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BRITISH FRESH-WATER COPEPODA

BY

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VOLUME I

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One may not doubt that, somehow, Good
Shall come of water and of mud;
And, sure the reverent eye must see
A purpose in liquidity.
Rupert Brooke.

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PREFACE.

The essential basis of all biology is the accurate determination of species. This is not, and cannot be made, an easy matter; but it is intolerably difficult for any but the specialist in a small field, unless the work of such specialists, scattered in small papers through an infinity of periodicals, in all languages, can from time to time be brought together into some form of monograph. Such monographs are necessarily out of date almost as soon as they are written, but at least they serve for a time to make easier the task of those concerned primarily with general problems of biology. The work involved is very great, and perhaps incommensurate with its results, but it is justified by its necessity. At the same time, with the works of Schmeil and of Sars before me, I feel some apology is needed. Both are so admirable that I cannot hope to emulate the thoroughness and sound judgment of the one or the perfection of illustration of the other; but Schmeil's book is now unprocurable, Sars deals mainly with marine forms, and, as the bibliography will show, a veritable flood of new work has poured forth since these monographs were published. As the illustrations of such a work are the most important feature, I have tried to give figures of every part that can have systematic value, and these figures, with very few exceptions, are original drawings made for this purpose. I have to express my thanks to the Ray Society for their liberality in reproducing so many. I am indebted to a number of friends for the loan or gift of specimens, but most particularly to Mr. R. A. Todd, who has, during the past three years, collected for me in about 200 localities in Devon, Dorset and Cornwall. Mr. Scourfield has been generous with specimens and information from his rich experience, and Mr. A. G. Lowndes has been most helpful.

ROBERT GURNEY.

Bayworth Corner,
Boars Hill,
Oxford;
November, 1930.

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GENERAL PART.

SYSTEMATIC PART.

BIBLIOGRAPHY.

The older papers, which are included in the bibliography published by Schmeil (1896), are not mentioned here unless referred to in the text. Papers dealing exclusively with Cyclopoida, or with Copepoda outside Europe and North Asia, are also omitted unless reference is made to them. For the rest, the literature is so extensive that an endeavour has been made to include only such papers as are regarded as real contributions to the systematics of Palæarctic Copepoda or to the biology of the group. The vast literature of freshwater plankton contains much that is of interest with regard to Copepods, but it is impossible to mention more than a few of such works. Only papers received up to May, 1931, have been included.

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THE BRITISH FRESH-WATER COPEPODA.

GENERAL PART.

I. HISTORICAL.

A. BRITAIN.

THE foundation of our knowledge of the British Copepoda was laid by Baird in his 'Natural History of the British Entomostraca,' published by the Ray Society in 1850; but of the fresh-water species almost nothing was known at that time, and practically no advance towards knowledge had been made since Jurine's great work of 1820.

When G. S. Brady took up the study of the Copepoda the work of Sars, Fischer, Claus and others had very greatly widened the field. Brady's Monograph, also published by the Ray Society, appeared in 1878–1880 and was a work of much merit, which greatly helped to advance knowledge of the group. His attention had been chiefly devoted to marine species, so that the number of species from fresh water included was comparatively small. From the time of the publication of this monograph progress has been rapid. Brady himself published, in 1892, a revised account of the Calanoida and *Cyclops* of fresh water, which was a great advance on his previous work, but still left much to be desired, and did not fully reflect the state of knowledge attained at the time.

T. Scott, during the period 1890–1900, carried out a thorough survey of the fresh-water fauna of Scotland, and revealed an unsuspected wealth of Harpacticids. His results are contained for the most part in a succession of papers in the 'Reports of the Scottish Fishery

Board,' and his illustrations, from the able hand of his son, Mr. Andrew Scott, are of the greatest value. Scott's skill as a collector can only be fully appreciated by one who has endeavoured to find again the species which he described.

So far as concerns the limnetic species, the work of the Bathymetrical Survey of Scotland, through the years 1897–1906, gave for the first time an insight into the distribution of the northern species of *Diaptomus*. Unfortunately the biological results were only published in very fragmentary form, generally as short notes by James Murray appended to the descriptions of the lake basins, and detailed information is not available.

I have found it necessary to work over myself a large proportion of the plankton samples, which are preserved in the Royal Scottish Museum, and have to thank Prof. Ritchie for permission to make use of them.

Mr. D. J. Scourfield, beginning with a careful survey of the fauna of Epping, has extended his investigations to many parts of Britain, and has contributed much to our knowledge. We owe two new species and many new records to his assiduous collecting and ingenuity in searching new habitats. His 'Synopsis of British Species,' published in 1903, is an excellent summary of the facts then available.

Mr. A. G. Lowndes has much advanced our knowledge of the British species of *Cyclops*, among which he has described two new species, and, by breeding experiments, has thrown most welcome light on some doubtful forms.

The position of the faunistic survey of Britain, so far as concerns Copepods, may be said at present to be this: Our knowledge is reasonably thorough for the whole of Scotland, the Lake District, Essex, Norfolk and the Marlborough district. Parts of North Wales have been explored with good results, and a good deal is known of the New Forest, but we have not yet a sufficient knowledge of the Harpacticids of the south—Dorset, Devon and Cornwall. The subterranean waters have not been sufficiently explored. One subterranean species, *Cyclops sensitivus*, has been found in a well at Ringwood associated with *Asellus cavaticus* and a number of *Cyclops* derived from surface waters, but without any Harpacticids. Further investigation of well waters is much needed.

Ireland may be said to be almost unexplored. We have a few scattered records, and a fairly thorough survey of Clare Island, but the south-west is untouched, and even the plankton of the lakes is only known in a few cases (*e.g.* Lough Neagh, Lough Derg). It is tempting to think that the peculiar Lusitanian flora of the south of Ireland may, perhaps, be accompanied by equally interesting fresh-water entomostraca.

B. EUROPE.

It is impossible to mention all who have contributed to our present knowledge of the fresh-water Copepoda, but there are certain milestones of progress which should not be forgotten.

Jurine's work of 1820 opens the period of accurate description and is one of remarkable merit. His observations on the life-history of some of these creatures still have their interest. It is to be hoped that his memory will be kept green by the retention of his names for *Cyclops* and *Canthocamptus*.

The species of *Cyclops* and *Canthocamptus* as we know them to-day rest mainly on the work of Claus and Sars. Claus was primarily a morphologist, but also a systematist of acute insight, whose researches covered the whole group of Crustacea. Claus's first paper on *Cyclops* was published in 1857, and in 1893 he issued a most valuable work on the genus, in which he discussed Schmeil's monograph and established a series of subgenera which are, for the most part, accepted to-day.

G. O. Sars's paper of 1863 on the Copepoda of Norway was unfortunately unaccompanied by figures, with the consequence that his species were not generally recognized, and in many cases have since been redescribed under other names. Sars, with an accuracy of observation which has never been rivalled, established even at that early date most of the species which we now know. Had his paper been accompanied by the beautiful figures which adorned his later publications much confusion of species would have been avoided. In his great work on the Crustacea of Norway he dealt with the fresh-water species, and established for the first time a satisfactory subdivision of the genus *Cyclops*, since Claus's subgenera had been generally ignored. It is to be regretted that he gave new names to his genera instead of using those of Claus, of which he was apparently unaware, and still more that he should have revived many of the specific names given by Koch about 1835. Both Claus and Schmeil had most thoroughly considered Koch's work, with the result that Claus considered every one of his species to be unrecognizable, and Schmeil adopted only one—*C. phaleratus*. Koch's descriptions are entirely worthless, and it is merely a matter of guess-work to recognize in his figures any species which we now admit. To argue that Koch must have had such and such a species before him, and that therefore such and such a figure must represent it, is wholly unjustifiable when we already have in use names based on adequate description and convincing figures.

The first part of Schmeil's monograph of the fresh-water Copepoda of Germany, dealing with *Cyclops*, appeared in 1892. This great work stands, and is likely to remain, unrivalled for thoroughness and accuracy of description and illustration. Schmeil, according to modern ideas, took much too broad a view as to the limits of certain species, but he was certainly right in doing so at that time and with the information then available. He did greater service by laying such a solid foundation of fact than he would have done by attempting to subdivide species on insufficient knowledge. It would have been well if some of his successors had shared Schmeil's caution. It would be strange if there were not faults to be found in such a monograph, but every worker in this field owes a debt to its author.

Mrázek's paper of 1893, on fresh-water Harpacticids, not only contained descriptions of a number of new and most interesting forms, some of which represented new genera, but opened up a new field for study which is not yet exhausted. He revealed for the first time the semi-terrestrial habitat of these Copepods, and stimulated search in every possible kind of surroundings.

Lilljeborg's account of the *Cyclops* and *Canthocamptus* of Sweden (1901 and 1902) has two disadvantages—that the greater part of the text is in Swedish, and that the illustrations are too few. He made known some of Sars's species which had hitherto not been recognized, and established some new species. In particular, he divided up satisfactorily the two collective species *Cyclops serrulatus* and *C. strenuus*. He did not recognize the genera of Harpacticids now accepted, but grouped all alike in the genus *Canthocamptus*.

Van Douwe's summary of the German species in the ' Deutschlands Süsswasser-Fauna ' (1909) is most useful. He succeeded in compressing into very small compass a wealth of information ; but even as an account of the German fauna it is already out of date, since so many new forms have been discovered.

During recent years a flood of papers has been poured out dealing largely with Harpacticids. Apart from purely faunistic work, attention has been devoted to the separation of new species and varieties and to speculations as to the influence of the glacial period upon distribution—speculations which our present information is not sufficient to support. Among the authors who have contributed most to our knowledge may be mentioned Chappuis and Kiefer. The former has made known a series of most interesting subterranean forms, and has published a revision of the Canthocamptinæ which marks a great advance.

Kiefer has quite recently (1929) published his long-promised volume on the Cyclopoida in ' Das Tierreich,' the product of great labour and industry. Further reference to this work will be made when dealing with the Cyclopoida.

It seems likely that the impetus given to the study of the fresh-water Copepoda by Schmeil's monograph has achieved its primary object, and that the period of discovery of really distinct new species in Europe is drawing to a close. In this country not many additions to the list are to be expected. The time seems ripe, therefore, for the publication of a successor to Brady's monograph, but confined, as is necessary with the growth of the subject, to the fresh-water species. To these it has seemed advisable to add certain brackish-water forms which are occasionally or frequently found in association with fresh-water species; but it has not been easy to know where to draw the line. In judging what species to include I have been guided mainly by my own experience in the Norfolk rivers, and have described those species which I have met with there. In including such a species as *Centropages hamatus* the limit has, perhaps, been stretched rather far, but it is one which is likely to be met with by anyone working in the tidal regions of a river, and it may be a convenience to find it dealt with among the rest. For the *Acartias* no excuse is offered. They play an important *rôle* in the estuarine fauna, and the absence of *A. bifilosa* from Sars's monograph has led, in my own case, and possibly in others, to some difficulty.

The region of brackish water is that to which attention should emphatically be drawn. Of its bionomics we know practically nothing, and it is most urgently necessary that limnologists should, in association with the chemist and physiologist, turn their attention to it. The study of the plankton of fresh water might well be suspended until the appalling weight of accumulated fact shall have been digested and assimilated. It is to be hoped, however, that the study of the brackish waters will not take the form that it has so often done in other branches of limnology, of the publication of vast masses of undigested fact. What is more needed is the accurate disentanglement of the many factors involved in the distribution of individual species. The environment is not stated when the salinity, temperature, etc., of the general body of water is ascertained. For bottom-living forms the environment may be the physical features of a minute area, and there is reason to believe that "salinity" is not the most important factor, and that a statement of pH is not more satisfying than the "blessed word Mesopotamia" (see Lowndes, 1928). Pantin's recent work (1931) on the environment of *Gunda ulvæ* is an excellent example of the accurate determination of the factors involved.

II. ECONOMIC IMPORTANCE OF COPEPODA.

A. As Food for Fish.

While a great deal of attention has been paid to the food of marine fishes and their dependence upon the plankton, the information as to fresh-water fishes, which are of so much less economic value, is comparatively small. That the Entomostraca are a very important source of fish food is certain, but the evidence goes to show that Copepoda are of much less importance than the Cladocera. Steuer (1910) gives instances. For example, *Coregonus schinzii* feeds almost entirely upon *Bythotrephes* in Neuenberger See, while *C. exiguus* in the same lake is less selective, eating also *Sida*, *Daphnia*, *Bosmina*, *Cyclops* and *Diaptomus*. *Coregonus albula* in Norwegian lakes feeds mainly on *Bosmina*, but in Swedish lakes often on *Limnocalanus*.

Juday (1907) gives an account of the stomach contents of 370 Trout. Of these 33 had eaten Crustacea, but only 5 contained Copepods. In the Twin Lakes of Colorado *Salmo stomias* had eaten only Cladocera, though *Epischura* and *Diaptomus* were commoner than *Daphnia*. In Lake Nipigon Black Bass (*Micropterus*) feeds to a large extent upon *Epischura*, and Whitefish upon *Limnocalanus* (Clemens, 1923). The nature of the food varies with the age and size of the fish. Bigelow (1923) gives an account of the food of the Sucker (*Catostomus commersonii*). At an average length of 1·9 cm. the food is almost exclusively plankton, of many species. At 2·3 cm. Cladocera (*Sida* and *Polyphemus*) are preferred; but at above that size it becomes a bottom-feeder, and eventually insectivorous. The Copepoda are a relatively insignificant source of food. In Lake Erie *Leucichthys* (Clemens, 1922) greatly prefers Cladocera. Southern and Gardiner (1926), in their study of Lough Derg, found that the fry of Perch, Bream and Tench (but not of Rudd) fed mainly on plankton, but here, again, Copepoda were of small importance compared to Cladocera. The adults of Trout, Perch and Pollan also feed largely upon plankton, but Copepoda are not mentioned in the table of stomach contents (p. 154).

Langhans (1928) gives notes of stomach-contents of Carp, which contained a high proportion of Copepods, but give the impression of indiscriminate feeding.

Dakin and Latarche (1913) discuss shortly the food of the Pollan in Lough Neagh (p. 85). Here it appears to be largely taken at the bottom (*Mysis* and *Chironomus* larvæ), but some specimens had fed upon *Daphnia* and *Bythotrephes*. Copepoda are not mentioned as a source of food.

Baird (1857) found that the Vendace of Castle Loch, Lochmaben, fed mainly on *Bosmina coregoni*, and that Trout and Char also eat Entomostraca.

The conclusion seems to be that feeding is very selective, and that Copepoda are of comparatively little importance as fish food.

B. COPEPODA AS INTERMEDIATE HOSTS OF PARASITIC WORMS.

That Copepods may serve as intermediate hosts for certain parasitic worms has long been known, and a few examples may be given.

Janicki and Rosen (1917) have proved that it is possible to infect *Cyclops strenuus* and *Diaptomus gracilis* with the eggs of the Cestode *Dibothriocephalus latus*, and the onchospheres could be distinctly seen in the body. Both these species are eaten by Perch, and it was found that the larvæ emerge from the Copepods and pierce the stomach of the fish, which is the second intermediate host of this parasite of man.

I have myself only once seen a cysticercoid in a Copepod. This was in a specimen of *Diaptomus laticeps* from the Orkneys, and it was identified, with some doubt, by Dr. H. A. Baylis as the larva of *Hymenolepis macranthos* (v. Linst.), the adult of which is found in the Goldeneye (*Bucephala clangula*) and the Merganser (*Mergus serrator*), two fish-eating ducks.

Copepods are also carriers of the larvæ of Trematodes, and the larvæ of *Hemiurus*, which, when adult, is parasitic in a number of marine fish, have been frequently noted (see Dollfus, 1923 ; Lebour, 1923).

Leiper (1906) observed that the larvæ of the Guinea Worm (*Filaria medinensis*) encysted in *Cyclops* remains quiescent for long periods. If a *Cyclops* containing the parasite is treated on a slide with ·2% hydrochloric acid, which is approximately the acidity of the gastric juice, the *Cyclops* dies, and the encysted larva becomes active, emerges, and swims freely.

A complete list of all species of *Cyclops* known as intermediate hosts of Helminths will be found in a paper by Hall (1929).

III. THE FOOD OF COPEPODA.

It is most difficult to determine the food, as it is generally impossible to recognize it from the contents of the gut. Birge (1898, p. 353) states that *Diaptomus* has a preference for *Anabœna* and *Aphanizomenon* over Diatoms when all are available. *Ceratium*, according to him, is eaten to some extent by *Cyclops*, but little by *Diaptomus* or Cladocera, and its maximum corresponds to a decline in the numbers of Crustacea.

Southern and Gardiner (1926, p. 147) found that *Diaptomus gracilis, Eurytemora velox* and *Cyclops strenuus* contained Diatoms, especially *Melosira* and *Stephanodiscus*.

De Lint (1923) traced *Melosira, Coscinodiscus, Cyclotella* and *Microcystis* in the alimentary canal of *D. gracilis*.

Kreis (1925–26, p. 314) states that *D. bacillifer* feeds on small algæ or on dissolved substances. The Calanoida are " filter-feeders " which cannot exercise any very marked selection ; but more information on this point is much needed, since thereby light may be thrown upon the distribution and seasonal fluctuations of the plankton species and the habitat preferences of others. Nothing at all is known of the feeding of Harpacticids, and very little about *Cyclops*. The latter is capable of feeding upon relatively large dead animals, and Spandl (1926, p. 64) states that they may attack and seriously injure small fish.

IV. HABITAT AND METHODS OF COLLECTING.

Taking the fresh-water Copepoda as a whole, there is hardly a collection of water, unless of quite transitory nature, in which some species are not to be found ; but to obtain a complete collection of them from any given area is not always easy, and requires a certain amount of experience and knowledge, coupled with a little luck. So far as the species are concerned which are members of the plankton no difficulty is to be experienced. A few minutes' use of a fine townet will almost certainly obtain a fair sample ; but this is not always true. For example, in Loch Shin *Diaptomus gracilis* and *D. laciniatus* are both to be found ; but, at least in late summer, the latter can only be caught at depths of over 50 ft., and it is quite absent from the shallower parts of the lake. It is therefore necessary in deep lakes to take samples from deep water as well as from the surface. In any case the plankton fauna is limited to few species. Throughout Scotland, for example, except in some eutrophic lakes of the lowland, there is but a single species of *Cyclops*—*C. abyssorum*—whereas in large ponds in the south, and in the Norfolk Broads, this species is replaced by *C. vicinus*, and the latter is accompanied by *C. leuckarti*, and often by *C. hyalinus*. Systematically the plankton species are fully known. What remains to be discovered concerning them is to what extent there is local and seasonal variation, and in what way species which appear only in summer—*e. g. C. hyalinus*—pass the winter.

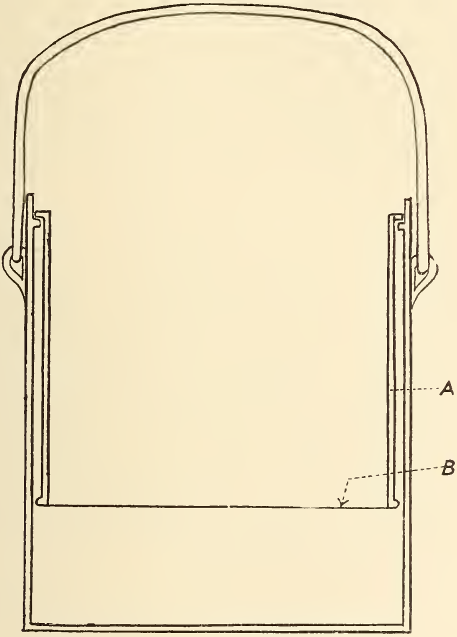

FIG. 1.—Section of filter-can for collecting Harpacticids. A, inner sleeve; B, bolting silk.

The many species of *Cyclops* and Harpacticids which inhabit the littoral region present more difficulties, and it is unlikely that the most expert collector will obtain all the species present in a richly populated water at a single visit. A small hand net about 6 in. in diameter is most convenient. Such a net, to screw on to a walking-stick, is supplied by Messrs. Flatters and Garnett. The net, which should be of bolting silk, 100 strands to the inch, has at the end a bottle of the same capacity as the corked tubes in which the catch is brought home. The net must be swept through weeds, scraped up the stems of reeds, and should skim the bottom so as to catch some of the top layer of mud and *débris*. The catch should be brought home and examined alive if possible, since it is extremely difficult to sort out the smaller species from among a quantity of mud, etc., when they are dead. If the material is set aside for a time the creatures will come to the surface of the mud and will be easily seen. Submerged moss, either at the edges of lakes or in small pools on peaty moors, should be carefully searched. This can be done by squeezing the moss into the net, but it is more satisfactory, when possible, to use a special filtering can for the purpose. Such a can may be made as shown in Fig. 1. The filtering surface is made of bolting silk, 40 strands to the inch, and allows all but the largest *Cyclops* to pass through. The filtered water can be passed through the fine net and the concentrated residue brought home for examination.

Though certain Harpacticids, such as *Canthocamptus staphylinus* and *C. trispinosus*, may be taken among weeds in the same way as *Cyclops*, many have very special habitats and are found with difficulty. We owe to Mrázek the discovery that some are almost terrestrial, and can live in the thinnest film of water on the leaves of moss that appears to be nearly dry. Some, such as *Epactophanes muscicola*, definitely avoid really wet moss. *Marœnobiotus vejdovskyi* is found, not only in moss, generally a little wetter than that chosen by *Epactophanes*, but also in decaying leaves and leaf-mould in woodland. Others, again, such as *C. cuspidatus*, prefer moss on rock faces where there is a constant slow trickle of water. The Morarias are generally found in wet or submerged moss. It is necessary, then, to wash carefully samples of moss from every kind of situation, and for this purpose the filter-can described above is invaluable.

At present nothing is known as to whether different species have preference for definite species or genera of moss, and this is a subject deserving attention. Some species, such as *Moraria sphagnicola* and *Canthocamptus weberi*, are constantly associated with *Sphagnum*, but it seems likely that limitation to one genus of moss, if it occurs, will be chiefly a question of the amount of moisture associated with it. Information as to the bionomics of these Copepods is much needed.

PRESERVATION.

While spirit is the best preservative for the Cladocera, it is by no means so for Copepoda. In spirit they become opaque, rigid, and the limbs brittle, and old specimens are often almost useless. Formalin (formaldehyde 4% or formol 10%) is much better for systematic purposes. In course of years the soft parts may be destroyed, but this may even be an advantage. The only objection to formalin is that it may occasionally deposit a white precipitate which clogs and ruins the specimens. I have seen specimens so ruined, but have never found this precipitate in my own collection. Formalin has the very great advantage of portability. A cigarette tin (of the usual flat type holding 50 cigarettes) will exactly hold seven corked tubes 2½ in. by ¾ in., and one of them can be filled with 40% formol, which is ample to preserve the contents of all the tubes.

