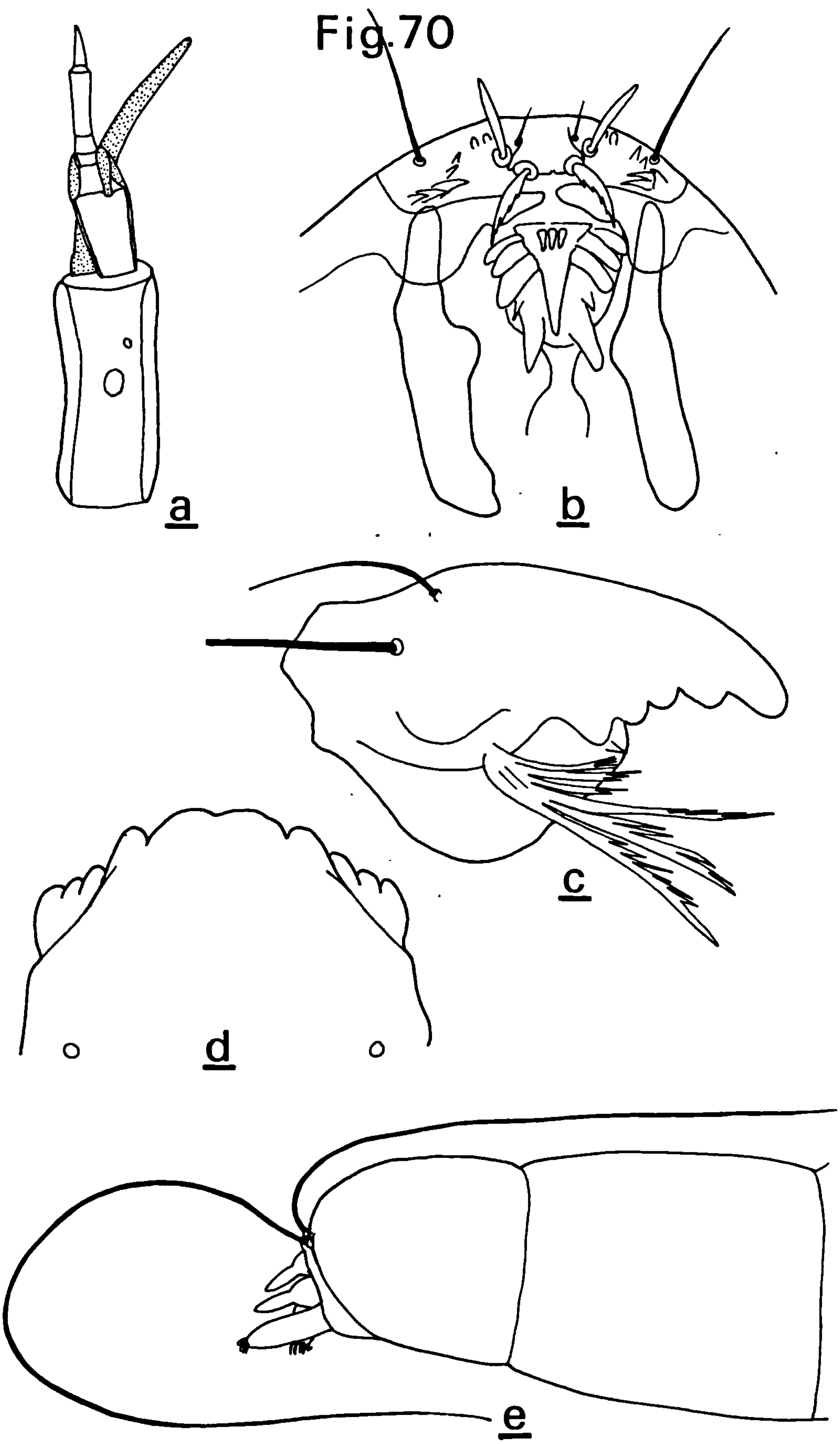


Figure 71

Pseudosmittia

a. - Antenna of undetermined species (011)

b. - Labrum and palatum of undetermined species (011)

c. - Mandible of undetermined species (011)

d. - Mentum of undetermined species (011)

e. - Maxilla of undetermined species (011)

f. - Anterior parapods of undetermined species (200)