V. DISTRIBUTION.

One of the most important problems relating to the fresh-water Copepods is that of their means of dispersal. Much has been written by Brehm, Zschokke and others on the relation of their present distribution to the glacial period, and many species have been claimed to be glacial relicts ; but such speculations are without foundation until we have some reasonable assurance that present distribution cannot be explained by present means of dispersal. Preference for low temperatures (cold-stenothermy) and a breeding period in autumn or winter have generally been regarded as strong evidence of northern origin. Taken by itself this kind of evidence does not seem to have any value at all, though it may be taken into account when the facts of distribution indicate a discontinuity of area explicable by the effects of the glacial period. In the case of crustacea producing floating resting eggs, almost unlimited dispersal by wind or by birds or insects is possible. Although actual demonstration of the means by which dispersal occurs is difficult, and has rarely been recorded, there are instances on record of ephippia of Cladocera having been seen sticking to the feathers of ducks, and the rapid colonization of new and isolated ponds is a matter of common knowledge, of which it is not necessary to give examples. The sporadic and temporary appearance of rare species is no doubt evidence of such transport. As examples I may give the appearance of *Alona elegans* and *Alona protzi* in Norfolk, both found only during a single season and disappearing again (Gurney, 1904, 1921). In the case of the Cladocera, in fact, means of dispersal are such that zoogeographical speculation founded upon them must be made only with great caution.

Very little is known as to the resting stages of Copepoda. The production of resting eggs has been proved for some species of Calanoida (*e.g. Limnocalanus macrurus*, *Diaptomus castor*, *D. denticornis*, *D. vulgaris*), and æstivation in cysts in the case of *Canthocamptus microstaphylinus* and *Cyclops bicuspidatus*, but resting eggs have not been demonstrated in any species of *Cyclops*.

Borutzky (1929) has found that *Canthocamptus arcticus* has resting eggs, and suggests that *C. rhæticus* and *C. cuspidatus*, which have eggs of apparently the same structure as in *C. arcticus*, may also be able to survive unfavourable periods in the same way.

The appearance of Calanoids in mud-cultures is quite usual, but very few cases are known for other Copepods. Claus was the first (1894) to make known the appearance of *Cyclops* (*C. minutus*) from mud-cultures, and he concluded that it was not the eggs, but the copepodid stages which survived. This is certainly the case in some other species. When a pond which has been dry is again filled, *Diaptomus castor* reappears as nauplii, but all the *Cyclops strenuus* first found are copepodid stages, and they may be covered with brown matter as if just revived from encystment in mud. Sars records the appearance of a specimen of *Cyclops inopinatus* from South African mud (1927) as the only case known to him ; but I have myself seen *C. affinis* appear from Indian mud, and *C. rubellus* and *Canthocamptus staphylinus* have " hatched " from drifted *débris* taken from Langmere in Norfolk and dried. It is probable that most if not all *Cyclops* have some means of surviving desiccation or cold periods, though there is no evidence for resting eggs, and that dispersal by resting eggs is certainly possible for some *Diaptomus*. Spandl (1926, p. 16) gives evidence that *D. gracilis* does not produce resting eggs ; but it seems probable that all species do produce them on occasions, if not regularly. Passive dispersal is, therefore, quite possible, and it is generally the agency of birds which is invoked. Gjorgjewic (1907B, p. 202) accounts for the distribution of the Diaptomidæ of the Balkans in this way. The line of migration of birds is roughly north and south, and he states that *D. laticeps* and *D. mirus* have been carried from the north, and *D. salinus* and *D. lilljeborgii* from the south. Zschokke (see Steuer, 1910, p. 516) points out that birds migrating south in autumn may drop into high alpine pools and so introduce northern species, but that the return journey in spring is made when these pools are still frozen, so that southern species cannot be carried northwards. Roy (1931) records the hatching of nauplii of *Canthocamptus bidens* from mud taken from the feet of *Rallus aquaticus* and *Gallinula chloropus*. Lowndes (1930) notes the finding of the ostracod *Pionocypris vidua* living in the rectum of a frog—an observation which suggests a possible means of transport for other Entomostraca. Distribution by wind is no doubt effective in many cases. In the Canaries the S.E. wind may bring clouds of dust from Africa (Richard, 1898), and with it Entomostraca. Zograf (1910) states that, during the sirocco, dust can be collected at Marseilles from which Rotifers can be hatched. He gives examples of the occurrence of certain Branchiopods which are supposed to have been transported by wind. He himself found a specimen of *Limnetis brachyura* floating on a bowl of water after a strong wind. The animal was dead, but its eggs were alive. Showers of fishes are well authenticated, and if fishes can be transported alive, copepods must often be so. Beal (1881) describes a "shower of *Cyclops quadricornis*" in Iowa. He found, after a shower of rain, the ground covered with "something that looked like blood." Half a teaspoonful of the substance contained about 500 *Cyclops*. Gudger (1929) records 71 cases of rains of fishes. For instance, a case is given from South Africa of the descent, in 1909, of hundreds of fishes up to 3 in. long. I have seen a miniature travelling tornado in the breckland of Norfolk which whirled up dust and clods of earth to a considerable height in the air. If this dust had contained eggs or resting stages, they could have been transported further by the wind.

Distribution throughout a drainage system is easily effected. At a time of heavy rainfall quantities of Entomostraca are washed out from lakes and carried alive to great distances. Even the violence of a Scottish burn in spate does not kill all it transports, and I have myself found living Copepods and Cladocera (even *Holopedium*) in such streams miles from their source in the outflow of a lake.

How far the transport of species living in deep water is possible is, however, very doubtful. Ekman excludes the possibility of transport in discussing the distribution of *Limnocalanus macrurus*, but it does not seem impossible that it might be effected, on rare occasions, by the intermediary of fish and fish-eating birds. One of the most remarkable cases of distribution is the occurrence of *D. laticeps* in Wocheiner See in the eastern Alps. This is, according to Pesta, a moraine-dammed lake, so that *D. laticeps*, which is a species of large lakes and deep water, must have been transported in post-glacial time.

In the case of the Harpacticids, active migration has probably been very effective in dispersal. Many of them can survive desiccation, and they require merely a film of water in which to move. After a heavy rain practically the whole country is a continuous sheet of water, in which movement could take place. This is most clear in the Scottish highlands.

The conclusion seems to be that, although in some cases (*e.g. Heterocope, Limnocalanus*) present distribution is probably due to the influence of the glacial period, the great possibilities of passive transport must always be borne in mind, and speculation founded on geographical distribution must be accepted with caution. Each species has its habitat preferences and, if means of dispersal are adequate, it will be found in those conditions wherever they occur. For instance, *Laophonte mohammed* is a typical species of inland saline waters, and it would be absurd to account for its distribution by supposing that it was at any time continuous. Similarly if a "cold stenotherm" species, such as *Canthocamptus cuspidatus*, is found (in association with *Polycelis cornuta*) in a stream near sea-level in Norfolk, it is not necessary to assume that it has survived there since the glacial period.

It must not, however, be supposed that the study of distribution is, for these reasons, without value. In our own country we have proof that there are factors at work of which we have no understanding. The distribution of *Diaptomus* in Scotland is at present wholly unaccountable, and presents a problem which, if it could be solved, would throw a flood of light on the biological relations of the fresh-water fauna. Another problem of the highest interest is presented by the occurrence of *Limnocalanus macrurus* in Ennerdale Water. Here undoubtedly is a problem which can only be solved by the geologist (see p. 105).

VI. DISTRIBUTION IN RELATION TO THE ORIGIN OF THE FRESH-WATER FAUNA.

Some speculations have been published as to the period of the origin of the fresh-water Copepoda (see Tollinger, 1911, p. 219); but one thing seems very clear—that the history of the Calanoida has not been the same as that of the Cyclopoida and Harpacticoida. The latter both contain cosmopolitan genera, and there are even species of *Cyclops* whose distribution is practically world-wide (*e. g. C. leuckarti*). As has been said above, we are by no means in a position to say that wide distribution is proof of anything more than extreme power of dispersal; but in the present state of knowledge it may be assumed that the universal occurrence of the genus *Cyclops* does indicate very ancient origin. Apart from the genus *Halicyclops*, it has no very near marine allies, and although the old genus has now been divided into a number of new genera and even subfamilies (Kiefer, 1929), there is no doubt that, in its wider meaning, it covers a closely related group of species of common origin dating back to a remote past—possibly even Precambrian, as Arldt supposed.

Much the same holds good for *Canthocamptus* in its wider sense, which is a distinctly circumscribed group of species of world-wide distribution without near allies in the sea. Chappuis has divided it into genera (here treated as subgenera), some of which show more or less restriction to definite areas; but it would be premature to apply present knowledge to zoogeographical speculation. All that can be said is that distribution here also indicates a presumption of great antiquity. The position is not the same with regard to the Calanoida. They do not form a single related group, but the genera represent, according to Sars's classification, five distinct families. Of these families one only, the Diaptomidæ, is confined to fresh water, and is comparable to *Cyclops* and *Canthocamptus* as containing genera so closely related that they may best be regarded as subgenera of *Diaptomus*. The comparison holds good also in this way—that while the subgenera *Metadiaptomus*, *Paradiaptomus* and *Hemidiaptomus* have a restricted distribution, the genus as a whole is cosmopolitan, and has no near allies in salt water. It seems most probable that we have here also a very ancient fresh-water genus which, in some areas, has given rise to subordinate groups.

The remaining genera may be of much more recent origin, and the adaptation of species to fresh water is probably a process that has continuously operated and may still be in progress.

In the Centropagidæ there are several genera allied to *Boeckella* found in South America and Australasia, but not in Africa, which are of ancient origin, but, on the other hand, there is *Limnocalanus*, the origin of which may date back to Pleistocene time only.

The Temoridæ have three genera in fresh water, *Epischura*, *Eurytemora* and *Heterocope*, of which *Eurytemora* at all events appears to be a recent immigrant into fresh water.

The remarkable genus *Senecella* (Juday, 1925) is the only representative of the family Pseudocalanidæ in fresh water, and it seems probable that it is of post-glacial origin.

The means by which colonization of fresh water has occurred are by no means clear. That in some cases it has taken place by separation of arms of the sea (relict lakes) is certainly true for a few species within the Baltic region, and perhaps in the region of the great North

American lakes and the Irish Sea; but there is no evidence that any considerable accession to the fresh-water fauna has been made in this way. Unless such separated areas are of exceptional size and depth, the change of conditions would no doubt be much too rapid to allow of acclimatization.

Högbom and others have recently introduced the "Stausee" theory to account for the distribution of certain relict Crustacea (see Ekman, 1930). According to this theory glaciers advancing across a relatively shallow sea may dam up parts of the sea against the land and raise the enclosed water above the level of the sea. In such freshening waters modification of the surviving population occurs, and the raised level permits invasion of inland waters which have never been directly connected with the sea.

The transfer from salt water to fresh has almost certainly taken place chiefly in the tidal regions of rivers, where it may even be in progress now. Perhaps the best example of apparently recent immigration is seen in the genus *Pseudodiaptomus*, in which there are purely marine species, species of estuarine regions, and species of fresh water. The species *Poppella guernei* is closely allied to *Pseudodiaptomus*, and inhabits both fresh and slightly saline waters.

The invasion of fresh water is more difficult for the species of the plankton than for those which live on the bottom, since they are more at the mercy of tidal currents, but it is easy to suppose that it might occur under such conditions as are seen in the Suez Canal. Here the tidal currents from the Red Sea penetrate as far as the Bitter Lakes, and many species of the plankton, and others with floating larvæ, have been able to establish themselves in the lakes. If these had contained brackish or fresh water it is quite probable that acclimatization might in time occur of species constantly introduced by the currents.

The Chilka Lake (Sewell, 1924) seems to offer opportunities for the adaptation of species from salt to fresh water and *vice versá*. This lake has a narrow opening into the Bay of Bengal, through which it becomes filled with salt or brackish water during the dry season; but during the season of rain (June–August) the salt water is almost entirely replaced by fresh water. While the species brought in by fresh water appear to be entirely destroyed in the saline period, some of the marine species (*e. g. Paracalanus crassirostris* and *Acartia centrura*, both of which are also at home in the Bitter lakes) have become permanent inhabitants of the lake. Whether we have in such a case an adaptation in the sense that the individuals of the present day are more euryhaline than their ancestors, or whether the species in question have always and everywhere the same powers of accommodation, is a question which is not answered by the faunistic facts.

While the plankton species of the estuarine region are limited to definite sections of the stream which can be defined in terms of salinity, such as *Acartia clausi* and *A. bifilosa* (see Percival, 1929; Gurney, 1930), some bottom-living forms (*e. g. Tachidius littoralis*) penetrate into regions where they are exposed for long periods to fresh water, or even beyond the range of tidal influence. The road to fresh water for such forms has everywhere and for nearly all time been open, while for the plankton forms acclimatization has only been possible under conditions which can have been comparatively rarely realized.

The problem of the relation of the marine to the fresh-water fauna is one of such exceptional interest and importance that it is surprising that it has attracted practically no attention from limnologists. It cannot be solved by speculation, and faunistic work can only reveal the complexity of the factors involved; but there is a wide field of research open to the experimental biologist in determining the influence of these factors.

One question that might be put to them is this: Have we any good reason to suppose that "brackish-water" species are more adaptable to fresh water, and consequently more likely to furnish new fresh-water species than marine species? A real answer to such a question would be most illuminating; but we have no information on the point at present. Such faunistic evidence as we have suggests that the answer would be in the negative, and that additions to the fresh-water fauna have, as a rule, been made, not by the gradual acclimatization of euryhaline species, but by physiological mutations, perhaps correlated with structural changes, permitting a complete change of habit (Gurney, 1913, p. 485). An interesting support to this suggestion is afforded by Needham (1930), who points out that the egg requires for its development a certain proportion of ash, and that it may have been "impossible for marine animals to colonize fresh water until, by some chance mutation perhaps, the capacity of providing enough ash within the egg is acquired."

VII. CLASSIFICATION.

The obvious convenience of the general classification of the Copepoda set out in Sars's 'Crustacea of Norway'* has won general approval, but it may well be that the Giesbrechtian system, or some modification of it, may eventually be restored, and there are some advantages in a combination of both. There is no dispute as to the validity of Giesbrecht's Gymnoplea, which corresponds to the Calanoida of Sars, and there may prove to be advantage in retaining his term in preference to that of Sars, since it seems not unlikely that divergent lines of evolution may be traced within the group, in which case the term "Calanoida" would be used for one division of the whole. The position is not so simple with regard to the Podoplea. Apart from the genera *Misophria* and *Benthomisophria*, which almost inextricably unite the characters of both suborders, and to that extent invalidate them, the definition of the Podoplea given by Giesbrecht undoubtedly does hold good for the unmodified free-swimming forms.

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* First propounded in 1886.

There are certain interesting exceptions to the rule that in the Podoplea the division between fore- and hind-body falls between the somites of legs 4 and 5.

(1) *Thaumatopsyllus*, Sars. Here the division falls between somites 3 and 4, somite 4 being very much reduced, and bearing a minute pair of uniramous appendages.

(2) The same is the case in the Artotrogidæ and Cancerillidæ of Sars. Indeed, unlike as they appear to be, it seems possible that *Thaumatopsyllus* is more nearly related to these families than to the Monstrillidæ.

(3) *Caligidium*, Sars. In this case leg 3 is rudimentary and leg 4 absent, somites 3 and 4 being very small. The division of fore- and hind-body then falls between somites 2 and 3.

These exceptions do not, however, really weaken Giesbrecht's definition, since we can regard them either as an extension of the process already begun in the Cyclopoida of the inclusion of one thoracic somite in the hind-body, or of the perpetuation of stages in the ontogeny which are passed through by all normal Copepods.

It can hardly be doubted that the parasitic forms have been derived, not from the Calanoid stem, but from one or other of the families of Cyclopoida or Harpacticoida. For instance, the Ergasilidæ are most nearly related to the Lichomolgidæ, and these probably to the Cyclopinidæ, while there is evidence of transition from the Ergasilidæ through the Caligidæ to the Lernæidæ on the one hand, and through *Nicothoë* to the Choniostomatidæ on the other. If this be so, there is no need to hesitate to accept a common group for all on the ground that the adults in so many cases do not fit the definition; the grouping remains phylogenetically sound.

Wilson (1910), in discussing the validity of the different systems of classification, took the view that the posterior appendages and somites are the most likely to become modified or suppressed. That, in fact, modification, when it occurs, proceeds from behind forwards. For this reason he considered that Giesbrecht's fundamental division, based upon modification affecting posterior somites, is unsound. On the other hand, Calman (1926) takes the opposite view, namely, that it is a "general rule among Arthropods that specialization begins anteriorly and works backwards; we should expect the posterior limbs to be the more primitive." Among the Copepods there does not seem to be any general rule, and Wilson's opinion that the anterior appendages are the most trustworthy for taxonomic purposes cannot be upheld without some reservation. While it is true that the structure of the head appendages has a fundamental similarity throughout groups which we judge to be related, yet they are subject to great modification within families or even genera. For example, in the Notodelphyidæ *Notodelphys* male has a prehensile antennule and *Doropygus* has not; within the genus *Ameiropsis* one species may have the mandible palp biramous and another unbranched. Many similar examples could be given.

If, on the other hand, we attempt to show that the posterior appendages are the more primitive and least subject to adaptational modification, we find great difficulties. There is, in the first place, the reduction or disappearance of leg 6—and perhaps of a seventh pair—and the modification from species to species of leg 5. In fact the structure of leg 5, throughout the group, is one of the most important specific characters. When legs are reduced or absent it is almost always from behind forwards. In the Calanoida leg 6 is always absent, and leg 5 is often lost in the female. In the Podoplea leg 5 is rarely lost, but leg 4 may lose its endopod (*Dyspontius*); or it and leg 3 may be reduced to vestiges (*Parartotrogus*). Although legs 5 and 4 are so frequently modified, it cannot be said to be a general rule even here that modification proceeds from behind forwards, for leg 1 provides valuable specific and generic characters, which legs 2 and 3 rarely do, except when there are sexual modifications.

Again, if we regard the series of limbs as a whole, we find modification, reduction and disappearance taking place in the middle of the series: for example, loss of maxillipede in *Cylindropsyllus* and Ergasilidæ; loss of mouth parts in Monstrillidæ, and so on. If any general rule is to be laid down it might be possible to say that the limbs fall into two series—fore and hind limbs—the limit being between the maxillipede and leg 1, and that generally modification proceeds in each series from behind forwards. But there are many exceptions to such a rule. In any case objection cannot be raised to Giesbrecht's system on grounds of this nature.

The most serious objection to Giesbrecht's system seems to be that it implies a fundamental difference between the Calanoida and all the rest which, while it can be upheld by insistence on the relation of fore- to hind-body, may actually be an overstatement of the case. The Misophriidæ, and to some extent the Longipediidæ, among the Podoplea, have certain definite Calanoid characters, and there are genera of Calanoida—*Pseudocyclops*, *Paramisophria*, *Platycopia*—which have features strongly suggesting a relation to the Podoplea.

Until the larval stages of these aberrant forms are known we are not likely to arrive at any final conclusion as to relationship. At present nothing whatever is known about any of them except *Longipedia* (Gurney, 1930A), whose larva differs much from that of typical *Harpacticoida*, and in some ways approaches that of normal Calanoida.

It seems that the only position to take up at the moment is that of admitting that the classification of the Copepoda is unsatisfactory, and of rejecting the Giesbrechtian arrangement for the moment, because it implies a phylogenetic system for which the evidence is not sufficiently good. The system of Sars has this merit—that it provides, as it were, a series of convenient pigeon-holes into which the genera can be fitted, without implying any deep knowledge of the phylogeny of the larger groups.

VIII. GENERA AND SUBGENERA.

In reducing a series of species to an ordered system two objects must be kept in view, namely methodical arrangement, and expression of phylogeny or relationship. These two objects may often come into conflict. For an arrangement to be methodical and convenient it is necessary that the species be divided into groups of reasonable size—the genera—all the components of which comply with a definition, and the more precise and rigid the definition can be made the better. On the other hand, evolution takes no account of precise definitions, and a complete evolutionary series would, in almost any case, be undefinable in precise terms. This difficulty is repeatedly met with among the Copepods, where we have to use, for example, the presence or absence of certain parts of appendages, or the number of segments in legs, as characters of genera. Nothing is more certain than that a reduction of segments may occur independently in one or more species in two related genera. The desire for methodical arrangement in such a case might lead to the grouping of these species in a third genus, whereas a phylogenetic arrangement would include them in their respective groups. In the first case we get three convenient and well-defined groups, and in the second two genera definable with difficulty, or not at all. An instance of this is the genus *Nitocrella*. The two species included in it are most nearly related to *Nitocra subterranea*, which itself is a rather aberrant member of *Nitocra*, not easily fitting the definition of the genus. If they are, for this reason, included in *Nitocra* they will be exceptions to the rule that the legs of that genus have the primitive 3-segmented endopod; whereas if the new genus is allowed to stand, the phylogeny of the species is obscured. There is no possible complete solution of this difficulty, and it extends also to the larger groups. It will be seen in the case of the Canthocamptidæ that it is almost impossible to give any satisfactory limitation of the family as compared with the Cletodidæ and Cylindropsyllidæ, and that within the family the genera, and within the genera the species, can often be grouped in series which seem to be related, and yet are not definable in a way which can be regarded as satisfactory.

It is most desirable for practical purposes that very large genera should be broken up into smaller ones if possible; but, if the large genus is in fact a natural group of related species, to split it up into a number of genera under new names implies a discontinuity which does not really exist, or at least obscures the relationship. The objection is largely removed if the new groups are treated as subgenera. For this reason, while wholly approving Chappuis's attempt to break up the genus *Canthocamptus*, I have regarded his genera as subgenera, and have not accepted his subgeneric divisions.

IX. SPECIES AND SUBSPECIES.

Faunistic research passes as a rule through three phases: first the pioneer phase of grand discovery; then revision of the earlier work, accompanied by accurate definition and addition of many species based upon less marked differences; with this phase closes the period of discovery. There follows intensive study, with the deliberate aim of searching for the smallest differences which can be appreciated, and the production of an infinity of new "critical" species, subspecies and varieties. The publication of Schmeil's monograph drew a line between the old and the new, but did not mark the end of the period of discovery. That period is now ending, so far as Europe is concerned, and the period of intensive study has begun. It will be seen that most of the fresh-water species, particularly of *Canthocamptus*, have been subjected to this scrutiny, and a number of subspecies and varieties have been described which it has been necessary to consider. In so doing the actual basis of fact must be estimated.

It must be remembered that the detailed examination of these minute creatures is a laborious business, and the material available is often small, consequently it is rare that more than a very few specimens can be brought into comparison. Again, the author of the new subspecies or variety commonly compares his own specimens with the published descriptions of specimens from other localities and not with the specimens themselves. In this way we have comparison of a population of which the variability is imperfectly known with others of which it may not be known at all. Further, the comparison takes account of such minute differences as the presence of one seta more or less on a limb, or even of the length and feathering of a particular seta, and it is expecting too much to suppose that the older authors, or even some of the present day, can be relied on to have described their material with such meticulous care as to justify such comparison. For these reasons alone, namely lack of knowledge of the limits of variability and of the degree of accuracy of original descriptions, it is necessary to view with scepticism much of the work that has been done in distinguishing subspecies.

There is another point which should be borne in mind, namely, the meaning to be assigned to the terms "subspecies" and "variety." This is a matter which cannot be discussed fully here. The answer to the question, "What is a species or subspecies?" must ultimately come from the geneticists; but until they have reached some agreement on the subject, those who are concerned with the identification and description of phænotypes can only be guided by their conceptions of what is practical and possible, rather than by theoretical speculation. It is indeed likely that it may never be possible to adapt the practice of the systematist wholly to the conclusions of genetics when dealing with material not amenable to exact experiment. It seems one should, for systematic purposes, conceive of a subspecies as a group of individuals, presumably genetically related, of recognizable parentage, and primarily occupying a continuous and limited area. The independent origin of the same species or subspecies from the same parent in distinct areas has no doubt occurred at times, but must be regarded as exceptional. As instances may be given *Limnocalanus macrurus* (p. 105), and the extinct elephants *E. melitensis* and *E. falconeri*, which are supposed to have originated independently in at least four areas from the parent *E. antiquus* (Vaufrey, 1929). It is not impossible that some forms which we know as subspecies, or even species, may be "adaptations" to particular conditions, without genetical relation between separate colonies. In rare cases such response to environment has been observed. Kreitmann (1927) records distinct structural changes in *Coregonus lavaretus* after a few years' establishment in the lake of Geneva. A particularly interesting case of such response is given by Bjerkan (1929). In this case a land-locked population of sprats, known to consist only of two generations, was examined, and the two groups were found to differ in the average number of vertebræ. Again, Robson (1928, p. 145) notes that *Limnæa involuta* and *L. prætenuis* have been regarded as localized lacustrine species; but in an isolated tarn in western Ireland local forms of *L. pereger* are found which approach these two species in shape and texture.

When we find the same subspecies in widely separated and dissimilar areas, some suspicion is aroused as to whether the facts are correctly known. The probability seems to be that further investigation would show that the subspecific characters are merely manifestations of individual variability throughout the range of the species. If we compare the records of subspecies in the Copepoda with the facts as ascertained for the birds, a group of which our knowledge is almost exhaustive, we find in the former sporadic and unaccountable distribution, and in the latter definite geographical limitation, often obviously bound up with climatic influence.

Therefore it appears that much of this work is premature. What is most needed now is not search for these new forms and the hasty emission of geographical speculations founded upon them, but painstaking study of variability, and experimental breeding. Such work as that of Mr. A. G. Lowndes on *Cyclops vernalis* and *robustus* (1929A) is of the highest value, and it is to be hoped that his example will be followed. In this case we know without a shadow of doubt that the very distinct form *C. robustus* is within the limit of variability of the parent species *C. vernalis*, and is repeatedly produced by it. It appears to have no adaptational significance, though this is a point to which attention might be profitably directed.

The word "variety" has had so many meanings that it is now almost without meaning. I have endeavoured to avoid its use in connection with forms bearing names. At the present moment it seems that, in giving names to distinguishable groups, attention should be confined to such as we may suppose, rightly or wrongly, to have the standing of species or subspecies. Variations, however distinct, if they are not believed to be common to a persisting population, should not be named. Literature is already too much burdened with excess of names, which may nowadays be given to single individuals distinguishable from others of the same population by perhaps a small difference in one leg of a pair.

It is most difficult to be consistent in practice, and some apology is perhaps needed for inconsistencies which may be noted in this book. For instance, I have given new subspecific names to two forms of *Marænobiotus vejdovskyi*, and have noted, without naming them, almost equally distinct races of *Epactophanes*. In the first case the races are clear-cut, recognizable without difficulty, and seem to be associated with special surroundings. In the second case there is no evidence of special adaptation, and separation of subspecies would, in practice, be difficult or impossible.

The two cases are precisely comparable, and the difference in treatment is dictated partly by convenience and partly by lack of knowledge of the ecological facts.

X. DISTRIBUTION OF ALLIED SPECIES.

According to the Darwinian theory of the origin of species, we are led to expect that the most nearly related species (or subspecies) will be found occupying areas which are distinct either geographically or ecologically, and this is generally true. For example, where two or more species of *Diaptomus* are found together they are generally structurally very distinct, or can be shown to have a different cycle, and it is rare to find two related species in the same plankton. But unfortunately, the rule is subject to such exceptions that it is of doubtful application. Krmpotic (1924) gives examples of associated species which are most difficult to understand. For instance, he found in one pool *D. gracilis*, *D. transylvanicus*, *D. intermedius* and *D. vulgaris*. While *D. gracilis* and *D. vulgaris* are quite distinct species which are often found together, the other two are so nearly related to *D. vulgaris* that they should be regarded as subspecies of it if they are to be recognized at all. Graeter (1903) states that *D. vulgaris* is never found with *D. transylvanicus*, nor *D. denticornis* with *D. laciniatus*, whereas *D. castor* may occur with *D. transylvanicus*.

The association of several species of *Diaptomus* in one shallow pool is not uncommon in countries which are richer in the genus than our own. For instance, in a pool in Tunisia *D. wierzejskii*, *D. incrassatus*, *D. cyaneus* and *D. ingens* were found together on two occasions, in March, 1906, and March, 1913—evidently no chance association. The following table shows the frequency with which different species were found associated by Krmpotic. It will be noticed that the more limnetic species were rarely found with those characteristic of ponds.

Table showing association of certain species of Diaptomus *in Croatia and Slavonia. Figures show number of occurrences of any two species together. Information taken from Krmpotic,* 1924, *pp.* 8–15.

	gracilis.	*vulgaris.*	*intermedius.*	*transylvanicus.*	*castor.*	*superbus.*	*sostarici.*	*lilljeborgii.*	*steindachneri.*	*laticeps.*	*wierzejskii.*	*tatricus.*
gracilis	—	6	4	3	..	..	..	..	..	..	..	..
vulgaris	6	—	5	3	..	..	..	1	..	..	..	..
intermedius	4	5	—	3	..	..	..	1	..	..	..	..
transylvanicus	3	3	3	—	1	..	..	2	2	1	1	
castor	..	..	..	1	—	1	2	5	5	..	..	1
superbus	..	..	..	..	1	—	1	1	1	..	..	1
sostarici	..	..	..	..	2	1	—	2	2	..	..	1
lilljeborgii	..	1	1	2	5	1	2	—	7	3	1	1
steindachneri	..	..	..	2	5	1	2	7	—	3	1	1
laticeps	..	..	..	1	..	..	..	3	3	—	1	..
wierzejskii	..	..	..	1	..	..	..	1	1	1	—	..
tatricus	..	..	..	..	1	1	1	1	1	..	..	..

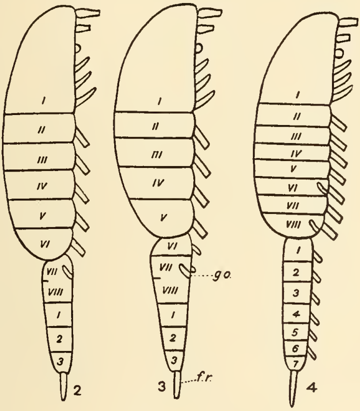
A remarkable example is seen in the occurrence in the same lakes in North Uist of *D. wierzejskii* and *D. laticeps*—two species which appear to have precisely the same cycle and are most difficult to separate. Indeed in the female separation can only be satisfactorily made by examining the 13th segment of the antennule, which in the former bears 1 and in the latter 2 setæ ! It is impossible to suppose that there can be any ecological separation is such a case.

Such associations of allied species seem to be contrary to all conceptions of the origin and persistence of species ; but the difficulty may be more apparent than real, and may arise simply from our ignorance of the biology of these animals, or in part from our relatively crude methods of collecting. It is difficult to see how such a problem can be attacked, but really detailed knowledge of the biology of any two closely allied species of *Diaptomus* would be a most valuable contribution to the " species problem."

XI. STRUCTURE.

1. Body.

Prof. Sars, in his 'Crustacea of Norway,' has adopted the terms "cephalosome," "metasome" and "urosome" for the regions of the Copepod body, on the assumption that the mesosome or thorax of the Malacostraca is not developed in the Copepoda. Although such a view does not need to be seriously discussed, there are some advantages in using a terminology different from that which we owe to study of the higher Crustacea, since the homologies of the somites are not altogether clear.



Figs. 2–4.

Fig. 2.—Calanoid or Gymnoplea type.
Fig. 3.—Cyclopoid or Podoplea type.
Fig. 4.—Malacostracan.
i–viii, thoracic somites; 1–7, abdominal somites; *g.o.*, genital opening; *f.r.*, furcal ramus.

There is strong evidence in favour of serial homology between the anterior appendages of the Copepoda and Malacostraca, and it is not unreasonable to extend it to the posterior appendages and their somites too.

The Copepod body may be said to include (1) head, with 5 pairs of appendages. (2) Mid-body with at most 7 pairs of appendages,* of which the maxillipede is the first. (3) A limbless region of at most 4 somites.

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* Including the vestigial pair on the genital somite.

The genital opening is upon the last somite of the mid-body. For the purposes of comparison we can ignore, for the moment, as being perhaps quite illusory, the division of the body into functional regions with other limits than these.

Now in the Malacostraca the thorax, or mid-body, includes 8 somites and the genital opening is upon the 6th (female) or 8th (male). The agreement is so nearly exact that it is tempting to suggest that in the Copepods there is a thorax corresponding to that of the Malacostraca, the last somite being the first legless somite which is so usually fused with the genital somite.

Speculations of this kind are attractive, but not, perhaps, of any serious value. Such an homology with the Malacostraca seems not unreasonable. In development the abdomen is the last part to divide, and it is quite possible that a functional shortening of the thorax, to which there is so strong a tendency in Copepoda, has led to a suppression of further division of the abdomen and its reduction to a maximum of 3 somites.

Some reference must be made in this connexion to the "Archicopepod," *Euthycarcinus kessleri*, described by Handlirsch (1914) and discussed by Pesta (1914). According to Pesta's interpretation the animal possessed the same number of somites as a modern Calanoid, but the somite of the maxillipede was free and bore a biramous appendage. Behind it there are said to have been 5 somites bearing biramous appendages, and an abdomen of 4 somites in the female and 5 in the male. If this is true then the Calanoid type of relation of thorax to abdomen is primitive, and it would not be correct to refer the somite of leg 6 in Harpacticoida to the thorax. On the other hand, reference to Handlirsch's paper shows that the grounds on which the detailed reconstruction was made are most uncertain. Nothing definite could be made out of the head appendages except the presence of an antennule. Handlirsch says, "Die übrigen Anhänge des Kopfes sind nur sehr schattenhaft als undeutliche Abdrücke zu sehen, doch glaube ich auf einer seite etwa acht Gliederreihen unterscheiden zu können, was vier gespaltenen Gliedmassen entsprechen würde." To assume, therefore, that the maxillipede somite was not included in the head is pure guesswork. The segmentation of the body seems to have been clear, but the evidence for the structure of the legs is weak. The abdomen consisted of 4 somites in two specimens and 5 in the third, but the reconstruction shows 4, with reduced appendages on the first 3 and a pair of rami on the last. If the homology with the abdomen of a Calanoid is as exact as Pesta would have it, and the specimens with 4 somites are female while the other is male, then somite 1 of the female should be compound, and approximately equal in length to somite 1 and 2 of the male. This is far from being the case, and it seems there must be some mistake. If the animal actually had only 4 somites, as shown in the reconstruction, then the assumption that the somite of leg 6 (genital somite) of modern Copepods belongs to the thorax receives strong support, but the following somite would be definitely abdominal. There is, however, so much that is speculative in the interpretation of this

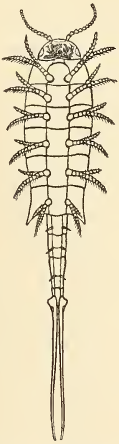


FIG. 5.—*Euthycarcinus kessleri*, reconstruction, after Handlirsch.

Triassic fossil that not much weight can be attached to it, and it is even doubtful if it has any relation at all to the Copepoda.

Giesbrecht has suggested that, in the protocopepod, the pre-genital somite bore an appendage of a form different from that of the thoracic series of limbs, and that this somite was lost in the Gymnoplea, while it was retained in the Podoplea, with corresponding loss of the last true thoracic somite. Although this assumption would make the homology more easy, the evidence for it is so weak as to be hardly worth considering.

Whether homology with the Malacostracan body be accepted or not, a terminology based upon it would have practical inconvenience for purely descriptive purposes. For such purposes we must accept the obvious divisions of the body as we find them, and these do not by any means correspond to head, thorax and abdomen of other Crustacea. A further difficulty is that, if we use a terminology based upon present structure, it is impossible to be consistent, for "abdomen" or "urosome" of the Gymnoplea does not correspond to that of the Podoplea. For the purposes of this work the following terms are adopted as a compromise between custom, convenience and homology :

Head : Including somite of maxillipede, which is actually a thoracic appendage.

Thorax : Including somites of legs 1–5.

Abdomen : Including genital somite, which is actually a thoracic somite and bears a vestigial pair of legs in most Podoplea.

2. The Somites.

The somites, when not actually fused, are capable of more or less free movement, and can, to some extent, be retracted one within another. This is particularly the case in the Harpacticids, so that great contraction of the body may occur when they are killed and preserved. For this reason measurements of length are very unreliable, and are of little or no assistance in determining species. Each somite consists of a cylinder of strong chitin, but anteriorly there is a flexible annular part which allows the cylinder to be pushed up within the preceding somite (Fig. 6). Posteriorly the rigid cylinder is generally continued into an exceedingly delicate and quite transparent membranous ring, the edge of which may be cut into a very fine fringe, which overlaps and perhaps protects the soft anterior part of the succeeding somite. The line of insertion of the membranous frill is commonly marked by a more or less complete ring of spines, the distribution of which is often a valuable specific character.

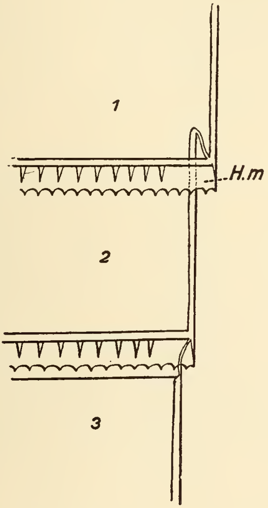


Fig. 6.—Diagram of three abdominal somites in a Harpacticid. Som. 2 is pushed upwards into som. 1, while som. 3 is shown fully extended. *h.m.*, hyaline membrane.

3. Setæ and Spines.

The cuticular outgrowths of the appendages take many forms, and the terms "seta," "spine," "hair," "tooth" or "denticle" are in use to describe them. It is impossible to be consistent in the use of these terms, since every possible gradation is found between them, and they cannot be accurately defined. On the other hand, they have great specific importance, and it is necessary constantly to refer to them. So far as concerns the typical seta and spine, the following definition may be given :

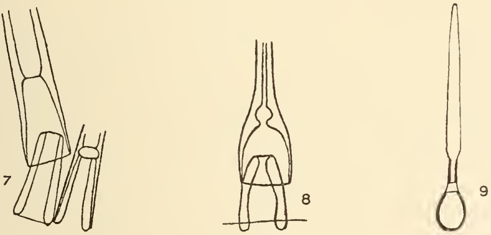
Seta : A relatively long, flexible organ, tapering to an infinitely fine point ; generally with a double row of fine hairs, giving it the appearance of a feather. The feathering may be so fine as to be almost invisible, or it may consist of conspicuous stiff hairs.

Spine : A short, strong, more or less inflexible organ ; generally armed on each side with a row of small denticles, giving a saw-like edge. More rarely smooth, or with marginal hairs, or with a marginal hyaline membrane.

The outer edge of the exopod always bears short, stout spines, which, on the last segment, increase in length distally. Commonly there is one long spine and a seta at the end of the segment, but it is just here that distinction becomes impossible. The outer organ may generally be distinguished as a spine, since it is strong and stiff, but it may have one margin denticulate and the other with marginal hairs. On the other hand, the inner one may be either a typical feathered seta, or may show every transition to a stiff spine denticulate upon one or both margins.

These structures are generally remarkably constant both in structure and position, and are therefore valuable specific characters. In the Harpacticoida each swimming-leg is generally distinguishable by the arrangement of the spines and setæ, and there are often marked differences between species. It is not easy to examine a sufficient number of specimens, but I have not yet found any individual variation in the number of the spines and setæ except in cases of malformation. Consequently I have made a practice of giving a " leg formula " for each species. Where setæ or spines are referred to in describing legs they are taken in order from proximal to distal or from outer to inner.

The two middle setæ of the furcal rami are often referred to as jointed or not jointed, and perhaps an explanation is necessary. These setæ in the first copepodid stage and in some adults are simple, and like any other setæ on the body; but in some Calanoida, and most Cyclopoida and Harpacticoida, they are "jointed" near the base in the adult. There is a definite break in the seta at this point, marked by the "helle Stelle" of Schmeil. There is a short cone attached to the ramus, and the base of the seta itself is hollowed out and fits over the cone (see Figs. 7, 8). The seta quite frequently breaks off at this point, and rarely it may be seen in process of becoming detached, revealing clearly the nature of the structure. When the seta is detached it does not actually break, but slips off as a glove from a finger. This structure was described by Schmeil (1892, p. 17), and by Claus (1893, p. 296).



FIGS. 7–9.

FIG. 7.—Furcal setæ of *Nitocra spinipes*, that on the left partly detached at the "joint."

FIG. 8.—Furcal seta of *Amphiascopsis cinctus* partly detached.

FIG. 9.—An æsthete from the antennule of the male of *Eurytemora velox.*

In addition to the setæ and spines there are, on the antennule, generally one or more sensory organs which have been called "sinneskolben" "sinnescylindren," or "æsthetasks" (Giesbrecht) (Fig. 9). These organs are, in some cases, modified setæ (Claus), but they are generally sensory organs of independent origin. They are alluded to in this work as "æsthetes." Their number and position are often of systematic importance.

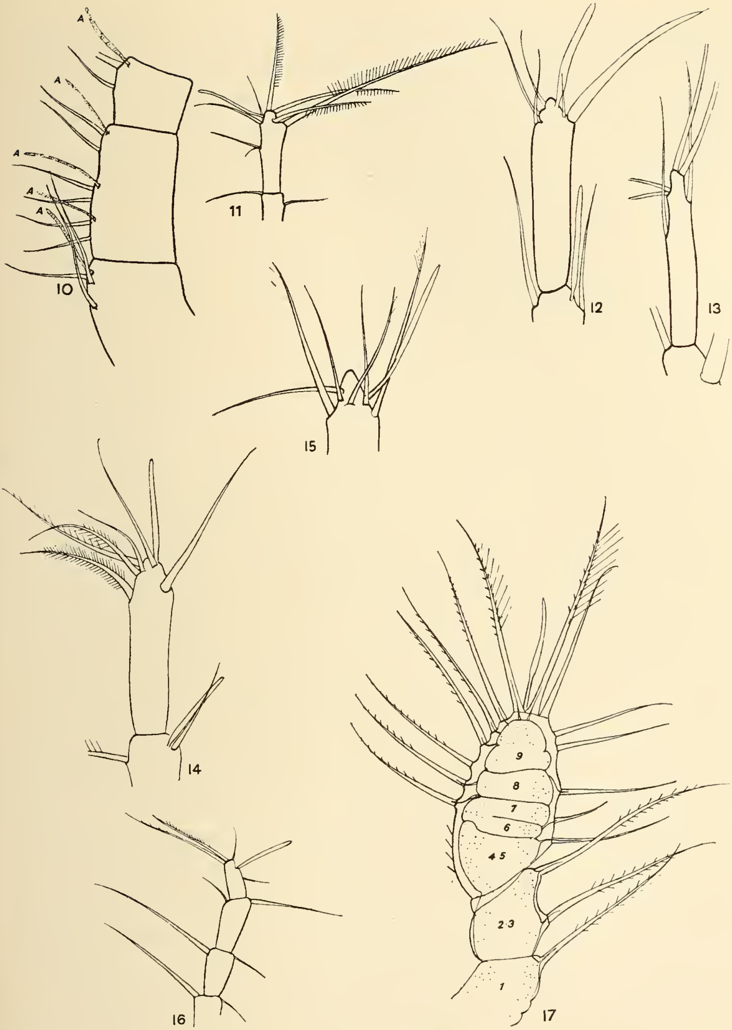
4. APPENDAGES.

Antennule.

A great deal has been written by Claus, Giesbrecht and others in an attempt to reduce the antennule of Copepoda to a common type, and to trace the origin of the segments of the adult from those of the nauplius and copepodid, and there is good reason to believe that the Calanoid antennule may be taken as the starting-point from which all forms of it have been derived by fusion of segments. Throughout the Calanoida, with few exceptions, the antennule is a long, many-jointed, balancing organ, in which the number of segments never exceeds 25. An antennule of 26 segments has been described by Cooper in *Adiaptomus* and by Methuen in *Metadiaptomus*, but in both cases by inclusion as a segment of the process of the head on which the limb is borne. Segs. 1 and 2 and 8 and 9 are often fused, and still more often segs. 24 and 25.

Each segment bears one or two setæ, often accompanied by an æsthete, and the number, arrangement and length of these structures provide valuable diagnostic characters upon which Giesbrecht and Schmeil have laid stress. As Lubbock (1853) was the first to point out, the typical arrangement, as found in such genera as *Calanus*, is that each segment bears 2 setæ and an æsthete, the group being designated by Giesbrecht as a "trithek." One or more members of the triad may be lost, but the arrangement is evidently fundamental, and can be traced in most genera of *Calanoida*. It is generally possible, by noting the arrangement of the setæ, to determine which segments have been fused in the antennules of less than 25 segments (*e.g. Ctenocalanus*, Giesbrecht, 1892, taf. x, fig. 21, segs. 8 and 9).

If, however, we accept the presence of a trithek on one segment of a 24-segmented antennule as evidence of the fusion of 2 segments, we must concede the same significance to their presence in an antennule of 25



FIGS. 10–17.—ANTENNULE.