Fig.71

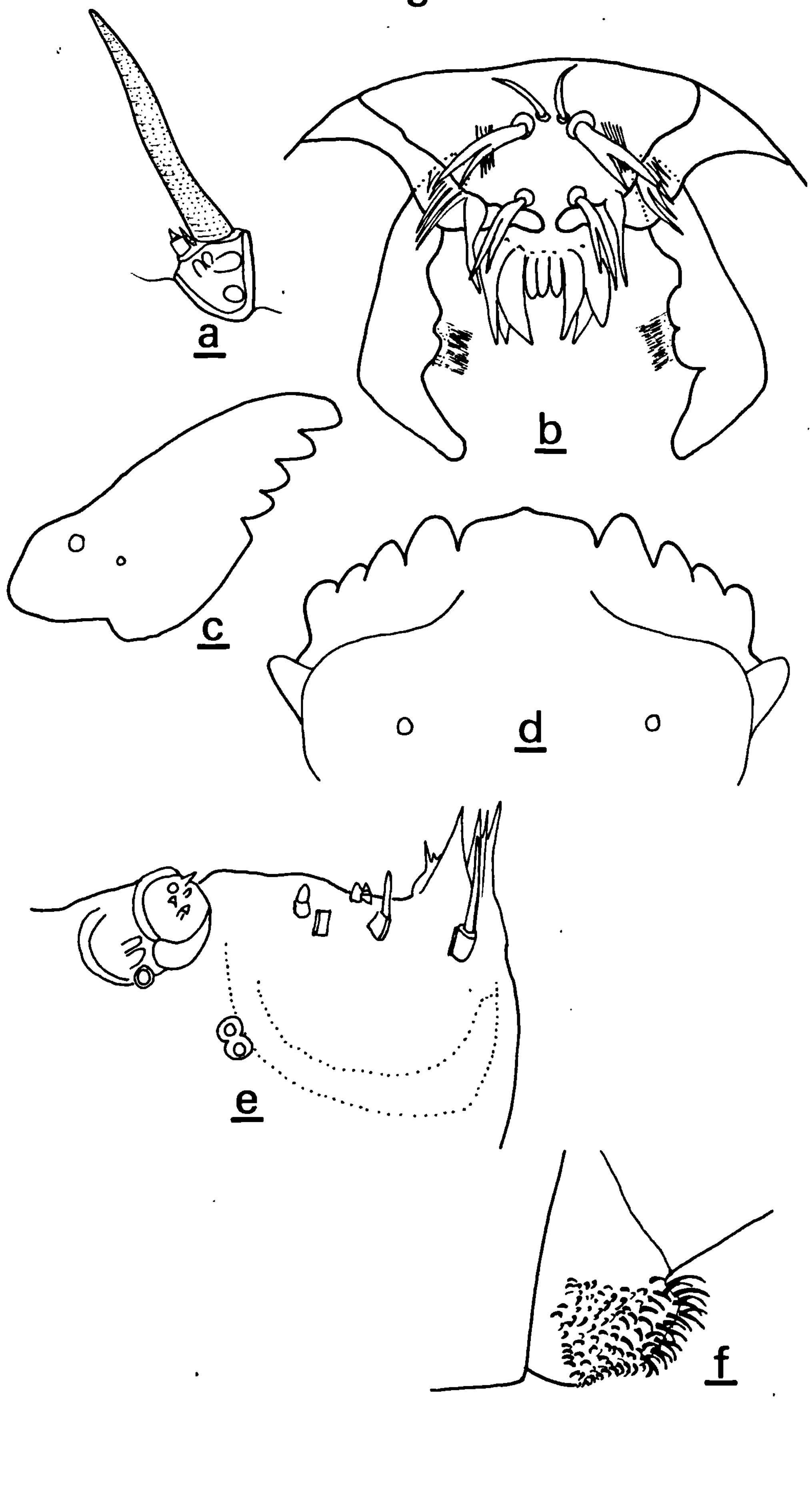


Figure 72

Rheocricotopus chalybeatus Edwards

a. - Antenna (011)

b. - Labrum and palatum (011)

c. - Mandible (400)

d. - Procercus (011)

e. - Maxilla (011)