(Figs. 11–16, terminal segments of certain Calanoida.)

FIG. 10.—Segs. 1–3 of *Calanus finmarchicus*, showing grouping of setæ and æsthetes in "tritheks." Seg. 2 has three complete tritheks.

FIG. 11.—*Parapontella brevicornis.*

FIG. 12.—*Temora longicornis.*

FIG. 13.—*Calanus finmarchicus.*

FIG. 14.—*Anomalocera pattersoni.*

FIG. 15.—*Eurytemora velox.*

FIG. 16.—*Stephos* sp.

FIG. 17.—Antennule of *E. velox*. Last nauplius, about to moult.

segments. In *Calanus finmarchicus*, for example (Fig. 10), seg. 2 bears 3 quite distinct tritheks, and should then correspond to 3 segments,* while seg. 1 in many genera has, in addition to a distal trithek, also a proximal seta which may indicate a lost joint. We may therefore conclude that the primitive antennule consisted of 27, and possibly of 28 segments.

The last 4 segments are differently armed, though the arrangement is reducible to the trithek scheme. The terminal segment varies much in the number of setæ borne, and it is commonly fused with seg. 24. In *Calanus* there are, in all, 5 setæ and an æsthete (Fig. 13),† but this is the greatest number found.

When the two distal segments are fused it may be difficult to distinguish the setæ referable to each, but in some cases it is quite clear. For instance, in *Anomalocera* (Fig. 14) the last segment bears near its end a pair of long setæ, corresponding to the 2 setæ of seg. 24, and a group of 4 setæ and an æsthete at the end. In *Centropages* and *Diaptomus* there are only 5 setæ in all, of which the 2 proximal correspond to seg. 24. In some genera (*e.g. Stephos*, Fig. 16) seg. 25 remains distinct, while segs. 8 and 9 are fused, so that a 24-segmented antennule may be arrived at in different ways. In *Eurytemora* (Fig. 15) there are 6 setæ crowded together at the extremity, but the arrangement is evidently the same. Considering the fact that the maximum number of setæ on any normal distal segment is 2, it is probable that fusion of distal segments has already begun in *Calanus*, and that the primitive antennule may have consisted of 30 or 31 segments.

Oberg (1905) has given a most detailed account of the development of the antennule in some Calanoida and in *Oithona*, tracing the fate of each segment from the nauplius to the adult. I have followed the development

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* Giesbrecht (1899, p. 133), has already noted this point, and states that in *Heterorhabdus* (in which segs. 1 and 2 are fused) the distal part of seg. 2 bearing a trithek, is divided off.

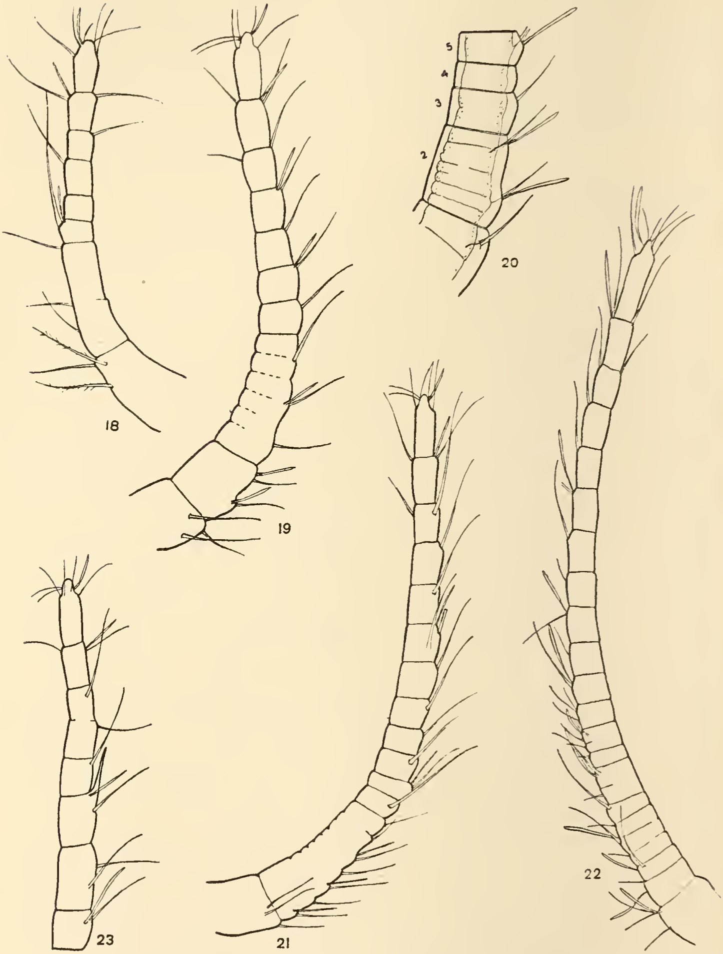
† Giesbrecht figures an additional small hair on the anterior side, but this I have not seen.

of the antennule in *Eurytemora*, and am fully in agreement with Oberg so far as concerns the derivation of the terminal segments, but am unable to confirm his results in some other respects.

At the moult of the last nauplius the antennule is transformed as follows :

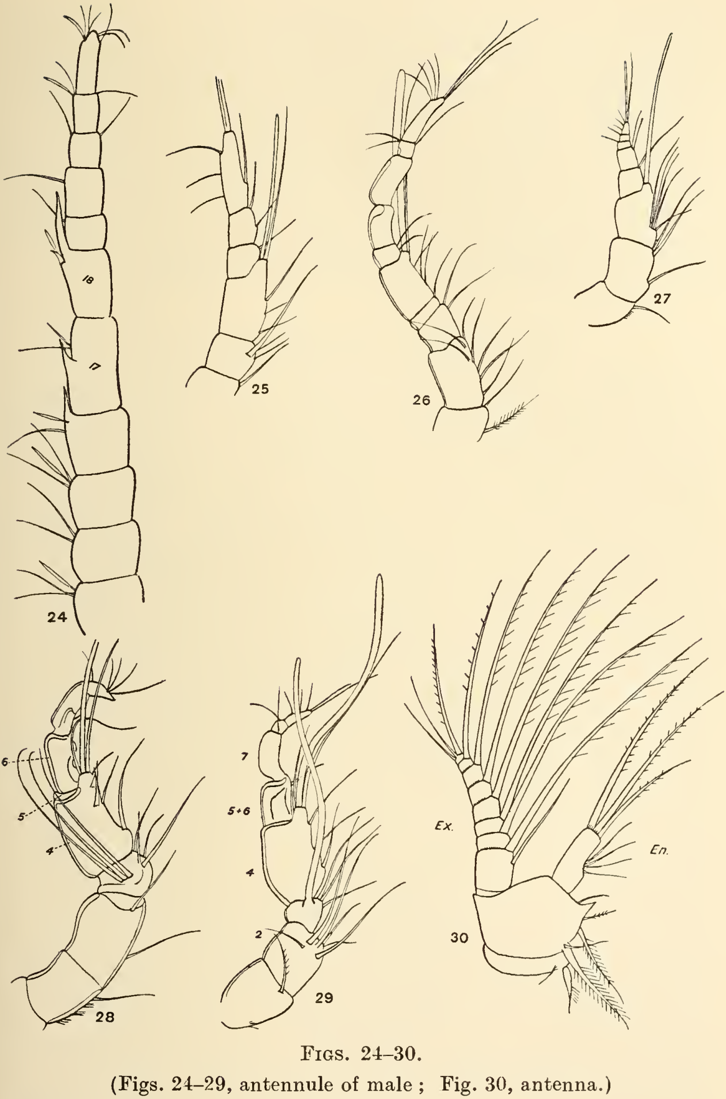
Nauplius.	1st copepodid.
Segment 1 . . .	Segment 1.
,, 2 . . .	Segments 2 and 3.
,, 3 . . .	,, 4–9.

That segment 3 becomes divided into a number of segments is quite clear if the limb is examined just before the moult; but it is by no means easy to determine the number positively, since the tissues are crumpled, and what appears to be a new joint may be no more than a wrinkle. It is possible to see threads of tissue entering setæ which will presumably be renewed (Fig. 17), but it is not necessarily certain that a seta without a thread will be lost. From copepodid 1 onwards these 6 segments (nos. 19–24) remain unaltered, and multiplication takes place entirely in the region corresponding to segs. 1 and 2 of the nauplius. At each moult the number of segments and setæ is increased till, in stage 5, the adult form is reached. Oberg claims that he was able to recognize at each stage the setæ of the preceding stage, and to determine in this way which segments had divided. I have spent much time in examining the antennule of *Eurytemora*, and find myself wholly unable to distinguish setæ acquired anew from those of the preceding stage renewed at the moult, so that I cannot confirm or deny Oberg's conclusions. Even when a specimen is about to moult there is no certainty as to the fate of existing segments and setæ, since the new appendage is to some extent retracted and thrown into folds which may or may not represent joints (Fig. 20). There is also this difficulty—that division of the proximal segments is often incomplete in stages 2 and 3, and always difficult to see. All that is clear in *Eurytemora*



FIGS. 18–23.—ANTENNULE OF *Eurytemora velox.*

FIG. 18.—Cyclopid I.
FIG. 19.—Cyclopid II.
FIG. 20.—Cyclopid II; segs. 1–5; about to moult.
FIG. 21.—Cyclopid III, male; basal segments not fully separated.
FIG. 22.—Cyclopid IV, female.
FIG. 23.—Cyclopid IV, male, distal part.



Figs. 24–30.

(Figs. 24–29, antennule of male ; Fig. 30, antenna.)

Fig. 24.—Cyclopid V, male, *E. velox.*

Fig. 25.—*Canthocamptus gracilis*; last Copepodid.

Fig. 26.—*Tisbe furcata*, showing seg. 3 divided.

Fig. 27.—*Thalestris rufoviolascens*, male ; last Copepodid stage.

Fig. 28.—*T. rufoviolascens*, adult.

Fig. 29.—*Amphiascopsis cinctus.*

Fig. 30.—*Longipedia* sp., nauplius.

is that the terminal 11 or 12 segments are separated in stage 2 and do not afterwards divide. The accompanying figures (18–24) show the fate of these segments. It is these segments that are modified in the prehensile antennule of the male, the hinge falling between segs. 18 and 19 (6 and 7 counting from distal end) and the next 6 (segs. 13–18) becoming more or less swollen. The terminal part of the male antennule corresponds therefore to the 3rd segment of the nauplius.

The Antennule of Harpacticoida.

The Harpacticid antennule never exceeds 10 segments, and is generally reduced to 8 or fewer. It is, in nearly all cases, separable into two parts, a proximal part of which the last segment bears a long æsthete, and a distal of not more than 5 small segments. The æsthete is generally borne upon seg. 4. This division into two parts is marked out in the copepodid stages. In *Canthocamptus* the last copepodid has an antennule of 6 segments, the æsthete being upon seg. 3 (Fig. 25), and at the next moult segs. 3 and 6 both divide into two. How far it is a general rule in the group that an addition may be made to the distal as well as the proximal part is uncertain, for in some cases (*e. g. Thalestris*) (Fig. 27) the terminal part is fully segmented while the proximal part consists of only 3 segments. Having regard to the general rule in Calanoida and Cyclopoida, that the terminal segments should be laid down in the first copepodid and thereafter remain unaltered, it is rather surprising to find an exception among the Harpacticids.

In the male the segmentation of the antennule may be the same as in the female, or it may have more segments, never less. This is also the case in those species of *Cyclops* in which the female has a reduced number of segments. Generally the æsthete is borne on seg. 4 as in the female, and the position of the hinge falls between segs. 6 and 7. The terminal part consists of from 3–5 segments, or they may be fused into two, or even one claw-like segment. Although as a general rule the æsthete is borne on seg. 4, there are many cases in which the proximal part consists clearly of 5 segments, seg. 3 apparently dividing into two.* This is particularly evident, for example, in *Tisbe furcata* (Fig. 26). This additional segment is found also in the female only in *Balænophilus*, a genus otherwise very specialized.

In some cases the prehensile antennule is as slender as it is in the female, and very little modified (*e. g. Tisbe furcata*). Generally segs. 4–6 are more or less swollen, and may bear modified spines, while there is a strong tendency to fusion of these three segments. Complete separation of them is seen, for example, in *Nitocra*; but seg. 5 is very commonly reduced or even absorbed into seg. 4 as in *Epactophanes*, for instance. In such cases the hinge appears to be between segs. 5 and 6. In some genera both segs. 5 and 6 unite with seg. 4 to form a single large segment upon which the distal claw folds back. This is so in *Tachidius* and most *Laophonte*. In such antennules the position of the æsthete may mark the place of the lost joint between segs. 4 and 5, but it may shift its position to the end of the combined segment, as in *Enhydrosoma curvatum*, for example.

The structure of the prehensile antennule is so exactly similar in all Copepods in which it occurs that it is almost certain that the position of the hinge may be regarded as a fixed point. In the Calanoida this point is always between segs. 18 and 19, the terminal part representing the segments produced from seg. 3 of the nauplius limb. In *Cyclops*, Claus (1893D, p. 284) found that the terminal 4 segments of the copepodid form the part distal to the hinge, and that this point corresponded to the hinge in Calanoida. As in the Calanoida, the succeeding 5 or 6 proximal segments form a more or less modified and swollen region. In the Harpacticoida the terminal part may consist of as many as 5 distinct segments (*e.g. Thalestris gibba*), or may be

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* Seg. 3 occasionally also bears a long æsthete, *e.g. Amphiascopsis cinctus* (Fig. 29), and *Ialysus rufus*, Brian (female).

reduced to an unsegmented claw. The swollen part is, however, reduced to 3 segments or fewer; but the numbers of setæ borne by these segments indicates that they are the products of fusion, and that this portion may well correspond to segs. 13–18 of the Calanoida. The basal 4 (or 5) segments should, then, be the equivalent of segs. 1–12 of the Calanoida. It is impossible, with any certainty, to suggest the steps in reduction. All that is of real interest, and seems to be clear, is that the prehensile antennule retains a more primitive segmentation than in the female, and that it is directly comparable to that of the Cyclopoida and Calanoida.

Detailed consideration of the Cyclopoid antennule, since it has bearing on the classification of *Cyclops*, is reserved for later treatment.

Antenna.

The antenna, though subject to much modification, presents no difficulties in interpretation, and it is only necessary to deal with Chappuis's recent (1929c, p. 473) proposition that the vestigial branch generally found in Harpacticids is the endopod, and not, as has always been supposed, the exopod. He states that, at the metamorphosis from the nauplius to the copepodid stage, the appendage is rotated so that the original endopod comes to lie on the outside of the appendage. Of such a rotation I have seen no evidence whatever, and comparison of the adult structure in various Harpacticids leaves no doubt that the unsegmented "accessory branch" of some *Canthocamptus*, for example, is homologous with the many-jointed branch in *Longipedia* and in the Calanoida. That this branch is the exopod in Calanoida cannot be disputed. It is only necessary to refer to Oberg's figures of the appendage in the nauplius and first Copepodid in *Centropages* (1905, taf. vii, fig. 2) to see how obvious is the correspondence of exopod with exopod in both. In *Longipedia* the antenna of the nauplius has an exopod of 7 or 8 segments (Fig. 30), and there is very little change at the moult to the

Copepodid (Gurney, 1930). It is hardly necessary to labour the point, the homology is so abundantly obvious, and it is to be hoped that Chappuis's new interpretation will not be adopted.

Mandible.

Hansen regards the corpus mandibulæ as the precoxa, and finds a minute segment representing the coxa between it and the large segment which he identifies as the basis. There certainly is, in many Calanoida, an "intermediate area" which might be regarded as a vestigial segment, but I am quite unable to see any sclerite in this region, and it has much more the appearance of a broad articular membrane giving extra mobility to the palp than a reduced segment. The development of the limb lends no support to Hansen's interpretation; in fact it most strongly suggests that the corpus mandibulæ is the coxa, and that the precoxa is lost.

Maxillule.

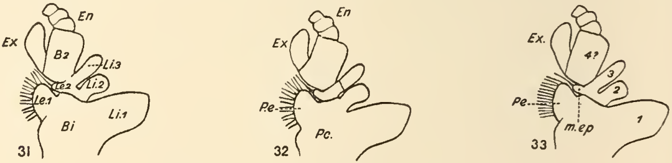
1. CALANOIDA.

The maxillule shows extraordinary diversity of form and reduction in the free-swimming Copepods, and it is by no means an easy matter to determine the homologies of its parts. It is necessary to start with what we must assume to be the most primitive form as found in certain Calanoida—*e. g. Calanus* (Fig. 34).

The interpretation of the appendage as given by Hansen (1925, p. 39) is as follows: The first segment, or precoxa, has two inner laciniæ, of which the first is a large spine-bearing gnathobase, and an outer plate or pre-epipod, bearing a number of long setæ. The second segment has an inner lacinia, and may bear a single outer seta. The third is a rather long segment bearing an outer moveable appendage which represents the exopod, and a terminal part which is the endopod and is two-jointed. Hansen's interpretation brings the limb into line with the scheme which he lays down for the crustacean limb in general, and it can be supported by reference to some of the numerous drawings given by Sars (see specially 1924).

The interpretations of Giesbrecht and of Borradaile differ from that of Hansen, and are shown in the diagram (Figs. 31, 33).

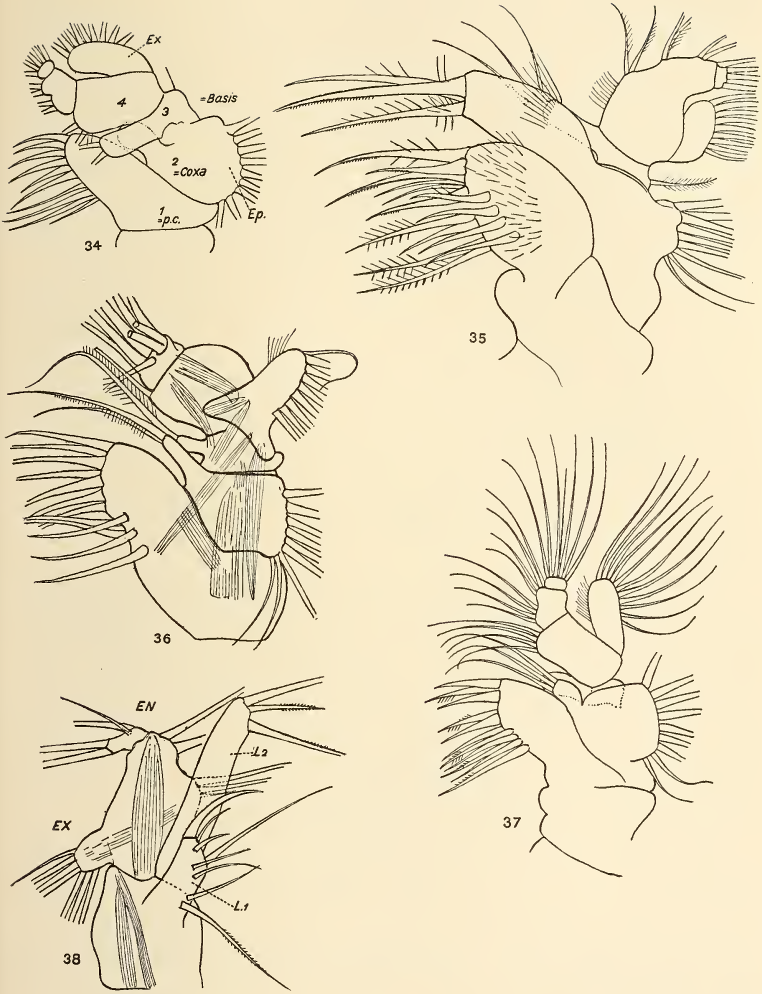
On the other hand, it is in some Calanoids most difficult to determine with certainty the lines of division between the segments, and my own observations lead me to disagree with Hansen in one important respect. The relations of the parts are specially difficult to follow in *Calanus finmarchicus*. Indeed it is possible to interpret them quite differently according as to whether the limb is examined from in front or behind. In other species, *e. g. Anomalocera pattersoni*, it is perfectly clear that there is a line of division between the gnathobase and the segment bearing the 2nd lacinia. In this and other cases lacinia 2 distinctly belongs to a segment bearing the outer setiferous plate (pre-epipod of Hansen). We have, then, 3 segments, which may be determined as (1) precoxa, (2) coxa, with epipod, (3) basis. But there is also the long segment, on the outer side of which is seated the exopod, and if we are to accept three preceding segments, then the exopod is borne on seg. 4, which would be unique.



FIGS. 31–33.—MAXILLULE.

FIG. 31.—Giesbrecht. FIG. 32.—Hansen. FIG. 33.—Borradaile. *B.i.*, *B.2*, segments of sympod; *L.e.*, *L.i.*, outer and inner lobes; *P.c.*, precoxa; *P.e.*, pre-epipod; *M.ep.*, metepipod; 1–4, endites or primary segments; *En.*, endopod; *Ex.*, exopod.

Borradaile (1926), taking the endites of a primary phyllopodium as the basis upon which the segmentation of the limb has been founded, concludes that the exopod



Figs. 34-38.—Maxillule.

Fig. 34.—*Calanus*. Copepodid V.
Fig. 35.—*Anomalocera*.
Fig. 36.—*Pareuchæta*.
Fig. 37.—*Pseudocalanus*.
Fig. 38.—*Candacia*.

may be borne either upon the third or the fourth segment, or upon these two fused into one. He says (p. 203): "The recognition of a three-segmented protopodite in the Crustacea is purely empirical, for the actual 3rd segment is not homologous in all cases, being sometimes the 3rd segment of the primary series, sometimes compounded of the 3rd and 4th, sometimes the 4th alone, and probably in a few instances compounded of the 4th and 5th, the actual 2nd segment in the latter two cases being compounded of the primary 2nd and 3rd."

Functionally the limb seems to be made up of two parts, namely segs. 1 and 2, and the whole terminal part (segs. 3 and 4 with exopod and endopod); for in the fresh limb of *Diaptomus*, for example, the whole of this distal portion is moveably articulated to the basal part, and there is no functional joint between segs. 3 and 4. This functional separation is indicated in Fig. 34, where the whole of the distal part is shown flexed upon the proximal.