Fig.72

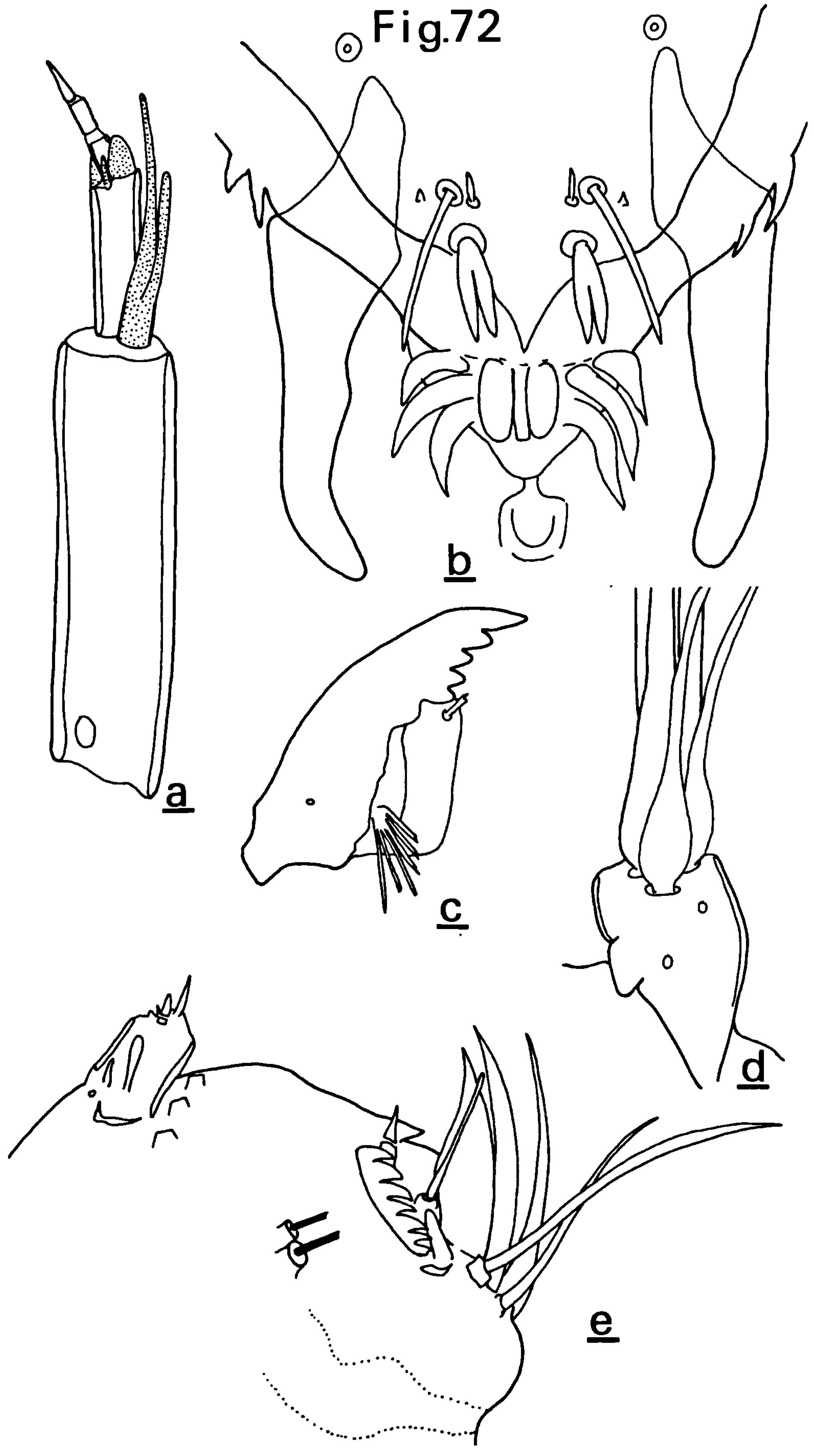


Figure 73

Rheocricotopus effusus Walker

a. - Antenna (Oil)

b. - Labrum and palatum (Oil)

c. - Mentum (400)

d. - Mandible (400)

e. - Maxilla (Oil)

Fig.73

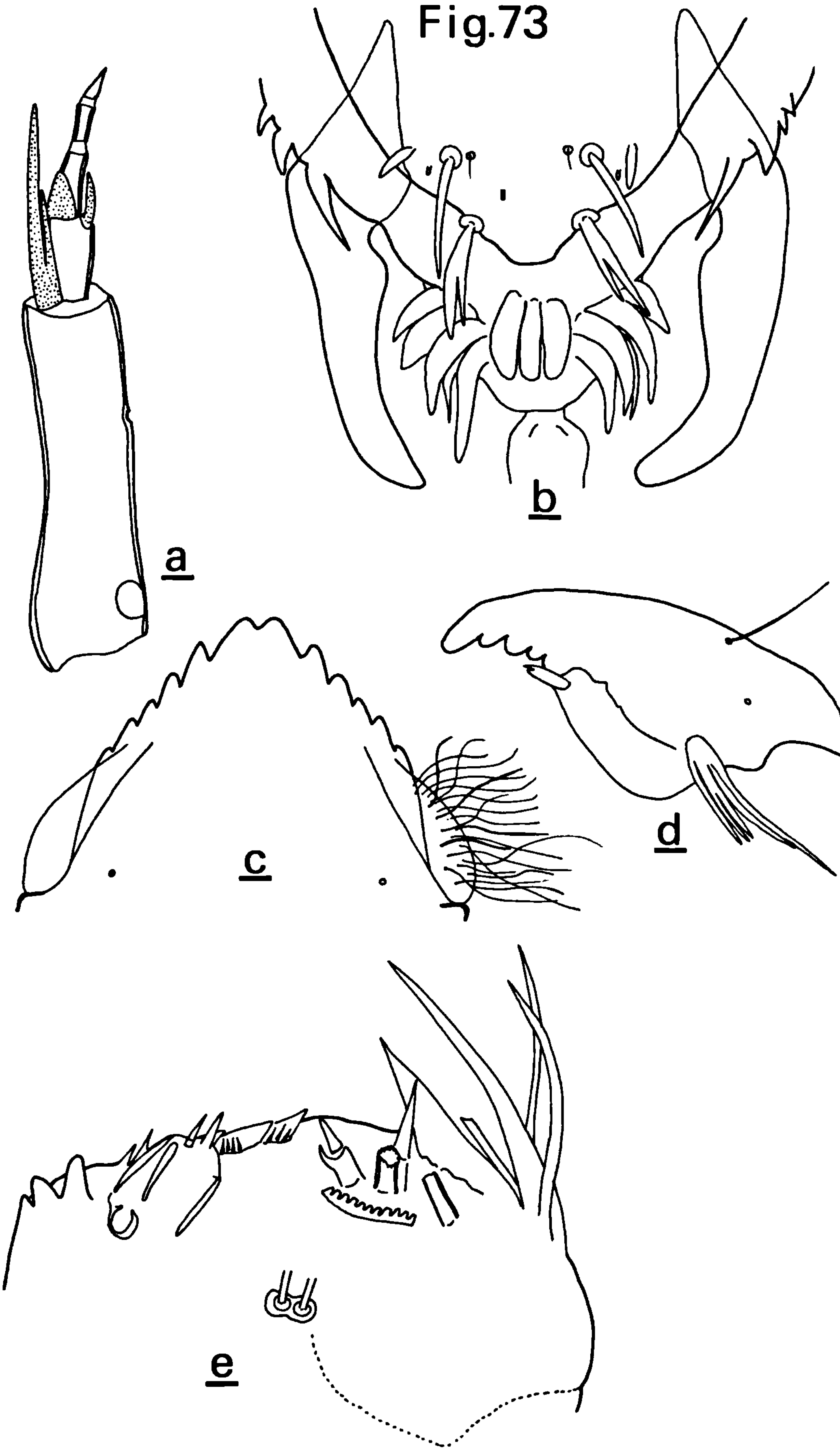


Figure 74

<u>Rheocricotopus fuscipes</u> (dispar)

a. - Antenna (011)

b. - Labrum (011)

c. - Mandible (400)

d. - Mentum (011)

e. - Maxilla (011)

f. - Procercus (011)