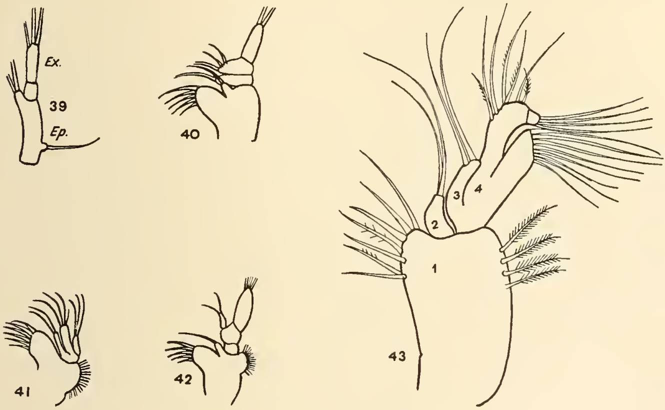
Within the Calanoida may be found many modifications of this appendage (Figs. 35–43). The fully-developed appendage, as found in *Calanus*, though with modification in form and some reduction of the endopod, is typical for the group, but in others one part or another may be reduced or absent. The gnathobase is always retained, though in *Augaptilus megalurus* (Fig. 39) it is reduced to a scarcely recognizable lobe.

The first part to be subject to reduction is the endopod, which becomes unjointed, shortened, or finally disappears altogether. In *Chiridiella* (Fig. 41) the form of this appendage recalls that of an Harpacticid. It seems quite clear, by comparison of a series, that it is the endopod and not the exopod which disappears, or rather becomes absorbed into the basis; but in some cases the exopod has the appearance of an endopod, being a continuation of the axis of the limb.

The epipod is traceable in almost all cases, but there are stages of reduction in the numbers of setæ until they may be reduced to one—*e. g. Augaptilus megalurus*

(Fig. 39), or disappear altogether as in *Pseudaugaptilus longiremis* (Fig. 40). Within the genus *Augaptilus* the number varies from one to five.

Among the most curious developments of the appendage is the form assumed in *Candacia* (Fig. 38). Here the 2nd lacinia interna is a long cylindrical rod directed along the axis of the limb, and lacinia 3 is lost. In this case the seta-bearing external lobe, which looks like the epipod, seems from its position to represent the exopod, the epipod being lost. Lacinia 2 in the Pontellidæ (Fig. 35) may become almost as large as the gnathobase. In *Anomalocera* Sars shows this lacinia as jointed, but I have not been able to see this joint.



Figs. 39–43.—Maxillule.

(Figs. 39–42, after Sars.)

Fig. 39.—*Augaptilus megalurus.*
Fig. 40.—*Pseudaugaptilus longiremis.*
Fig. 41.—*Chiridiella macrodactyla.*
Fig. 42.—*Scottula abyssalis.*
Fig. 43.—*Parapontella.*

Another remarkable line of development may be traced from the foliaceous type of limb to a simple linear appendage. The loss of the endopod is the first step; then the inner lacinia may be reduced or lost, until finally a simple linear series of segments is attained.

For instance *Pseudaugaptilus longiremis* has lost epipod and endopod (Fig. 40). The parts are easily homologized, but an approach to a linear, 4-segmented, limb is made. The tendency of the exopod to continue the direction of the stem increases the appearance of linearity. The last stage is seen in *Augaptilus megalurus* (Fig. 39), where the epipod is reduced to a minute papilla with one seta, the gnathobase is almost lost, and segs. 2 and 3 are fused, forming a 3-segmented cylindrical appendage.

2. Harpacticoida.

The maxillule in most Harpacticoida is so much reduced that, taken by itself, it would scarcely be possible to relate it to the fully developed Calanoid appendage. Giesbrecht (1892, p. 43) distinguishes in the Calanoid limb exopod and endopod, but refers to the epipod as lacinia externa, the outer seta corresponding to lacinia interna 2 in some forms being lacinia externa 2. He regards the three inner laciniæ as belonging to seg. 1 of the protopod, and the segment bearing exopod and endopod as seg. 2. In describing the appendage in *Euterpina* (Harpacticoida) he refers to the gnathobase and succeeding lacinia as L.i.1 and 2, and the terminal segment as B2 plus endopod.

Sars is not consistent in his terminology, but alludes to the outer two small lobes in Canthocamptidæ as epipodal and exopodal lobes. With this interpretation I do not agree.

It is only in the Longipediidæ that all the elements of the Calanoid limb can be definitely identified, but the epipod is reduced to a bunch of setæ (2 in *Canuella*) springing from seg. 2, and segs. 3 and 4 are fused (Fig. 44). Even here the homologies are not entirely clear; but it is reasonable to assume that the bilobed inner edge of the third segment represents lacinia 3 and the vestigial lacinia of seg. 4. The endopod would then be 2-segmented as in *Calanus*.

Figs. 44–50.—Maxillule. Harpacticoida.

Fig. 44.—*Canuella.*
Fig. 45.—*Dactylopus.*
Fig. 46.—*Amphiascopsis cinctus.*
Fig. 47.—*Diosaccus.*
Fig. 48.—*Phyllothalestris.*
Fig. 49.—*Aspidiscus.*
Fig. 50.—*Canthocamptus.*

(Homologous parts in Figs. 48, 50 lettered B, C, D.)

In all other Harpacticoida the epipod is lost, unless some small setæ occasionally found (*e. g. Dactylopus tisboides*) (Fig. 45) on the outer margin may represent it. In many other forms the remaining parts are distinctly recognizable (see Figs. 46, 47, *Amphiascopsis cinctus*, *Diosaccus tenuicornis*); but whereas seg. 2 is generally more or less clear, with its inner lacinia, the precise homology of the distal parts is obscure. It seems that seg. 3 remains generally distinct, and with a tendency for its inner lacinia to become very much larger than that of seg. 2 (see Fig. 48, *Phyllothalestris mysis*, *Diosaccus tenuicornis*), and that the exopod, endopod and seg. 4 tend to fuse and become reduced to a single segment in which the separate elements are lost. Even seg. 3 may become merged into this composite part.

In its most reduced condition, as in *Canthocamptus* (Fig. 50), there appear to be only the gnathobase followed by two small laciniæ. The first of these laciniæ is clearly seg. 2, while the second is all that is left of segs. 3 and 4 and of exopod and endopod.

Stress should, I think, be laid upon the fact that in all cases there is quite clear separation between the segment of the gnathobase and that of lacinia 2. This strongly confirms the conclusion arrived at with regard to the Calanoida—that the outer seta-bearing lobe belongs to seg. 2 and is therefore an epipod and not a pre-epipod, as in Hansen's interpretation.

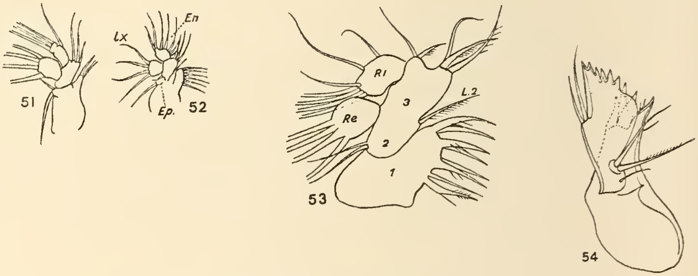
If, instead of starting with the Calanoid appendage, we were to start with that of *Canuella*, the interpretation of the limb in the terms of the normal biramous Crustacean appendage would be easy, since it falls naturally into a 3-segmented sympod bearing on the third segment the exopod and endopod. Possibly this is, after all, the most primitive form, and it may be held that the Calanoid type of limb has been derived from it by separation of seg. 3 into two parts, rather than that the Longipediid limb has been derived from the Calanoid by fusion of segs. 3 and 4. This is a question which cannot be definitely answered. The general view is that the Calanoida are the more primitive, and that therefore it is more likely that the Longipediid limb has been derived from the more fully segmented form. The Harpacticoida show such a strong tendency to fusion and suppression of parts that some reduction is to be expected in the Longipediidæ. Assuming the Calanoid type of limb to be the more primitive, the maxillule then consists of a 3 or 4-segmented sympod with 3 inner laciniæ. Seg. 2 may bear an epipod in Calanoida only. In the Harpacticoida segs. 3 and 4 are not separated, but there may be vestiges of the exopod and endopod. In some cases, *e. g. Canthocamptus*, they are only traceable with doubt as groups of setæ. In the figure these groups are lettered to correspond to the parts in *Phyllothalestris*, where the homologies are clear. When they are definitely traceable they are to be referred to as exopodal and endopodal lobes. Where reduction has gone so far that no distinct parts are recognizable, the whole terminal part may be described as the "palp."

3. Cyclopoida.

The Cyclopoida, as defined by Sars, include a very large number of parasitic or semi-parasitic forms in which the mouth parts are much modified, and it is only in the more primitive families, such as the Oithonidæ and Cyclopinidæ, that we find a maxillule directly comparable with the Calanoid type, and even here the homologies are obscure.

In order to understand the Cyclopoid form of maxillule it is best to take as the starting-point the maxillule of the Notodelphyoida, which can readily be homologized with the hypothetically primitive type. In this group there is a tendency to the loss of lacinia 2 and the fusion of its segment with that of lacinia 1. Thus, in *Doropygus* L.i. 2 is represented by a single seta, and the combined segs. 1 and 2 bear a single seta representing the vestigial epipod. Seg. 3 has no inner lacinia, but bears an outer and a terminal plate representing exopod and endopod (Fig. 51). In *Agnathaner* the basal segment seems to represent segs. 1 and 2 completely fused, and with a single small inner lacinia (Fig. 52).

The most complete form of maxillule in the Cyclopoida is found in *Cyclopina.* In *C. schneideri* (= *C. brevifurca*, Sars) the appendage distal to the gnathobase consists of a single large segment bearing 2 outer plates (Fig. 53). There are 2 setæ on the outer side at the base, probably representing the epipod, and an inner seta, which is perhaps the vestige of lacinia 2. This large plate corresponds exactly to seg. 3 of *Agnathaner*, with the exception that seg. 2 is fused to it instead of to seg. 1. The movable plates are, then, exopod and endopod, while the main segment represents segs. 2–4 of the Calanoid appendage. There are two small terminal lobes which may be the vestiges of lacinia 2 and 3. Exactly the same parts are recognizable in *Oithona*, though the endopod is reduced to a minute lobe, and the exopod is a dorsally directed prolongation of the segment. In these cases the whole distal part of the appendage may well be called the "palp," since it is a single entity distinct from the gnathobase. Even in the Calanoida the whole of the distal part of the limb from seg. 3 onwards moves and functions as one part.



FIGS. 51–54.—MAXILLULE.
FIG. 51.—*Doropygus porcicauda*, after Sars.
FIG. 52.—*Agnathaner typicus*, after Canu.
FIG. 53.—*Cyclopina Schneideri.*
FIG. 54.—*Euryte longicauda.*

In the Cyclopidæ the limb is reduced further to the gnathobase and a single small segment hinged to it. In *Cyclops* (*e. g. C. strenuus*) this small plate has two outer lobes, which may represent the vestiges of endopod and exopod, but in *Euryte*, apart from a pair of setæ on the outer edge, no trace of them is left (Fig. 54).

We have, then, the appendage reduced to the first segment or gnathobase, and a small, simple palp which is the sole remains of the whole of the rest of the Calanoid appendage.

In the *Ascomyzontidœ* the limb appears to consist of a small basal segment bearing 2 setigerous branches, and it is probable that the larger of these really represents the gnathobase, which is the most persistent part in other forms, and the other the small palp seen in *Cyclopidœ.* The gnathobase is not separated from the base by a suture, whereas the palp is jointed off.

Coming to the *Pœcilostoma* of Sars, we are faced with a peculiar difficulty. According to Sars the mandibles are entirely absent, and the maxillules are represented by an appendage having the character of the gnathobase of other Copepods, bearing a small unsegmented palp. Such an appendage is easily derived from that of *Cyclops*, and indeed the " maxillule " of *Hemicyclops* is very like that of Cyclops ; but not only does it seem most improbable that the mandible should be lost, but also in some cases it is quite clear that the " palp " is a structure distinct and separate from the " gnathobase." This is certainly the case in *Thersitina*, and I consider that the " gnathobase " is really the mandible itself, and the " palp " is the maxillule reduced to a vestige in which separate parts are indistinguishable.

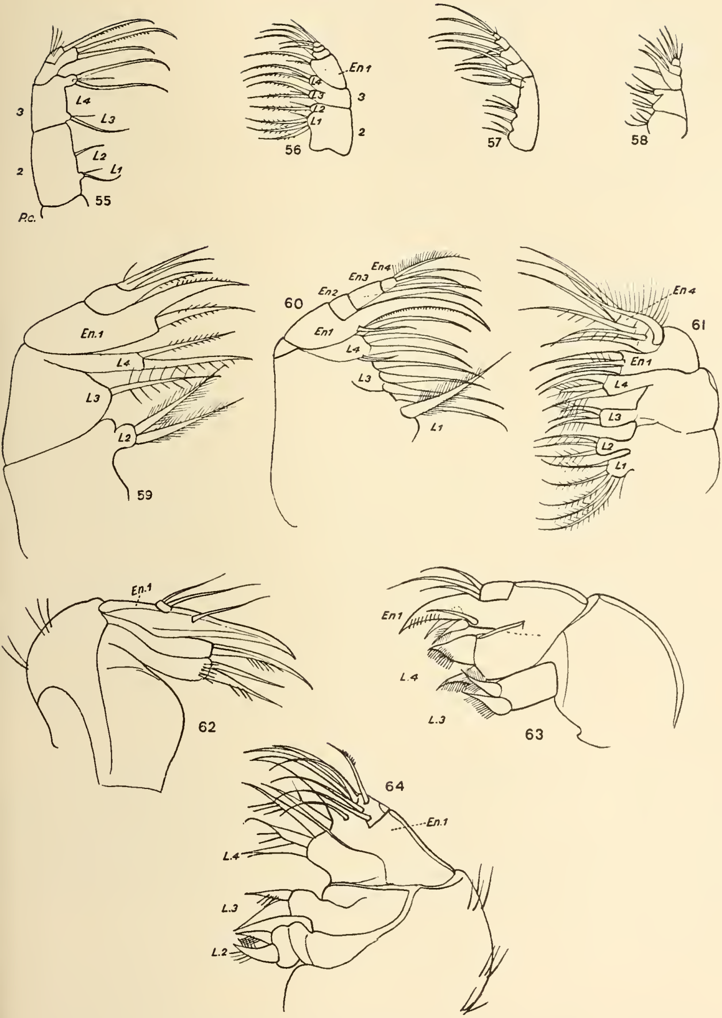
Maxilla.

The interpretation of this appendage is reasonably clear, but it can best be understood if the limb in *Calanus* is considered together with that of certain other genera in which its segmentation is more distinct, *e. g.*

Heterorhabdus (Fig. 55) and *Heterocope* (Fig. 56). Hansen's interpretation is doubtless correct ; but I have not seen the cuticular sclerites as represented by him. In appendages such as this there are often lines visible which have the appearance of joints or of delimiting sclerites, but are sometimes merely folds of no significance. It is only when the limb develops into a strong pediform appendage that it is possible with certainty to distinguish definite joints.

There is, in many cases, a small precoxal segment, but this is apt to become absorbed in the body and indistinguishable. The next two segments are large, each bearing a pair of endites, and correspond to coxa and basis. Finally there is an endopod of not more than 5 segments. Seg. 1 is nearly always large, in *Calanus* produced into a large endite, and armed with one or more large spines. The remaining segments are reduced, and show a tendency to disappear. There is never a trace of an exopod, unless the seta inserted on the outer side of the appendage in *Calanus* may be interpreted as a vestige of it. Hansen regards it as such, but its position, in my own experience, and also in Giesbrecht's and Sars's figures, is not as shown by Hansen. It appears to belong to seg. 2, and not to seg. 3.

Giesbrecht apparently regards the 4 proximal endites as belonging to the coxa (B.1) and the segment of endite 5 as representing the basis (B.2), and indeed in many cases the segment is so large that it might well be supposed to belong to the sympod. If it were so the latter would be of 4 segments, as appears to be the case in the maxillule of Calanoids. Apart from the general postulate that the sympod normally consists of not more than 3 segments, there is nothing to attach the segment of lacinia 5 to the endopod rather than to the sympod. Giesbrecht is, however, certainly wrong in so far as he overlooked the precoxal segment and attributed endites 1–4 to his B.1, whereas it is quite clear in many cases that they belong to two distinct segments.



FIGS. 55–64.—MAXILLA.

(Figs. 55–58, after Sars.)

FIG. 55.—*Heterorhabdus.*	FIG. 60.—*Notodelphys.*
FIG. 56.—*Heterocope.*	FIG. 61.—*Longipedia.*
FIG. 57.—*Oithona.*	FIG. 62.—*Canthocamptus.*
FIG. 58.—*Cyclopina.*	FIG. 63.—*Diosaccus.*
FIG. 59.—*Cyclops strenuus.*	FIG. 64.—*Amphiascopsis cinctus.*

If the comparison is extended to the Cyclopoida, *e.g. Oithona*, we find exactly the same type of limb, and in this case it is fairly clear that there is a distinction between the unsegmented sympod with 4 vestigial endites and the endopod of 4 segments, of which endite 5 belongs to the first. For this reason I accept Hansen's interpretation.

CYCLOPOIDA.

In the Cyclopoida the limb of *Oithona* is precisely comparable to that of some Calanoida, *e.g. Heterorhabdus*, but the precoxa is not distinguishable, and coxa and basis may be fused. In *Cyclopina* endites 1–5 are distinguishable (Fig. 58), and it is fairly clear in *C. elegans* that no. 5 belongs to the endopod. It has developed a large inner spine which remains a constant feature in other Cyclopoida in which the limb is reduced. The remaining segments of the endopod become reduced to a small papilla—*e. g. Cyclops* (Fig. 59).

In the Pœcilostoma the limb becomes reduced to a basal segment representing segs. 1–3, without endites, and a distal segment which appears to represent seg. 1 of the endopod only, the remainder of the endopod being completely lost, *e.g. Hippomolgus*, *Pseudanthessius.*

In the Siphonostoma, *e. g. Parartotrogus*, the limb has the form of a 2- or 3-segmented prehensile claw. The slender distal part probably here also represents endopod seg. 1, the apparent terminal segment sometimes seen being merely the spine of the former.

HARPACTICOIDA.

In the Harpacticoida the Longipediidæ possess a maxilla of typical form (Fig. 61), with a 2-segmented sympod bearing 4 well-developed endites, and an endopod of 3 or 4 segments, of which seg. 1 is large, with a large endite bearing strong spines. In the majority of genera the limb is very much reduced and simplified, with loss of one or more endites and of the segments of the endopod ; but throughout it appears that, as in Cyclopoida, seg. 1 of the endopod with its large spine is retained, while the endites are lost from the base upwards (Figs. 62–64), endite 4 persisting always even when 1–3 are lost.

The degree of reduction does not characterize large groups, for various stages of reduction may be found within a single family. For example, in Canthocamptidæ, while *Phyllopodopsyllus* has all 4 endites and a 3-segmented endopod, in most genera the endopod is reduced to seg. 1 with a seta-bearing papilla representing the remainder. In *Ameira*, for example, only endite 4 is retained. The *Tachidiidæ*, which, on other grounds, must be regarded as an unnatural assemblage of genera, include one genus, *Tachidiopsis*, with an apparently 5-segmented endopod (Sars), while in the other genera it is reduced to a small papilla. The appendage is peculiarly modified in Ectinosomidæ, and difficult to interpret. It seems probable that the long segment 2 represents seg. 1 of the endopod (*e. g. Bradya*).

Maxillipede.

1. CALANOIDA.

According to Hansen the maxillipede consists of a 3-segmented sympod and an endopod of not more than 5 segments—*i. e.* "at most 8 joints." So far as concerns the sympod, 3 segments are easily demonstrated, but it is equally clear that 6 segments may be detected in the endopod—a point of some importance, since I hope to show that the swimming-legs also are potentially 9-segmented.

In *Calanus* (Fig. 65) and many other forms there is a small spine-bearing lobe at the end of seg. 3 of the sympod which has generally been reckoned as part of it. In some cases, *e. g. Temora* (Fig. 67), there is no sign at all of separation from seg. 3, but even in *Calanus* it is sometimes clearly separated and partly united with seg. 1 of the endopod. Examination of the figures in

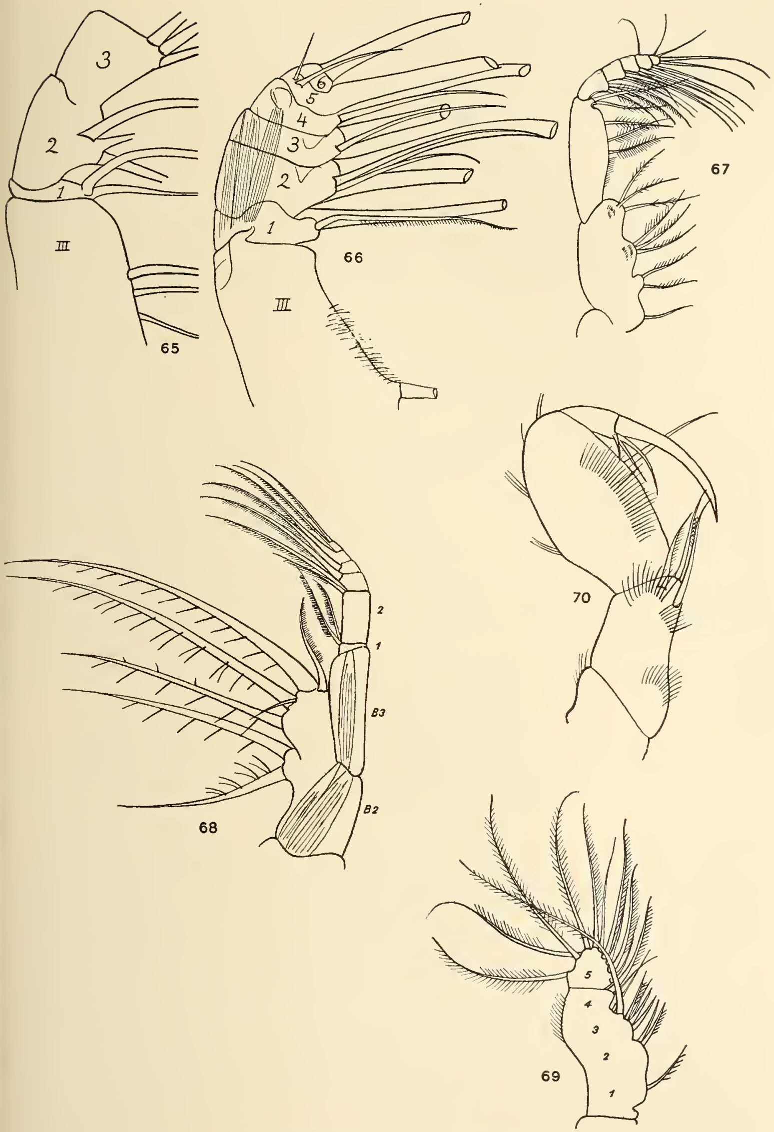
Sars's plates shows many cases in which there is partial separation of this segment, but in *Euchæta* it is quite clearly a separate segment and the first of a 6-segmented endopod (Fig. 66). In *Pseudeuchæta brevicauda* (Sars, 1924, pl. xxix) the endopod is of 5 segments only, but the segment in question is distinct and it is a terminal segment which is lost.