Fig.74

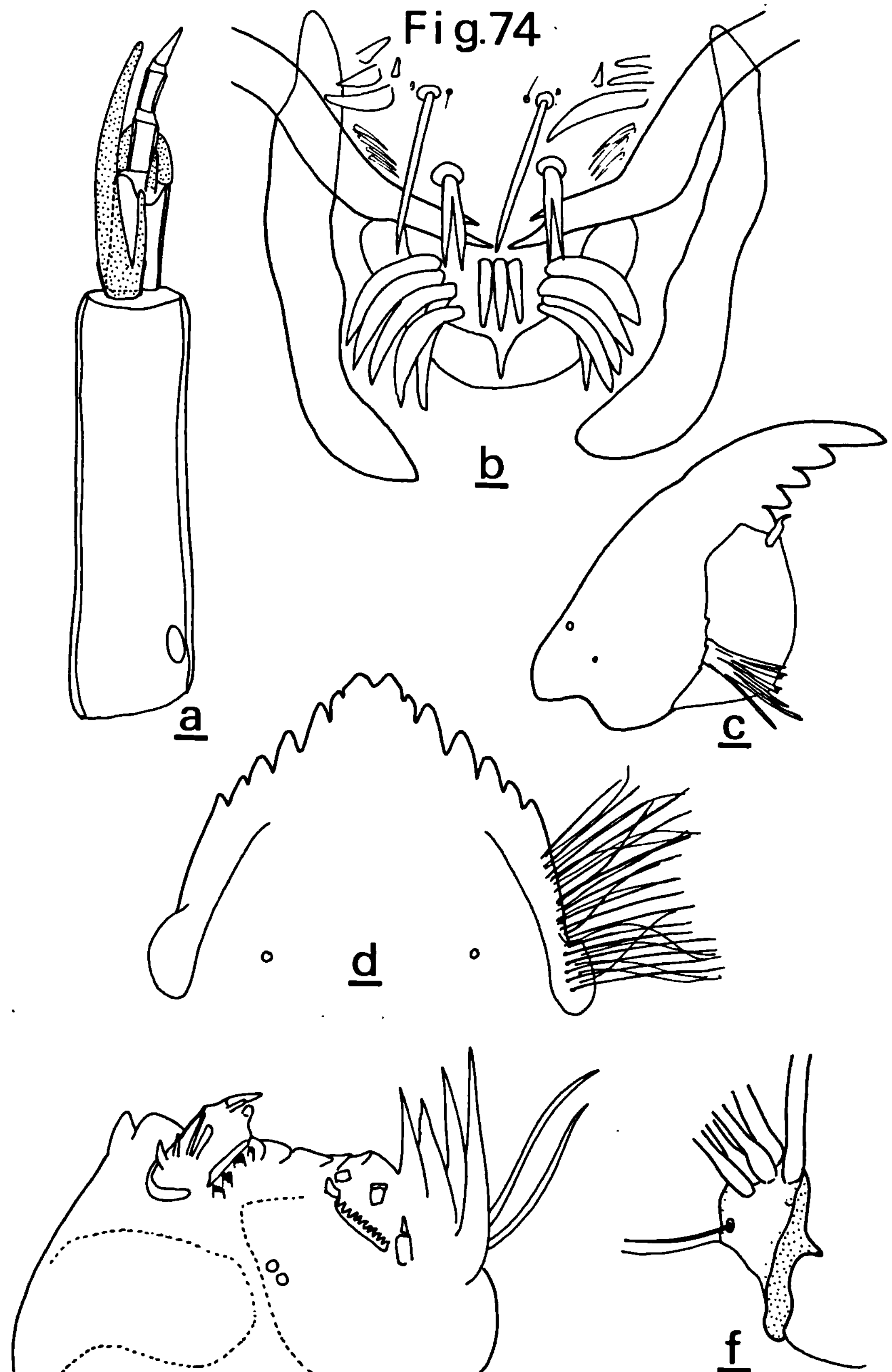


Figure 25

Smittia ? contingens (Walker)

a. - Antenna (O11)

b. - Labrum and palatum (O11)

c. - Mandible (O11)

d. - Mentum (O11)

e. - Maxilla (O11)

f. - Ventral view of anterior parapods (O11)