In seg. 2 of the sympod the marginal setæ are arranged generally in 3 groups, which in some cases, *e. g. Temora*, are elevated upon lobes which seem to correspond to the endites of the maxilla. But in other Crustacea no single segment bears more than 2 endites. In some cases (*e. g. Isias*) there are 4 groups of setæ, and, if these represent endites, then we should have 4 endites corresponding to 2 primary segments, and the sympod would be interpreted as of 4 segments as in the maxillule of *Calanus*. It should be noted as supporting such a conclusion that it is the proximal endite which is liable to be lost, and this is in accordance with the fate of the endites in the maxilla.

In some families the maxillipede is reduced, becoming smaller than the maxilla, *e. g. Heterorhabdus*, *Parapontella*, *Acartia*. In *Pontellidæ* and *Acartia* the appendage is of very peculiar form. The sympod is very short and broad, bearing several long pectinate spines, while seg. 3 is slender and seems at first sight to be seg. 1 of the slender endopod. The homology is not clear in *Acartia*, but it is evident in such genera as *Calanopia* that the long segment is the basis, and it is followed by 6 segments, of which seg. 1 is traceable with difficulty (Fig. 68).

2. Harpacticoida.

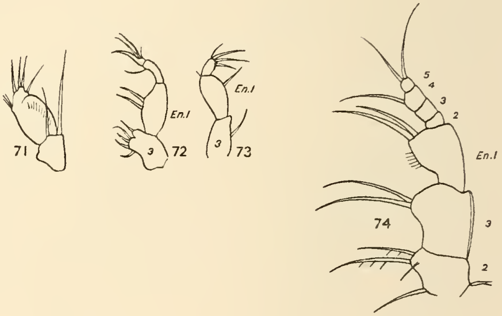
The Harpacticoida are divided by Sars into two main groups—Achirota and Chirognatha—on the ground that in the former the maxillipede is not prehensile, whereas it is a clawed prehensile organ in the latter. A distinction of the two groups founded upon this limb is impossible. Not only are there species of Chirognatha



Figs. 65–70.—Maxillipede.

Fig. 65.—*Calanus*.
Fig. 66.—*Euchæta*.
Fig. 67.—*Temora*.
Fig. 68.—*Calanopia*.
Fig. 69.—*Canuella*.
Fig. 70.—*Amphiascopsis cinctus*.

in which the limb is as little prehensile as it is in Achirota (*Stenhelia palustris*, *Ceylonia*, etc.), but there are transitional forms among the Tachidiidæ. In *Tachidiella minuta* and *Tachidiopsis cyclopoides* the maxillpede departs from the prehensile type and becomes comparable to that of *Bradya* (Fig. 71). In fact the appendage of *T. minuta* is almost exactly as it is in *B. dilatata* (see Sars, 1911). Sars's figure of the appendage in *T. cyclopoides* does not show the joints clearly, but it gives the appearance of a minute additional terminal segment not found in any other Harpacticid except among "Achirota," *e.g. Cerviniopsis.*



Figs. 71–74.—Maxillipede.
(Figs. 71–73, after Sars.)
Fig. 71.—*Bradya dilatata.*
Fig. 72.—*Tachidiella minuta.*
Fig. 73.—*Tachidiopsis cyclopoides.*
Fig. 74.—*Cyclopina Schneideri.*

Among the Achirota the Cerviniidæ show an appendage of typical form consisting of 5 segments, of which the last 3 no doubt represent the endopod. In the Longipediidæ the appendage becomes flattened, but retains in *Sunaristes* the same number of segments. In *Canuella* it is possible to distinguish 4 or 5 segments (Fig. 69). In the Ectinosomidæ there are 3 segments, of which the last seems to be all that is left of the endopod.

The "Chirognath" type of appendage, in its prehensile form, is at first sight difficult to harmonize with the fully segmented limb of the Calanoid or of *Cerviniopsis* for example, since it apparently consists only of 3 segments, of which the last is a claw hinged upon seg. 2. Comparison of the many different genera shows that there has been loss of segments at both ends. The precoxa is never traceable in any Harpacticid, while the coxa is commonly lost also. In *Alteutha* there are 3 segments besides the claw, and it appears that the first of these represents the coxa, and the third the enlarged seg. 1 of the endopod. In *Amphiascus* and other genera (Fig. 70) the first traceable segment would then be the basis. The terminal claw results from fusion of segments of the endopod. In *Amphiascus* it shows clearly a separation into 2 segments, and indications of such a separation may be seen in other genera.

For the purposes of description seg. 1 of the endopod upon which the claw is hinged may be called the palm.

3. CYCLOPOIDA.

The appendage never attains the development seen in Calanoida. The precoxa is not distinguishable, and the endopod is much reduced. In *Oithona* seg. 1 is long, but is followed by only a single segment. In *Cyclopina* there may be 5 free segments in the endopod (*C. schneideri*) (Fig. 74), but in Cyclopidæ the appendage becomes modified as a prehensile organ (*Euryte*) or reduced. In *Halicyclops* it is reduced to a 2-segmented appendage, probably by total loss of the endopod, but in *Cyclops* the endopod is 2-segmented (or 1-segmented in *C. phaleratus* and *C. affinis*). In the Siphonostoma it is a prehensile claw in which 5 or 6 segments may be distinguished (*Ascomyzon*). In Pœcilostoma the appendage resembles that of the Cyclopidæ in which the endopod is most reduced (*Hemicyclops*), or it may be a prehensile organ much as in Siphonostoma, though in this case reduced to 3 segments. The condition in *Lichomolgus* resembles closely that found in Harpacticoida. Evidently the terminal claw represents a fusion of the endopod segments. In some cases there is sexual dimorphism, the appendage in the male having a longer claw than in the female (*e. g. Hermannella*), while it is altogether lost in the female of *Ergasilus*.

The Swimming-Legs (*Legs* 1–4).

Infinite as is the variety of form assumed by the four pairs of swimming-legs in the Copepoda, they are all reducible to a common biramous type with, primitively, a 3-segmented stem and two 3-segmented branches. Hansen found some difficulty in proving the existence of a precoxa in Copepods, but demonstrated in *Megacalanus* the existence of a sclerite which might be attributed to it. On the other hand, it can certainly be traced in some Harpacticids (*Canthocamptus*) and also in *Cyclops*. In the latter the two legs are united by a plate which, if the leg is examined when turned backwards, extends forwards beyond the base of the coxa. Just in front of this point it has a transverse suture indicating a division into two parts (see Fig. 75). This anterior portion corresponds to the precoxa, which is represented by a strongly chitinized lateral part, which moves with the limb, and a membranous inner part.

It seems to be characteristic of copepod appendages that each segment should have an inner seta and an outer spine or seta. The coxa in nearly all Calanoida (*Acartia* is an exception) and in most Cyclopoida retains the inner seta, but it is lost in nearly all Harpacticoida (*Longipedia* retains it). There is never an outer spine or seta. The basis usually has an outer seta, and very generally in the first leg it also has an inner spine or seta. The presence of outer and inner spine or seta on the basis of leg 1 is practically universal in Harpacticoida. The inner seta is present in most Cyclopoida, with curious exceptions in the genus *Cyclops*, but absent from a number of semi-parasitic forms (*e.g.* Lichomolgidæ). It is rather remarkable that the outer seta of the basis, which is rarely, if ever, absent from Cyclopoida or Harpacticoida, is generally not present in Calanoida, though the inner seta on leg 1 is commonly found. So far as concerns the sympod of the legs, then, the Calanoida seem to be less primitive than other Copepods.

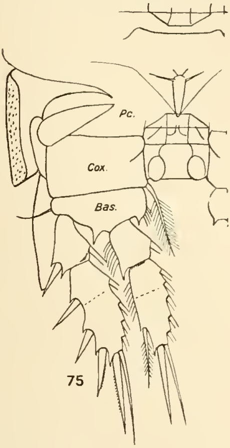


Fig. 75.—Leg 2, etc.; *Cyclops*, copepodid V. *Pc.* Precoxa.

In the branches the presence of an outer spine and an inner seta is the general rule in segs. 1 and 2 of the exopod; but there are, of course, exceptions, generally involving loss of the inner seta on seg. 1, and more rarely of an outer spine (*e.g. Oithona*). In the endopod segs. 1 and 2 never have an outer spine, but it is commonly the case that seg. 2 has 2 inner setæ.

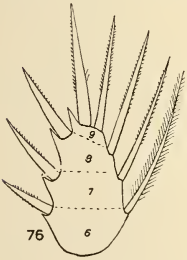
Seg. 3 in both branches has a number of setæ, the exopod also having from 1–3 outer spines. The greatest number of spines and setæ is shown in Fig. 76 (*e.g. Cyclopina gracilis, Cyclops vernalis-robustus*). If we assume that each outer spine in the exopod and each inner seta in the endopod represents an independent segment, we have in each case evidence of the fusion of 4 segments into one. In other words the whole limb would primarily have been of 9 segments, precisely as it is in primitive Malacostraca, if we accept as part of it the pre-coxa and pre-ischium. The following evidence for such a fusion of segments is offered: (1) In the copepodid stages the branches of the legs are at first unsegmented, then 2-segmented, and finally divided into 3. In the 2-segmented stage, seg. 2, which represents segs. 2 and 3, bears the same number of outer and terminal spines as the adult leg, either 3 or 4 as the case may be, and the division at the last moult takes place at the position of the first spine. At this stage there are, in species such as *Cyclops strenuus*, 3 inner setæ only, corresponding in number and position to the outer spines. In the adult there are 2 additional setæ on seg. 3. It is suggested that, inasmuch as the first outer spine and inner seta do in fact correspond to a segment which becomes free, so the succeeding spines indicate segments which once became separated, but are now suppressed. In the case of *C. strenuus* only 3 segments can be postulated, but in others (*C. vernalis-robustus*) 4 can be distinguished.

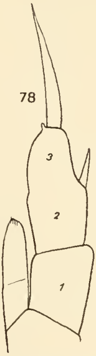
(2) Leg 5 of the Calanoida, which is so generally more or less modified in both sexes, is unquestionably derived from the normal swimming-leg, and indeed in some genera it is scarcely at all modified, and each branch is 3-segmented. Even when the modification is considerable (*Diaptomus* female), or very great (*Diaptomus* male), it may be possible to trace the 3 segments in the exopod, even though they are entirely lost in the endopod. In female *Diaptomus* the exopod is distinctly 3-segmented, though seg. 3 is very much reduced, and may be absent. At the junction of this small vestigial segment with the large seg. 2 the latter generally bears a small spine. In the copepodid stage V seg. 3 is not separated from seg. 2, but it is much larger in proportion than it is in the adult, and the spine which marks the position of the future division is

relatively large. The 3-segmented branch is quite recognizable, though not complete (Fig. 79).

In stage IV these appendages show scarcely any sexual difference; the outer branch is unsegmented, and bears 2 terminal spines (Fig. 77).

In the male in stage V the adult form is more or less indicated, but, apart from a difference in size, the right and left legs are the same. The exopod is 2-segmented as in the female, and seg. 2 bears an outer spine and one (or in some species 2) terminal spine, but no inner spine such as is present in the female. There is no question that in both sexes the limb is on precisely the same plan (Fig. 78).





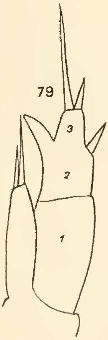


Fig. 76.—Leg 3, exopod 3; *Cyclops vernalis* var. *robustus*.
(Figs. 77–79, development of leg 5, *Diaptomus castor*.)
Fig. 77.—Male, stage IV.
Fig. 78.—Male, stage V.
Fig. 79.—Female, stage V.

Now in the male the outer branch of the right leg remains unsegmented, bearing a strong outer spine and a long moveable terminal claw. But, since the outer spine is obviously homologous with the outer spine in the female, which is inserted on the outer corner of the separated seg. 2, it is obvious that in the male also it indicates a joint which, in this case, is never developed. In stage V there is sometimes a very slight notch on the inner side of the last segment, opposite to the spine, which may indicate the position of the lost joint (Fig. 78).

Now if it can, as I think, be definitely proved that this outer spine marks a lost joint in a highly modified limb, and if, in the case of the swimming-legs, the spines corresponding to segs. 1 and 2, which are later separated, appear in their proper position before the separation is effected, I suggest that the outer spines in seg. 3 of the adult represent also joints which are now suppressed.*

It must be conceded that the argument above developed rests mainly upon the development of the exopod, whereas in the Malacostraca the exopod is generally flagelliform, without any fixed number of joints. It is not, however, necessary to assume that there has always been such a separation of function between exopod and endopod as now exists, and it is probable that the two branches were primitively similar. Also it is possible, in the Copepods, to extend the same interpretation to the endopod, though the facts are by no means so convincing as for the exopod.

That the Copepod limb originally possessed more segments is not a new idea. It was suggested in 1892 by Grobben, though the reason given was not very satisfying—" was die Gestalt des *Argulus* Beines erschliessen lässt" (p. 255). Chappuis also (1929c, p. 473) says, " die Äste hingegen werden ursprunglich beider 6-gliedrig gewesen sein. Dass der Endopodit eine solche Urgliederzahl hatte, ist schon deshalb anzunehmen weil der Innenast bei allen Crustaceen ursprunglich diese Gliederzahl aufweist; beim Exopoditen hingegen kann man aus den vorhandenen Randborsten und -dornen erkennen, dass das Endglied aus vier verschmolzenen Einzelgliedern zusammengesetzt ist." The evidence here presented from the male limb of *Diaptomus* is so clear that what was otherwise merely an assumption becomes a reasonable proposition.

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* Smirnov (1931, p. 325) holds that certain abnormalities described by him prove that the terminal claw includes seg. 3 of the exopod—"Das dritte Exopoditen-glied des rechten Fusses beim Männchen ist mit dem Greifhaken vollkommen verschmolzen, und nur durch die Anschwellung des Basalteiles des Hakens angedeutet." The evidence from abnormal structures of this kind (supernumerary setae) is of doubtful value, and I see no reason to modify the view expressed above.

The Fifth and Sixth Legs of the Harpacticoida and Cyclopoida.

It has been suggested by Giesbrecht (1899) that it is possible that the 5th leg of the Podoplea is not homologous with that of the Gymnoplea, and that it and the 6th leg found only in the former may belong to a series separate from the series of the thorax.

Leg 5 of the Cyclopoida and Harpacticoida is generally so much reduced that it is impossible at first sight to see how it could be derived from the normal biramous type of leg. There is nothing to be learnt from developmental stages, but fortunately there are some species in which the reduction has not gone so far, and from which homologies may be deduced.

In the normal leg the coxa bears an inner feathered seta, and the basis a slender smooth (or sometimes feathered) outer seta. Now in practically all Harpacticoida, and in most Cyclopoida, the basal segment of the 5th leg has a slender outer seta, and seems to correspond to the basis. This conclusion is confirmed by the fact that there are species of Cyclopidæ in which this segment is preceded by another which, in some cases (*Cyclopina elegans*, *Pterinopsyllus insignis*) (Figs. 80, 83), bears an inner seta. It seems certain, then, that we can recognize here the coxa and basis, and that in most cases the former has been lost.

The homology of the distal part of the limb is less clear. In the Harpacticoida it is typically a flattened oval plate with rarely more than 6 setæ. It is possible to surmise, on the analogy of the 3rd segment of the swimming-leg, that this plate may have arisen by fusion of segments to a maximum number of 4, represented now by their outer or inner setæ, and there is at least some evidence that such fusion has occurred.

In *Microthalestris forficula* (Figs. 88, 89), the leg of the female has 8 symmetrically arranged setæ, but that of the male is definitely 3-segmented, the 3rd segment bearing 4 setæ in two pairs. The male limb is, in effect, the same as the female limb, but with 3 out of the possible 4 segments separated.

In *Eucanuella spinifera* male (Fig. 86), there are also 3 definite segments, the 3rd again bearing 4 spines and perhaps representing 2 segments.

In the Cyclopoida the limb rarely consists of more than 2 segments, of which the 1st represents the basis; but there are species among the more primitive forms (*Cyclopina longicornis*, male, and *Pterinopsyllus insignis*) in which it is 3- or 4-segmented (Figs. 82, 83). The last segment then bears 4 setæ and may be regarded as a fusion of 2 segments, making the equivalent of the 3-segmented ramus.

There is, I think, no doubt that we can see the steps in the transformation from a primitively 4-segmented branch to an unsegmented limb, but it is not quite clear whether this branch represents the endopod or the exopod.

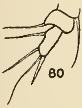
Where one branch has been lost it is generally the exopod, but in this case such evidence as there is points to the conclusion that it is the exopod that is retained. The evidence is admittedly slender.

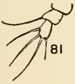
(1) In *Eucanuella* (Fig. 86) the 3-segmented appendage has the apparent character of an exopod in that each segment has an outer spine. I cannot find any Copepod in which there is an endopod with an outer spine on either of the first 2 segments of the endopod.

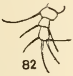
(2) In the Calanoida it is always the endopod of the 5th leg which is reduced or absent.

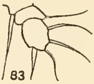
(3) The inner extension of the basal segment (basis) of the Harpacticoida may, perhaps, represent the endopod fused to the basis. It never bears more than 6 setæ or spines—a total number such as is frequently found on the endopod of leg 4 (*e.g. Microthalestris forficula*). This leg commonly bears fewer setæ than leg 3, indicating a progressive reduction in number from behind forwards. It is also commonly the case that the endopod itself is smaller and of fewer segments than that of leg 3, though the exopod may be longer and with more setæ.

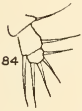
(4) A 5th leg extraordinarily like that of a Harpacticid is found in *Scottula abyssalis*, Sars (Calanoida) (Fig. 92). In *Scottula inæquicornis*, Scott, the basis bears an inner seta, but no inner extension at all. On the other hand, in *Paramisophria cluthæ* there is a small inner process bearing a small spine and a seta, and it is permissible to suggest that in the series *S. abyssalis*, *P. cluthæ*, *S. inæquicornis*, we see three stages in the reduction of the endopod.

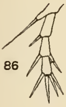


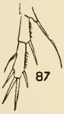


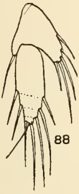


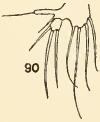


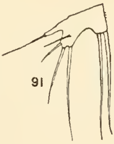












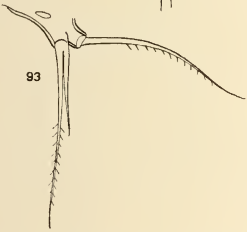


FIG. 80.—*Cyclopina elegans.*
FIG. 81.—*Cyclopina longicornis*, female.
FIG. 82.—*C. longicornis*, male.
FIG. 83.—*Pterinopsyllus insignis*, female.
FIG. 84.—*P. insignis*, male.
FIG. 85.—*Cyclops fuscus.*
FIG. 86.—*Eucanuella spinifera*, male.
FIG. 87.—*Cerviniopsis clavicornis.*
FIG. 88.—*Microthalestris forficula*, female.
FIG. 89.—*M. forficula*, male.
FIG. 90.—*Zosime major.*
FIG. 91.—*Z. valida.*
FIG. 92.—*Scottula abyssalis* (a Calanoid).
FIG. 93.—Leg 6, *Phyllothalestris mysis*, female.

(Figs. 80–85, leg 5 of certain Cyclopoida, after Sars; Figs. 86–92, leg 5 of certain Harpacticoida, after Sars.)

There can be no doubt that the so-called 6th leg is actually a reduced leg of the same series as the preceding leg 5.

In the female it is reduced to a papilla bearing at most 2 setæ, lying by the opening of the oviduct; but in the male it is rather more distinct, and consists of a slight ridge bearing generally 3 setæ. Of these the outermost is a slender seta of exactly the same form as, and obviously homologous with, that of the basis of the 5th leg. This is particularly clear in *Eucanuella spinifera* or *Phyllothalestris mysis* (Fig. 93). Stages of reduction to this condition can easily be traced in the 5th leg of the male of many species. For example in *Rhizothrix gracilis* (Sars, 1903, supp., pl. xlviii) the 5th leg is reduced to a simple plate bearing 5 setæ, and the outer basal seta. In *Sunaristes paguri* (Sars, 1903, pl. vi) that of the female is merely, as in leg 6 of so many forms, a simple series of small papillæ bearing 3 very small setæ and a long basal seta. It is, in fact precisely the same as the 6th leg with the exception of having one more seta.

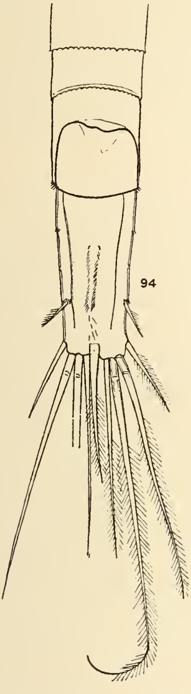
It is clear from the foregoing that the 5th and 6th legs are derivable from the normal biramous type and must belong to the same series. Further, that there is no reason to accept Giesbrecht's suggestion that the 5th leg in Gymnoplea and Podoplea may not be homologous. One further piece of evidence may be finally adduced which seems to bear upon both propositions. In the Cancerillidæ (*e. g. Parartotrogus arcticus*, Scott (Sars, 1915, pl. 79), the 4th somite is reduced to the same size as the 5th, so that the articulation between fore- and hind-body seems to fall between the 3rd and 4th somites of the thorax. In accordance with this reduction the 4th leg is also reduced. The basis is fused with the somite so that its seta springs from the edge of the somite, and the limb itself is a small papilla bearing 2 setæ, even smaller than the 5th leg, which bears 3 setæ.

5. Abnormal Structures.

Abnormal structures, such as supernumerary setæ, or deformed setæ or spines, are not very uncommon, but do not seem to have any significance. Examples of abnormalities in the secondary sexual characters are on record, but have not come under my notice (see

Richard, 1889 ; Bremer, 1914 ; Mrázek, 1893, etc.). It seems, however, worth while to mention two abnormalities in *Cyclops* which I have met with. In both cases the furcal rami are fused together to form a single plate.

(1) *Cyclops vicinus* (Fig. 94).—The anus opens into a dorsal depression on som. 5. The two rami are completely fused, but they retain all their normal setæ except the dorsal seta, and even the inner fringe of hairs is represented as a double line of hairs on the dorsal face. In place of the two dorsal setæ there is one large median feathered seta.



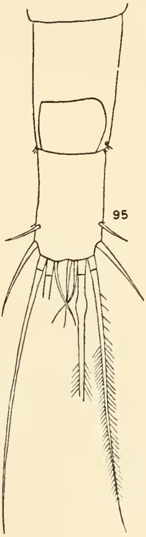


FIG. 94.—Abnormal furcal rami, *Cyclops vicinus*.
FIG. 95.—Abnormal furcal rami, *Cyclops serrulatus*.

(2) *C. serrulatus*, male (Fig. 95).—The specimen was taken at Misurina (Dolomites) in May, 1929. Abdominal somites 4 and 5 united. Here the fusion of the rami into

a simple plate is so complete that there is no indication of a median division. The setæ are again normal, except that only one of the dorsal setæ is present, and is inserted a little below the others.

Steuer (1910B, p. 1018, fig. 3) describes an exactly similar example of union of the rami in *Corycæus brehmi.* The resemblance of these furcal plates to the Decapod telson, and more particularly to that of the Euphausiacea, is very striking. In the Ægisthidæ* the long slender furcal rami are normally fused throughout their length, but the fusion is not complete, as there is a median line of demarcation in *Ægisthus.*

XII. METAMORPHOSIS.

The main features of the development of the Copepoda were fully described by Claus as early as 1858, but it is only in recent years that the full details of the changes from stage to stage have been established. The most important works on the subject are those of Oberg (1906), Grandori (1912), Chappuis (1916), Dietrich (1915), Brian (1921) and Borutzky (1925).

It is typical for the Copepoda as a whole that the larva passes through 6 nauplius and 5 copepodid stages, but development may be to some extent abbreviated, and this is particularly the case in the parasitic forms, where also various special changes are sometimes introduced.

In the Calanoida, so far as is known, there are always 6 nauplius stages, but in the Cyclopoida there may be only 5, even in the free-swimming forms. The full number is retained in *Oithona*, but in *Cyclops* there are 5, and the stages are not precisely comparable with those of *Diaptomus*, for instance. Among the Harpacticoida 6 nauplius stages are found in *Phyllognathopus* and *Epactophanes*, but in general there are only 5, and often fewer.

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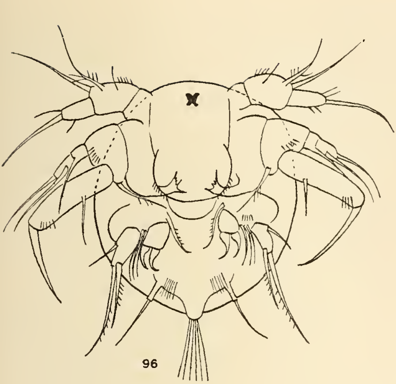
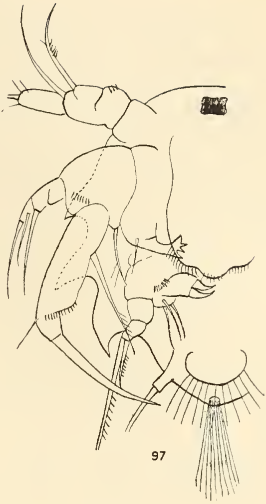
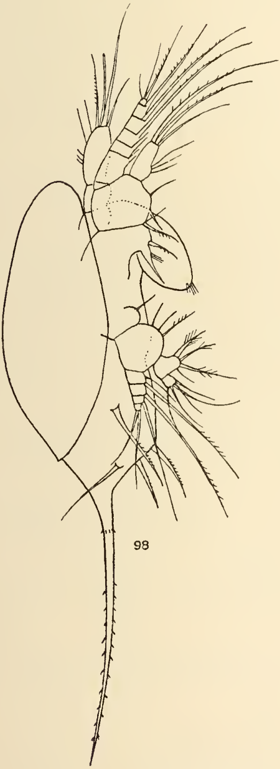
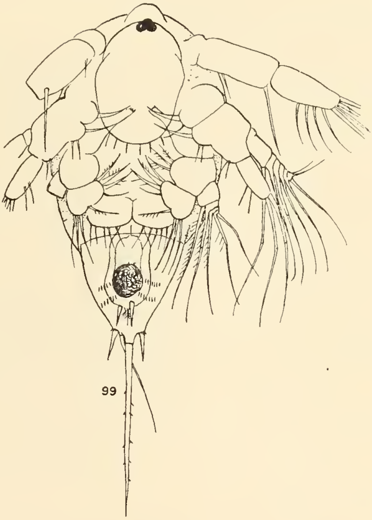
* This group of genera has been three times independently separated as a new family:

1. Ægisthidæ, Giesbrecht (1892, p. 78, footnote).
2. Hensenellidæ, Dahl (1895, p. 171).
3. Pontostratiotidæ, A. Scott (1909, p. 232).









FIGS. 96–99.—COPEPOD NAUPLII.

FIG. 96.—*Laophonte brevirostris.*
FIG. 97.—*Laophonte cornuta.*
FIG. 98.—*Longipedia* sp.
FIG. 99.—*Centropages hamatus,* stage IV.

In their general form, and in the structure of the appendages, the nauplii of the Calanoida, Harpacticoida and Cyclopoida (taking *Cyclops* as typical) are readily distinguishable, and detailed study and comparison shows that it is possible to discover generic and even specific characters. As an extreme case of such specific differences the accompanying figures of the nauplii of two species of *Laophonte* are given (Figs. 96, 97).

Increased knowledge of these larval stages is necessary, and probably without it we shall never reach a satisfactory classification of the Copepoda. For instance, the nauplius of *Longipedia* (Gurney, 1930*) differs so fundamentally from that of any known Harpacticid nauplius that its position in the group becomes very doubtful (Fig. 98). Unfortunately no new grouping can be suggested until the development of other allied genera is known.

The characters of the nauplii of the three chief groups of Copepoda may be summarized as follows :

(1) Calanoida : Body rather laterally compressed.

Antennule with terminal segment flattened, the marginal setæ increasing in number at each moult.

Antenna with exopod of 6 well-developed segments. Coxal segment with small spines, but no masticatory process.

Mandible a simple biramous limb, with coxal mandibular process in early stages.

Maxillule appearing in stage 3 ; maxilla in stage 5 ; maxillipede and large rudiments of legs 1 and 2 in stage 6.

Furcal setæ usually asymmetrical after stage 1 (Fig. 99).

(2) Harpacticoida (excluding *Longipedia*) : Body very flattened, often wider than long.

Antennule cylindrical, with few setæ.

Antenna with exopod reduced, of 3–5 small segments.

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* I take this opportunity of mentioning that Hansen fully described the larva of *Longipedia* as that of an unknown Copepod in 1899. ('Ergeb. Plankton-Exp. Cladoceren und Cirripedien ').

Endopod prehensile, the terminal seta modified as a moveable claw. Coxa with large mandibular process.

Mandible with exopod small, 2-segmented, with very long terminal seta. Endopod modified,* unsegmented, with 2 stout spines in the form of pincers and a group of setæ. No coxal mandibular process in early stages.

Maxillule appearing in stage 2. Maxilla and small rudiments of maxillipede and legs 1 and 2 in stage 5.

Furcal setæ symmetrical, 1–3 pairs.

(3) Cyclopoida: Body more or less pear-shaped, never laterally compressed, but sometimes flattened.

Antennule with seg. 3 not as a rule so flattened as in Calanoida, but with marginal setæ increasing in number at each stage.

Antennule with exopod of 6 segments, seg. 2 the longest. Coxa with strong masticatory claw.

Mandible with well-developed exopod; endopod 2-segmented, seg. 1 with broad inner lobe with 3 large spines. Coxal mandibular process absent.

Maxillule appearing in stage 2; maxilla and other limbs appearing together in stage 5, but maxilla and maxillipede scarcely distinct till copepodid.

Furcal setæ symmetrical, 1–3 pairs.

The nauplii of the semi-parasitic forms have limbs of very simple form since, in the first stages, they do not apparently take food. The larva hatches with a large amount of yolk, and the number of nauplius stages may be reduced to two.

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* In *Ectinosoma* the endopod has simple, unmodified setæ and the endopod of the antenna is scarcely prehensile.

SYSTEMATIC PART.

CALANOIDA.

CLASSIFICATION.

THE division of the Calanoida by Giesbrecht into Amphascandria and Heterarthrandria, according to the structure of the male antennule, was adopted by Sars, with the addition of the group Isokerandria to include a number of rather anomalous genera, most of which were unknown to Giesbrecht. Sars's grouping differs only from that of Giesbrecht in that he raised the latter's subfamilies to the rank of families, and in some cases divided one subfamily into two new families (*e. g.* Temorina=Temoridæ and Metridiidæ). Sars himself later realized that a division founded upon the structure of the antennule was untenable. Two examples may be given: (1) *Platycopia* has the male antennule unmodified, but is in other respects related to *Pseudocyclops*, which is classed with the Heterarthrandria. (2) *Bathycalanus* is a true member of the Calanidæ, but has the right antennule of the male geniculate.

There can be very little doubt that both antennules were primitively prehensile in the male, and that the unmodified antennule of the Calanidæ is secondary. There are species in which there is fusion of certain segments without formation of a hinge, and, as Giesbrecht has pointed out, such fusion must be regarded as the last trace of a geniculate arrangement rather than an incipient stage. The example of *Bathycalanus* is the strongest possible evidence for this view, and the fact that in the genus *Pleuromamma* one species may have the right antenna prehensile (*P. abdominale*) and another the left one (*P. gracile*), shows that both appendages have the same tendency to modification. There is not, therefore, in this respect any profound difference between the Calanoida and the "Podoplea."

We are left, then, with a series of families not allotted to larger groups, although a primary grouping is desirable, and should be practicable. This is hardly the place to deal with so difficult a subject, neither am I qualified by experience of the marine Calanoida to attempt it; but it may be permissible to suggest certain points which seem worthy of attention.

In the first place, reliance on the character of the antennule has led to an unnatural grouping of the Amphascandria, and to neglect of the form of leg 5, which is of great importance. Among the Amphascandria the Calanidæ alone have leg 5 little modified in either sex, and natatory in both; in all the rest it is greatly reduced or absent in the female, and much modified in the male. There is also pronounced sexual dimorphism in the reduction of the mouth-parts of the male. The Calanidæ appear to be more nearly related to the Centropagidæ than to the other members of the Amphascandria, and one would suggest that a more natural arrangement would be to place the Centropagidæ in the position now occupied by the Calanidæ as the most primitive family.

Secondly, it is possible to indicate certain associations of families which might be regarded as super-families. For instance, with the Centropagidæ would be placed the Heterorhabdidæ and Lucicutiidæ, and possibly also the Metridiidæ, while the Amphascandria, with the Calanidæ, and perhaps the Eucalanidæ, removed, would form another natural group. The Isokerandria of Sars includes a rather heterogeneous assemblage of families, but they can at least be brought within a clear definition. Other groups which appear reasonable would be an association of the Temoridæ, Diaptomidæ and Pseudodiaptomidæ in a superfamily Temorina, and of the Pontellidæ, Parapontellidæ and Acartiidæ. On the other hand, the Arietellidæ, Pseudocyclopidæ and Candaciidæ remain difficult, if not at present impossible, to relate to other families.

Probably no final and satisfactory system can be evolved solely on the basis of adult structure, but the difficulty of discovering the larval forms of those Copepods that do not carry their eggs and are not easy to isolate and keep alive, is so great that such a final system is a remote ideal. For the present it seems necessary to abandon the larger sections, and to retain the families of Sars.

A SUGGESTED REGROUPING OF THE CALANOIDA.

I. CENTROPAGINA.—One antennule of male prehensile. Mouth-parts of male not reduced. All legs with endopod 3-segmented. Leg 5 natatory in female.

- Centropagidæ.
- Heterorhabdidæ.
- Augaptilidæ.
- Lucicutiidæ.
- (Metridiidæ ?).

II. CALANINA.—Antennule of male not modified. Mouth-parts of male not reduced. Endopods of 3 segments, and leg 5 natatory in both sexes.

- Calanidæ.

III. PARACALANINA.—Antennule not prehensile. Mouth-parts of male reduced. Leg 1 with endopod of 1 or 2 segments. Leg 5 of female reduced or absent.

- Paracalanidæ.
- Pseudocalanidæ.
- Ætideidæ.
- Euchætidæ.
- Scolecithricidæ.
- Phaënnidæ.
- (Eucalanidæ ?).

IV. TEMORINA.—Right antennule of male prehensile. Mouth-parts of male not modified. Endopods reduced. Leg 5 of female not natatory, uniramous, or with endopod much reduced.

- Temoridæ.
- Diaptomidæ.
- Pseudodiaptomidæ.

V. DIAIXINA (ISOKERANDRIA).—Antennule slightly modified in male. Mouth-parts of male not reduced. Leg with 1 endopod unsegmented; endopod of leg 2 of 2 segments. Leg 5 of female reduced or absent.

Diaixidæ.
Stephidæ.
Tharybidæ.
Pseudocyclopiidæ.

VI. PONTELLINA.—One antennule prehensile. Mouth-parts of male not reduced. Sympod of maxillipede greatly reduced. Endopods of legs 2–4 of 2 segments. Leg 5 of female reduced, generally biramous.

Pontellidæ.
Parapontellidæ.
Acartiidæ.

VII. Position uncertain.

Arietellidæ.
Pseudocyclopidæ.
Candaciidæ (Pontellina ?).

CENTROPAGIDÆ, Sars.

Somite of leg 1 distinct, and usually also that of leg 5. Frontal filaments present (absent in *Calamœcia*). Abdomen of 3 somites except in *Gladioferens*, which has 4. Furcal rami hairy on inner side. Antennule of female of 24 or 25 segments. Right antennule of male prehensile. Mouth-parts of male not reduced. Rami of legs in marine forms three-segmented, but number of segments reduced in some fresh-water genera (*Metaboeckella*, *Calamœcia*, *Brunella*). Leg 5 of female natatory, with a prominent inner spine on seg. 2 of exopod. Leg 5 of male generally with endopod well developed and bearing setæ. Occasionally reduced and without setæ (*Boeckella*).

Female, in fresh-water genera, bearing one egg-sac.

The family, as thus restricted by Sars, includes two marine genera, *Centropages* and *Isias*, and a number of genera in fresh water. These are :

Boeckella, De Guerne & Richard, 1889.
Brunella, Smith, 1909.
Calamœcia, Brady, 1906.
Gladioferens, Henry, 1919.
Hemiboeckella, Sars, 1912.
Limnocalanus, Sars, 1863.
Metaboeckella Ekman, 1905.
Osphranticum, Forbes, 1882.
Parabroteas, Mrázek, 1901.
Pseudoboeckella, Mrázek, 1901 (Ekman, 1905).

With the exception of *Limnocalanus* and of *Osphranticum*, which is North American, these genera are confined to South America, Antarctica and the Australian region. One species of *Boeckella* occurs in Central Asia. None are found in South Africa, which is occupied by *Diaptomus* and the related genera *Paradiaptomus* and *Metadiaptomus*.

The family was taken in a much wider sense by Giesbrecht & Schmeil (1898), and included also the Metridiidæ and Arietellidæ of Sars, which seem to be very remotely related to the rest. If these two be excluded, the remainder of Giesbrecht's family fall naturally into two series, the first including the Heterorhabdidæ, Centropagidæ and Augaptilidæ of Sars, and the second the Diaptomidæ, Pseudodiaptomidæ and Temoridæ. The former group is characterized by the general retention of a more or less natatory leg 5, which is a distinctly primitive character.

The second group includes nearly all the remaining fresh-water genera of Calanoida, while the Temoridæ are, if not fresh-water, at least generally littoral.

The union of these two groups into one family cannot be defended, and, as suggested above, they may better be regarded as forming two superfamilies.

CENTROPAGES, Kröyer.

1848–49. *Centropages*, Kröyer, Nat. Tidsskr. N.S., II, p. 602.
1853. *Ichthyophorba*, Lilljeborg, De Crust. ord. tribus, p. 184.
1892. *Centropages*, Giesbrecht, F. Fl. Neapel, XIX, p. 59.
1898. *Centropages*, Giesb. & Schmeil, Tierreich, p. 53.
1902. *Centropages*, Sars, Crust. Norw. IV, p. 74.

Somites of legs 1 and 5 distinct. Abdomen of female of 3 somites, the genital somite somewhat asymmetrical. Antennule of 24 segments, the 24th and 25th being fused. Exopod of antenna longer than endopod. Maxilla with setæ of endopod very long and strong.

Legs 1–4 with endopod of three segments. Exopod 3 of leg 4 with 3 outer spines. Leg 5 of female natatory, exopod 2 with a long inner spine. Endopod of leg 5 in male 3-segmented, natatory. Exopod of left leg 2-segmented, that of right leg 3-segmented and modified to form a claw.

Type.—*C. typicus*, Kröyer.

About 23 species of this genus have been described, most of which are confined to the Pacific and Indian Oceans and the Red Sea. All are true marine species. Two species only occur in North European seas—*C. typicus*, Kr., and *C. hamatus* (Lillj.); but the latter penetrates into brackish estuarine regions, and for that reason is included here.

The two British species may be separated as follows:

Segments 1, 2, 5 of antennule with a spine.
  Genital somite of female with dorsal setæ . *C. typicus*, Kr.
These segments of antennule without spines.
  Genital somite without setæ . . . *C. hamatus* (Lillj.).

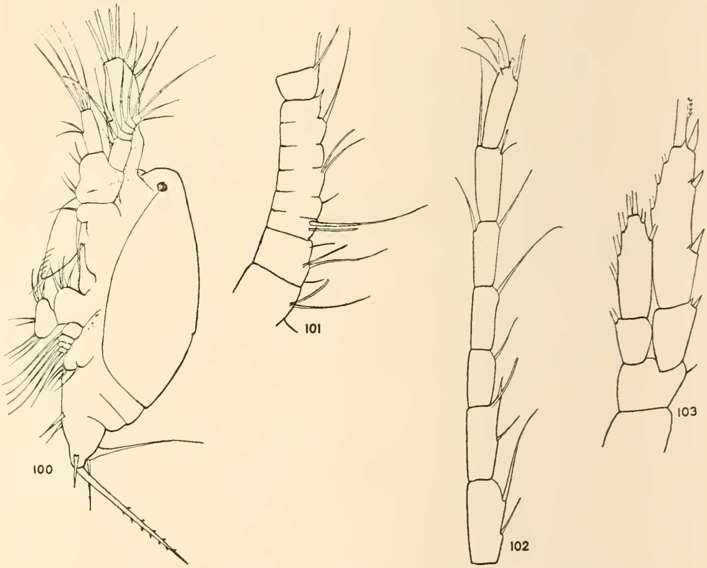
DEVELOPMENT OF CENTROPAGES HAMATUS.

(Figs. 99, 100.)

See Oberg, 1906, p. 42, *C. hamatus*.
Grandori, 1912, p. 421, *C. kroyeri*. 1925, *C. typicus*.

Nauplius more or less pear-shaped, greatly constricted behind, and not ventrally flexed in late stages. In this straightness of body it differs from *Temora*, which it otherwise resembles. Primary pair of furcal setæ symmetrical in stage 1, but becoming asymmetrical at first moult. Throughout later stages the left seta is strong and spine-like, continuing the axis of the body, while the right one is slender, directed dorsally and to the left side. In later stages there is a pair of lateral and one of ventral spines.

Labrum large, fringed with a few stiff hairs. Antennule of 3 segments, seg. 2 with 2 setæ only. Seg. 3 without setæ on anterior edge except in last stage, when there may be one (Oberg). Apex with 3 setæ and æsthete. Exopod of antenna of 6 segments, the setæ jointed about the middle. The setæ of the endopod, and also of the exopod of the mandible, are similarly jointed. Mandible with broad unsegmented endopod, with pronounced inner projection bearing stout spines. Coxa from stage 4 onwards with a large chewing process—the corpus mandibulæ of the adult.



Figs. 100–103.—*Centropages hamatus* development.
Fig. 100.—Nauplius, stage IV.
Fig. 101.—Copepodid V, antennule of male; basal segments.
Fig. 102.—Copepodid V, antennule of male; distal segments.
Fig. 103.—Copepodid V, leg 5, male.

Stage 6 with well-developed rudiments of legs 1 and 2, and their somites clearly marked.

There are 5 copepodid stages. The sexes are distinguishable in stage 4 with difficulty. In both sexes at this stage the abdomen is of 3 somites, and leg 5 unmodified. The only distinction seems to be that in the male seg. 19 of the right antennule (*i. e.* 6th from end) has a terminal spinous process.

In stage 5 the male has 4 somites in the abdomen and the female 3, but the structure of the appendages is much the same. In the prehensile antennule of the male there is a marked constriction between seg. 8 and 9, and seg. 19 has a spinous process (Fig. 102). Seg. 24 has a finger-like terminal process ; but the last 5 segments are separate, and there is no modification of seg. 18. Leg 5 in female with inner basal seta of exopod 2 modified into a short spine ; but in the male there is no modification of the exopod (Fig. 103). Apparently the whole of the changes in this leg and the antennule take place at the last moult.

In *C. typicus* the exopodite of the right leg in stage 5 is markedly stouter than in the left, and the endopods of both legs are 3-segmented.

Grandori (1912, p. 422) states that he has found evidence of a moult in the adult male. This stage 7 differs only in its larger size from the normal male.

Centropages hamatus (Lilljeborg).

(Figs. 104–116.)

1853. *Ichthyophorba hamata*, Lilljeborg, De Crust. Ord. tribus, p. 185, figs.
1857. *Diaptomus bateanus*, Lubbock, Ann. Mag. Nat. Hist. (2), XX, p. 404.
1863. *Ichthyophorba angustata*, Claus, Freileb. Cop. p. 199, figs.
1864. *Centropages hamatus*, Boeck, Forh. Vidensk Selsk. Christ. p. 244.
1878. ,, ,, Brady, Mon. Brit. Cop. I, p. 67, figs.
1881. ,, ,, Giesbrecht, Freileb. Cop. Kiel, p. 156, figs.
1888. ,, ,, Nordquist, Calaniden Finlands, p. 26, figs.
1892. ,, ,, Giesbrecht, F. Fl. Neapel, XIX, p. 304, figs.
1902. ,, ,, Sars, Crust. Norway, IV, p. 76, pl. 52.

Female.—Length 1·1–1·2 mm. (North Uist).*

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* This is a relatively small form. Giesbrecht and Schmeil give 1·3–1·42, while the Baltic form is only ·9 mm. (Nordquist).