Fig. 75

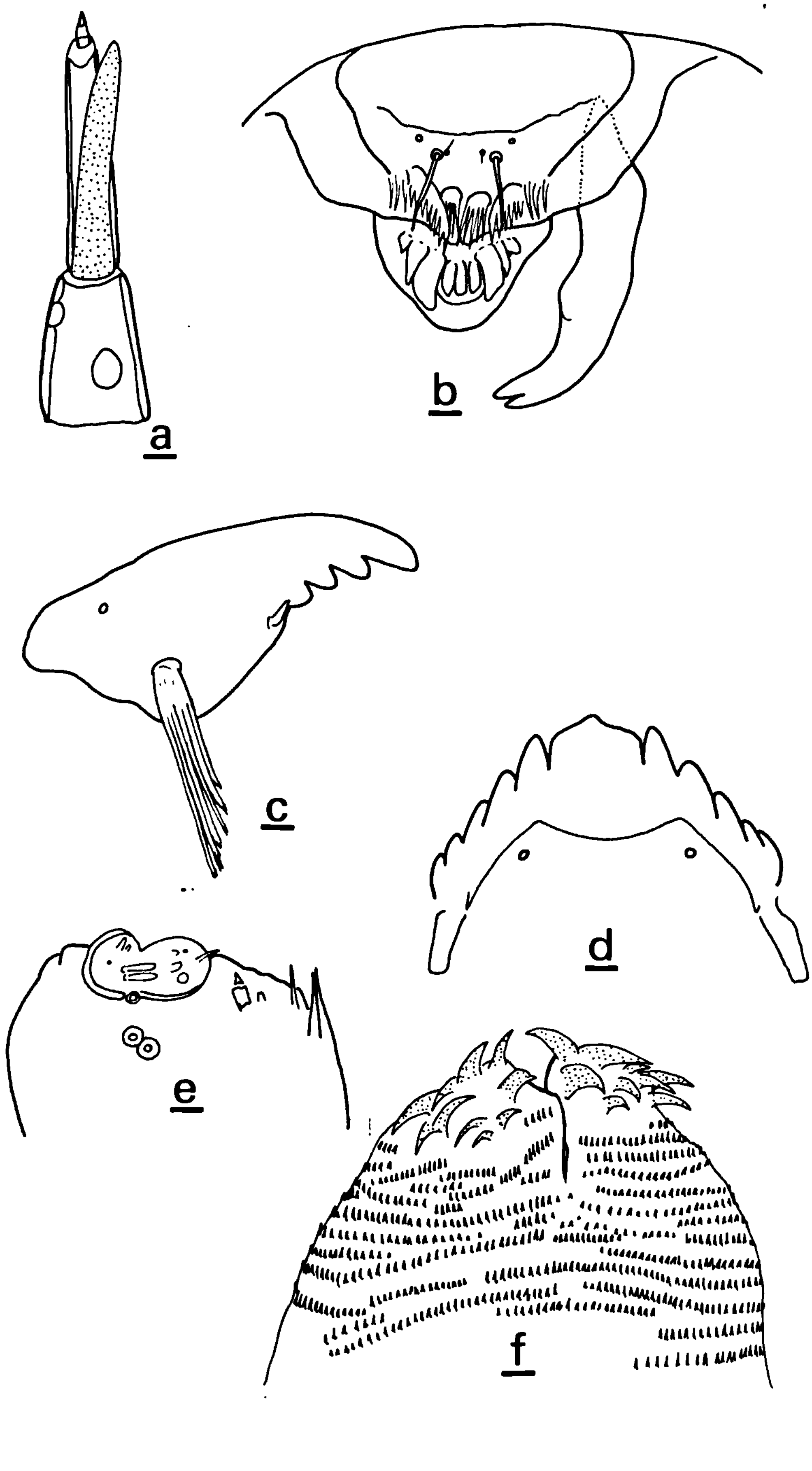


Figure 76

Synorthocladius semivirens (Kieffer)

a. - Antenna (011)

b. - Labrum (011)

c. - Premandible, lateral view, (011)

d. - Mandible (011)

e. - Maxilla (011)

f. - Mentum (400)

g. - Abdominal segment showing stellate and simple setae (400)

Fig.76

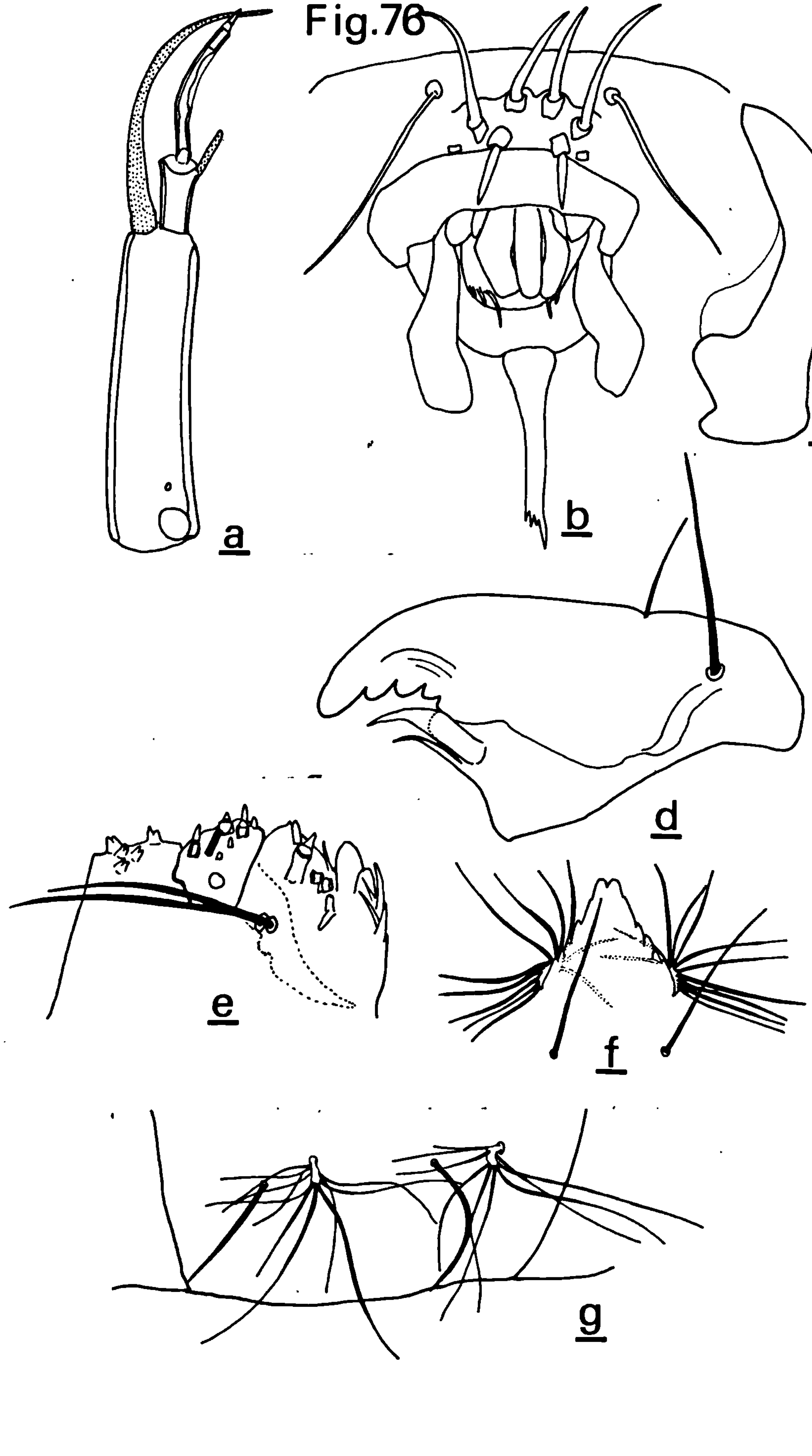


Figure 77

Thienemanniella

a. - Dorsal view of head capsule of T. *clavicornis* (Kieffer) (

b. - Labrum of T. *species B* (011)

c. - Mandible of T. *fusca* (Kieffer) (011)

d. - Antenna of T. *fusca* (011)

e. - Maxilla of T. *species B* (011)

Fig.77

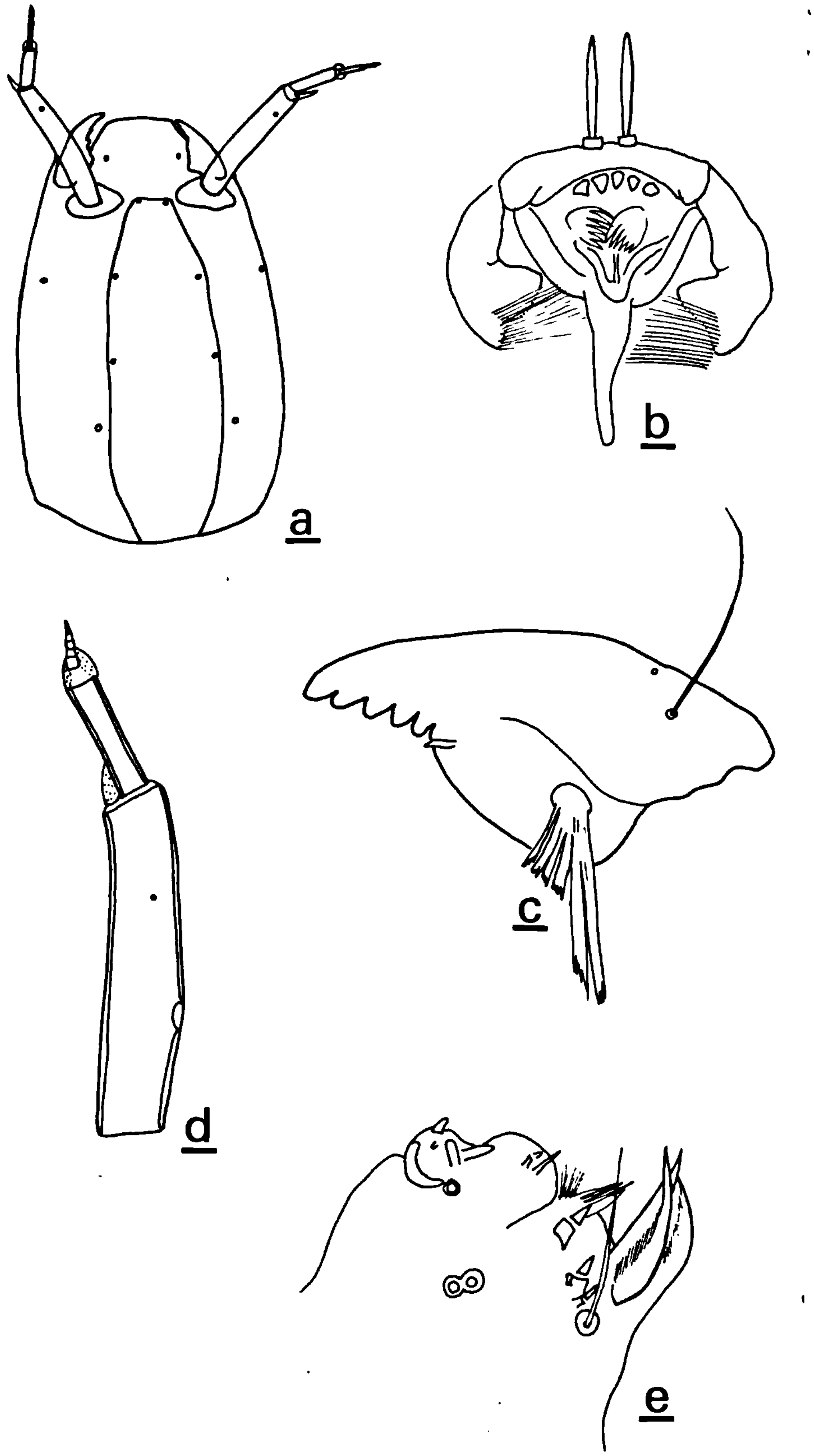


Figure 78

Thienemanniella

a. - Mentum of *T. clavicornis* (Kieffer) (011)

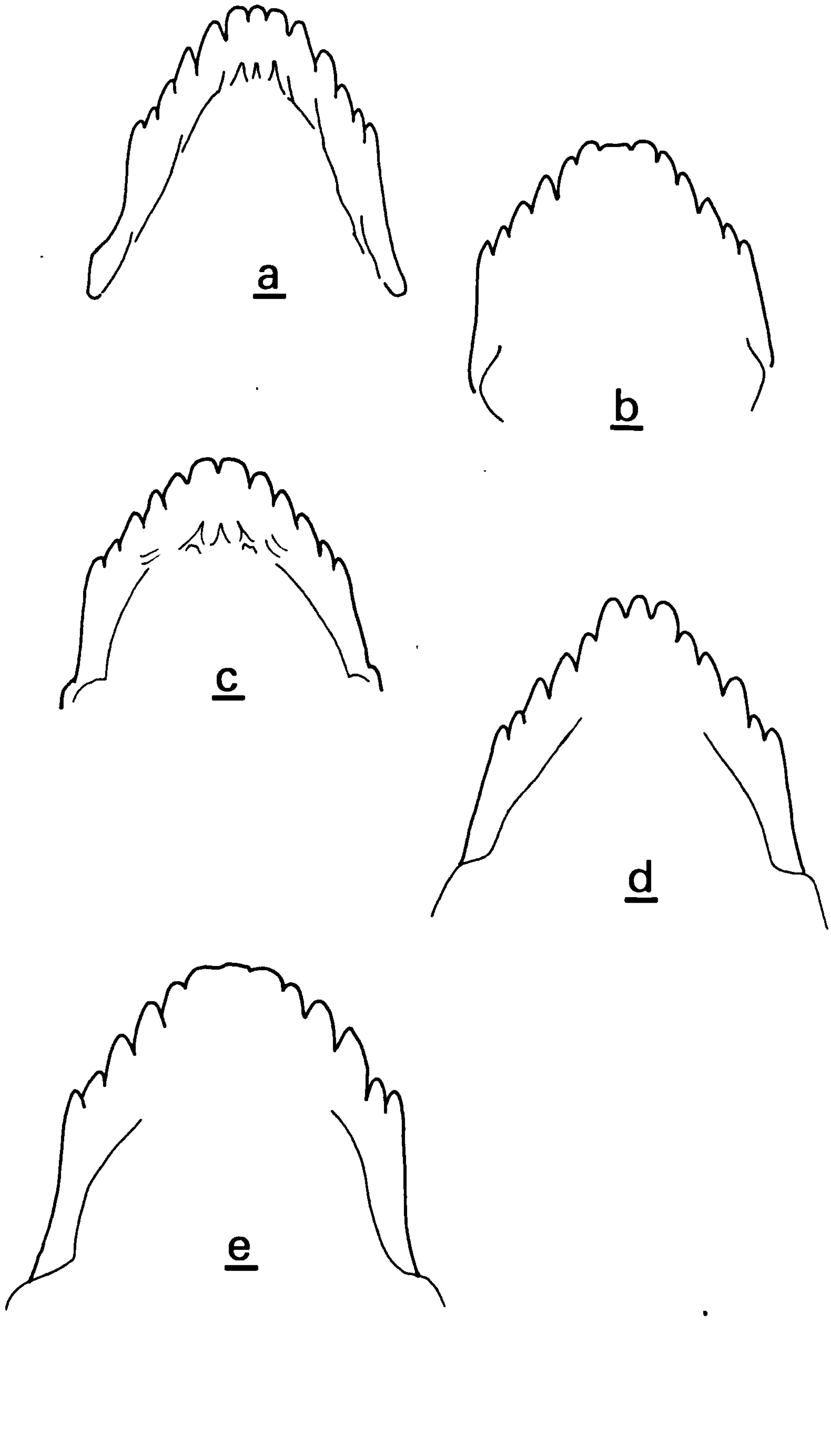
b. - Mentum of *T. fusca* (Kieffer) (011)

c. - Mentum of *T. species A*

d. - Mentum of *T. species B* (? *lutea* (Edwards))

e. - Mentum of *T. species C* (? *majuscula* (Edwards))

Fig. 78



<u>Figure 79</u>

? genus *acutilabis* Konstantinov

a. - Antenna (Oil)

b. - Labrum (Oil)

c. - Premandible (400)

d. - Mentum (400)

e. - Mandible (400)

f. - l_4 seta on abdomen (400)

Fig.79