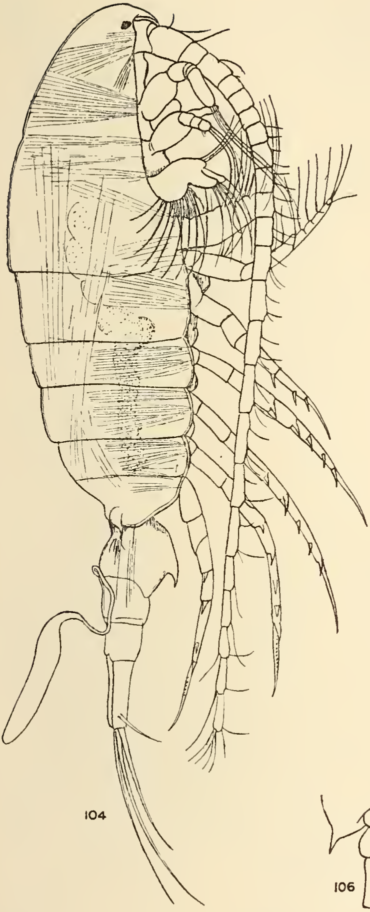
Body rather slender, the greatest width in the region of the head. Last th. somite distinctly separated and asymmetrical, produced on either side into a point which on the right side is directed outwards and curved backwards. Rostral filaments long and slender. Abdomen of three somites, the genital somite about equal to the two following somites combined, and with a group of hairs on either side. The genital operculum bears a large, backwardly-curved spine. Furcal rami about three times as long as wide, hairy on inner side; longest seta a little shorter than abdomen. Antennule reaching to end of furca, consisting of 24 segments, with setal formula as follows:

Centropages hamatus, *female: Table showing Setæ and Æsthetes on Antennule.*

1	2	3	4	5	6	7	8
2 s., a.	3, a.	s., a.	2 s., a.	2 s., a.	s.	2 s., a.	s , a., sp.
9	10	11	12	13	14	15	16
2 s., a.	2 s., a.	2 s., a.	2 s , a.	2 s., a.	2 s , a.	2 s., a.	2 s.
17	18	19	20	21	22	23	24 & 25
2 s., a.	2 s., a.	2 s., a.	s.	s.	s. + s.	s. + s , a.	s. + s. 4 s., a.

s. = seta; a. = aesthete; sp. = spine; s. + s. = seta on either side.

Antenna with outer branch slightly longer than inner and of 7 segments, the second markedly short and swollen. Mandible palp biramous, exopod of 5 and endopod of 2 segments. Maxillule with sympod distinctly 3-segmented. Seg. 2 bears a large epipod with 9 setæ. Seg. 3 with outer seta. Endopod of 2 segments and exopod of 1, with 9 setæ. Maxilla consisting of a strong stem bearing 4 endital lobes, the first with 4 and each of the others with 3 spinous setæ. Distal part, representing endopod, with 4 short segments, bearing



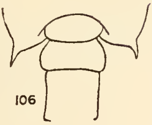
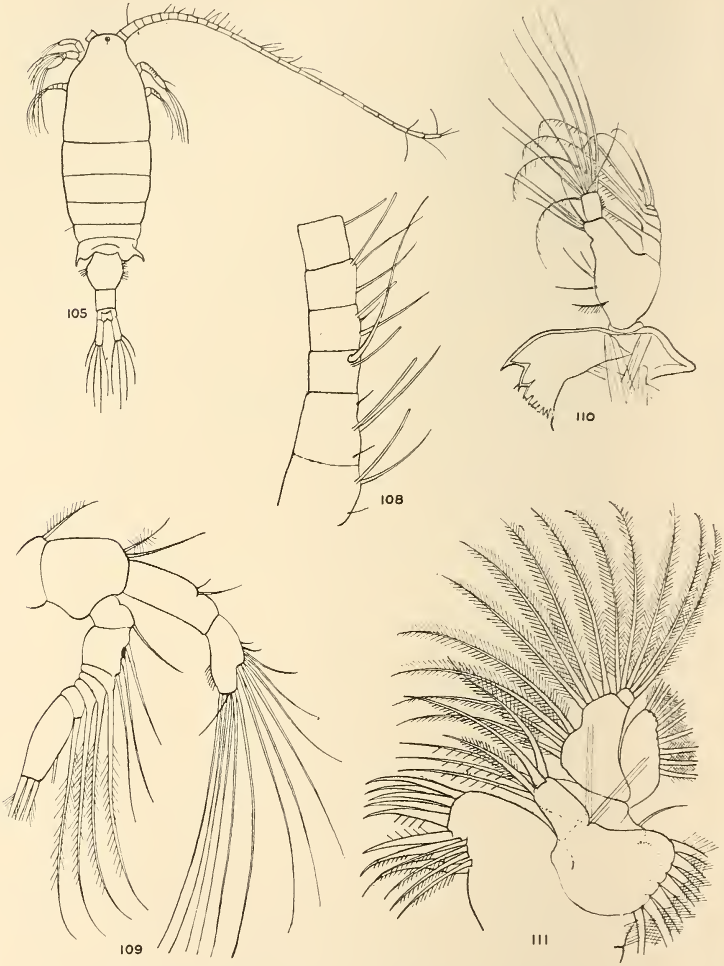


Fig. 104.—*Centropages hamatus*, female, side view.
Fig. 106.—Male, th. som. 5.
Fig. 107.—Antennule, male.

long claw-like setæ. Maxillipede long and slender. Seg. 2 with 3 inner lobes bearing 2, 3, 4 setæ. Terminal part (endopod) of 6 segments, the first partly fused with seg. 3 of sympod or distinctly separated (Fig. 113). Segs. 5 and 6 sometimes fused. Legs 1–3 have both rami



Figs. 105, 108–111.—*Centropages hamatus.*
Fig. 105.—Female. dorsal view.
Fig. 108.—Antennule, female; segs. 1–6, showing æsthetes.
Fig. 109.—Antenna.
Fig. 110.—Mandible.
Fig. 111.—Maxillule.

3-segmented, the endopod much shorter than exopod. Seg. 3 of exopod with 3 short outer spines, a strong terminal spine with a saw-like membrane on outer edge, and 5 inner setæ. Leg 5 differing little from preceding legs. Exopod with no seta on seg. 1. Seg. 2 with a strong inner spinous process curving downwards and about as long as the segment. Seg. 3 has 2 outer spines, a terminal spine and 4 inner setæ. Endopod of 3 segments, the second with 1 seta only, and reaching just beyond seg. 2 of exopod.

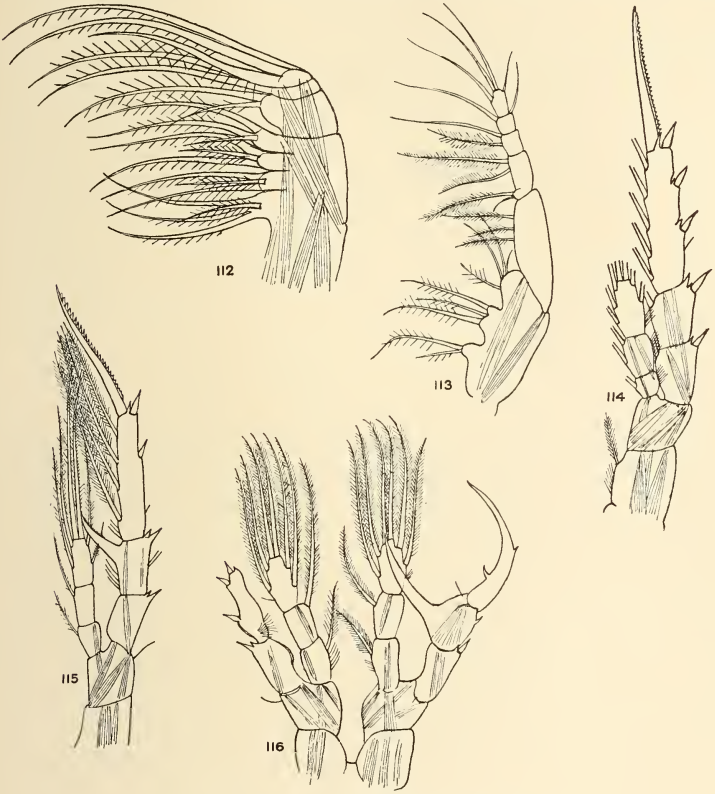


Fig. 112–116.—*Centropages hamatus.*
Fig. 112.—Maxilla.
Fig. 113.—Maxillipede.
Fig. 114.—Leg 4, female.
Fig. 115.—Leg 5, female.
Fig. 116.—Leg 5, male.

Male.—Length 1·0 –1·14 mm. (North Uist).

More slender than female ; th. som. 5 symmetrical, with small outer points. Abdomen of 4 somites. Prehensile antenna flexed at 18th segment. Segs. 17, 18, 19 with a comb of short spines. Terminal part of 3 segments, the first of which represents segs. 19–21 inclusive. Leg 5 with endopod 3-segmented, alike on each leg. The seta of endopod 2 is longer on left leg than on right. In right leg exopod 2 bears, as in the female, a very large inner spinous projection, which forms, with the sickle-shaped seg. 3, a sort of pincer. Exopod of left leg 2-segmented, seg. 2 with 2 small outer spines and 2 small terminal spines. The right leg differs from that of *C. typicus* in having the spine of exopod 2 and 3 more slender.

DISTRIBUTION IN BRITAIN.

Distributed all round the British Islands, but relatively rare in the south. Included by Norman and Scott in the fauna of S. Devon, having been taken at Starcross and near Plymouth, and recorded from Weymouth by Lubbock (*D. bateanus*). Norman and Scott state that it is not so common inshore as in the open sea, which is quite contrary to the general opinion and my own experience in other regions. Brady, on the other hand, notes that he had once taken it in rock-pools in Durham. Farran has only a single record for the species on the Atlantic slope of Ireland, but refers to it as characteristic of littoral waters of low salinity, and found it abundant in inshore waters off Clare Island.

It is common on the east coast, penetrating into the estuaries of the Thames, Blackwater, Stour, Orwell and Alde.

In Norfolk it is found in the lower reaches of the Bure and Yare, and is often carried far up the river by the tide, even to 20 miles from the sea.

In North Uist the Scottish Lake Survey took it in numbers in Loch Obisary, which is the largest lake in the island, communicating with the sea by a single narrow opening. The water is salt, but it is stated that it contains fresh-water weeds. The plankton consisted only of *Evadne nordmanni*, *C. hamatus* and *Acartia clausi*, even at the end furthest from the sea.

In the Shetlands it occurred in Loch Strom, which is also tidal. In both these cases the water can hardly be entirely salt, having regard to the large amount of fresh water draining in.

At Wells, in Norfolk, I have taken it in tidal pools on a salt marsh flooded by spring tides.

DISTRIBUTION ABROAD.

This is an Atlantic species, occurring between 40° N. and 70° N. (With) in water of mean temperature of 9·7° C., and salinity 33·58$^{\circ}/_{\circ}{}^{\circ}$ (Cleve). It is, however, a species capable of tolerating low salinities, and is characteristic of coastal waters. De Lint (1922) gives its range of salinity as between 13·5 and 23·9 per mille. It is common in the Zuider Zee, and in some parts of the Baltic, *e. g.* Gulf of Bothnia and Gulf of Finland, but not in the freshest parts.

Found by Derzugin (1925) in a "relict" lake in the island of Kildin (Murmansk coast). In this lake the surface waters contain fresh-water species.

In the Schwentine estuary in Kiel Bay it is found only in the outermost part, and is not actually at home in the estuary (Kuhlgatz, 1898), being brought in by the currents from the open sea.

Found also in the estuaries of the Elbe and Jade (Poppe) in salt and in brackish water, but in the latter not so commonly as *Eurytemora affinis*.

BIONOMICS.

Most abundant between June and September. The eggs are laid free and are taken in the plankton. The development has been described by Oberg.

Both Nordquist and Kuhlgatz note an excess of males over females, and there is the same excess in my own specimens from North Uist.

Nordquist notes that, in the Baltic, the females of this and other species of Copepod are of reduced size, while the males are not affected. The male may then be larger than the female, whereas normally it is smaller.

In the North Sea it forms a considerable item in the food of Whitebait Herring. The adult Herring feeds mainly on *Temora longicornis* and *Calanus finmarchicus*, these two together making up 96% of the Copepod food. *C. hamatus* amounts only to about ·97% (Hardy, 1924, pp. 13 and 23).

LIMNOCALANUS, Sars, 1863.

1863. *Limnocalanus*, G. O. Sars, Forh. Vidensk Selsk. Christ. 1862, p. 228.
1889. ,, De Guerne and Richard, Mem. Soc. Zool. France, II, p. 127.

Body slender, the abdomen about two-thirds of thorax. First and last th. somite distinct. The latter rounded or pointed, but not expanded. Abdomen of 3 somites in female, and 5 in male, the genital somite not dilated. Furcal rami long and slender, covered with hairs. Antennules of 25 segments in female, the right limb prehensile in male, but not much widened. Antenna with exopod much longer than endopod, of 7 segments. Mandible with palp biramous, the anterior branch of it reflexed. Maxilla with the setæ of the terminal segments modified into long, flattened spines. Maxillipede very long and slender. Swimming-legs with both rami 3-segmented, exopod 3 with 2 outer spines. Leg 5 of female with both branches natatory, but little modified ; exopod 2 with a strong inner spine ; exopod 3 with 2 outer spines and 4 inner setæ. Leg 5 male with endopod natatory and unmodified. Exopod of both legs 2-segmented, seg. 2 of right leg truncated and with strong inner spine. Eggs laid free.

Type.—*L. macrurus*, Sars.

To this genus have been ascribed the following species :

L. macrurus, Sars.
L. grimaldii (De Guerne), 1886.
L. sarsii, Daday, 1901.
L. sinensis, Poppe, 1889.
L. johanseni, Marsh, 1920.

L. sarsii is a synonym of *Parabroteas michaelseni* Mrázek, while *L. sinensis* has been made the type of a new genus *Sinocalanus*, Burckhardt (1913). This genus, which includes 3 species from China, is very closely allied to *Limnocalanus*, but differs markedly in the structure of the antenna, which is, indeed, unlike that of any other Calanoid. The only genus having nearly the same form of antenna is *Acartia*, to which *Sinocalanus* has no relationship. *Eucalanus* resembles it slightly.

L. johanseni differs from *L. macrurus* in having the furcal rami very much shorter, but its most striking feature is the presence in the right 5th leg of the male of a structure which Marsh regards as a modified 3rd segment. In this he is no doubt right, and the retention of this segment seems to prove this species to be more primitive and more nearly related to *Centropages* than the other species.

L. grimaldii, which inhabits the Baltic and the Arctic seas, differs so little from *L. macrurus* that it is difficult to separate them. Indeed they are united by transitional forms, and there can be no doubt that *L. macrurus* is a recent derivative from *L. grimaldii*.

Burckhardt has attempted, by tabulation of a number of characters, to make a numerical estimate of the relation between *Limnocalanus*, *Sinocalanus* and *Centropages*, and concludes that, though there is no direct descent between the three genera, *Centropages* is the most primitive. Speculations as to the phylogenetic relation of one genus to another are generally unsatisfactory and conclusions elusive. In this case all that can be said is that there is probably no direct relation between *Limnocalanus* and *Sinocalanus*, but that both are more closely related to the marine *Centropages* than to any fresh-water genus of the family. Within the family these three genera stand together and apart from the rest of the group.

Limnocalanus macrurus, Sars.

(Figs. 117–132.)

1863. *L. macrurus*, Sars, Forh. Vidensk. Selsk. Christ. 1862, p. 228.
1888. ,, and *L. grimaldii*, Nordquist, Calaniden Finlands, p. 31, figs.
1889. ,, De Guerne and Richard, Mem. Soc. Zool. Fr. II, p. 77, figs.
1902. ,, Sars, Crust. Norway, IV, p. 81, pls. lv, lvi.
1911. ,, Tollinger, Zool. Jahrb. Syst. XXX, p. 190.
1913. Ekman, Int. Rev. Hydrob. IV, p. 335, figs.
1913. ,, Ekman, Zeit. Ind. Abstamm. VererbLehre XI, p. 39.
1923. ,, Gurney, J. Linn. Soc. London, XXXV, p. 426, figs.

Female.—Length 2·10–2·27 mm. (average 2·18 mm.) (Ennerdale).

General form slender, greatest width of thorax, which falls in som. 2, not much exceeding one-third of length (51 : 139). Abdomen and rami together more than half thorax (78 : 139). In side view the head region is distinctly marked off from the rest of thorax by a slight depression at the insertion of the mandibular muscles. From this point the outline slopes at first very gently and then sharply downwards, but is not vaulted as in the typical extreme form from Lake Mjösen.

The various races of *L. macrurus* are distinguishable by the dorsal outline of the head, and almost every transition may be found between the even slope downwards and forwards in *L. grimaldii* to the high arched form from Lake Mjösen, in which the vertex rises well above the horizontal line of the thorax. Ekman (1913 (A)) has devised a system of measurement to express these differences, and gives tables for the comparison of the local races.

Last th. somite evenly rounded. In *L. grimaldii* and some individuals of the American races it has a small apical point in side view. Abdomen of 3 somites, the relative lengths of which are 24 : 17 : 13. Genital somite not dilated, and but little broader than succeeding somites. Som. 2 with a posterior circlet of small spines, and there are usually a few on the dorsal side of som. 1. Furcal rami long and slender, covered with small spines and hairy on inner side. In the Ennerdale form their length is about 13% of the whole body-length, but this proportion varies with different races, and tends to be higher in those judged, on other grounds, to be the more primitive. In the parent form, *L. grimaldii*, they are 16 or 17%. Furcal setæ long and slender, the longest of the four terminal setæ being nearly twice the length of the ramus.

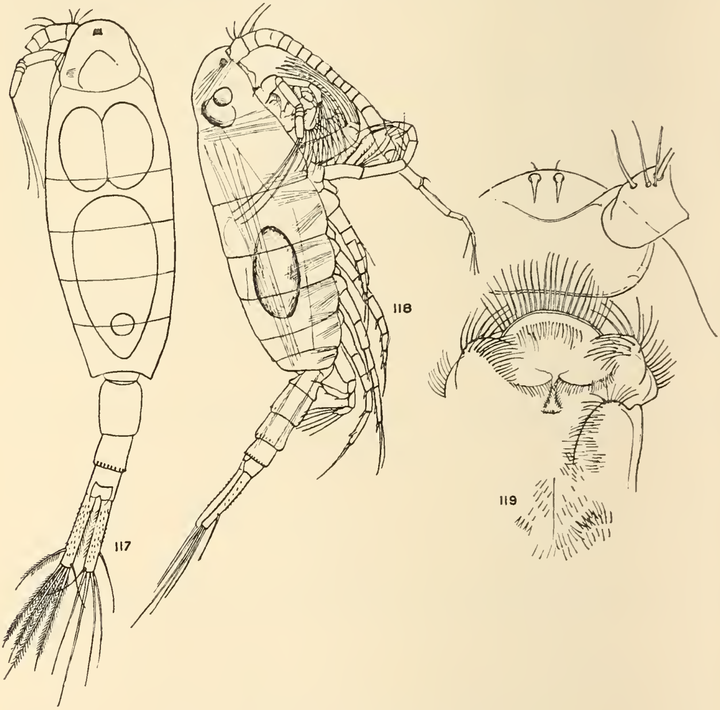
Upper lip with large median and lateral lobes, covered with long hairs (Fig. 119). Antennule reaches about to end of genital somite, of 24 segments, the 25th being fused with the 24th. The disposition of the setæ and æsthetes, is much the same as in *Centropages*. It differs mainly in the absence of an æsthete from segs. 17 and 18. Seg. 6 appears at first sight to have no seta, but a small one is present on the dorsal side. Antenna: Endopod much shorter than exopod, 2-segmented, seg. 1 long and slender; exopod of 7 segments. Mandible with

L. macrurus, *female: Table showing Setæ and Æsthetes on Antennule.*

1	2	3	4	5	6	7	8
3 s., a.	2 s., a.	2 s., a.	2 s.	2 s., a.	s	2 s., a.	s., a., sp.
9	10	11	12	13	14	15	16
2 s., a.	2 s., a.	2 s., a.	s., a., sp.	2 s., a.	2 s., a.	2 s., a.	2 s., a.
17	18	19	20	21	22	23	24 & 25
2 s.	2 s.	2 s., a.	s.	s.	s. + s.	s. + s., a.	s. + s. 4 s., a.

s. = seta; a. = æsthete; sp. = spine; s.+s. = seta on either side.

very broad blade, the 2 outer teeth very large, pointed, and widely spaced. There are 5 other blunt-ended teeth close together and a pair of small hairs on inner angle. Palp biramous, the basal segment of stem not clearly defined, seg. 2 very long, with 4 unequal setæ. Exopod of 4 segments, not well defined, with 6 setæ in all ; endopod 2-segmented, reflexed towards the exopod.



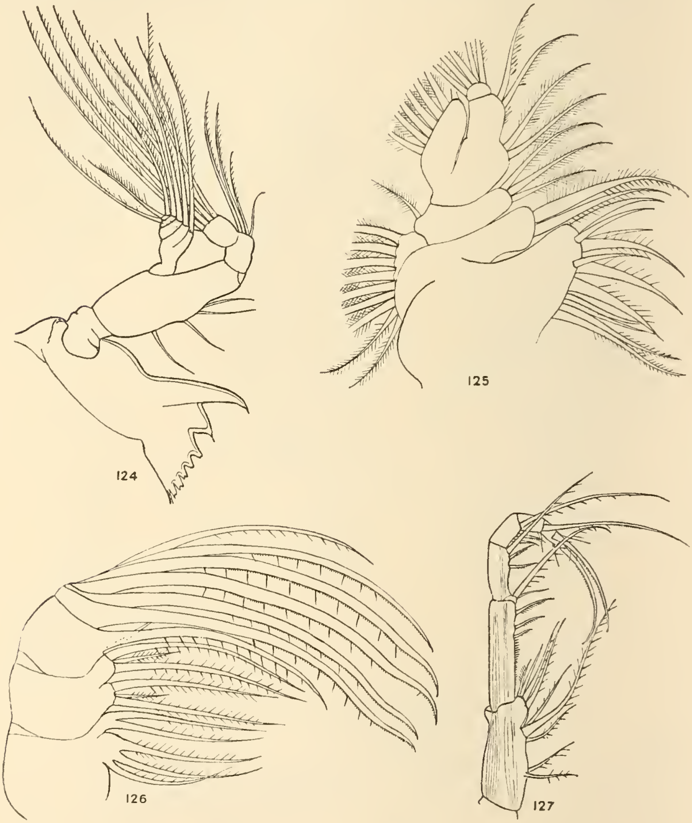
Figs. 117–119.—*Limnocalanus macrurus.*
Fig. 117.—Female, dorsal view, showing oil-globules.
Fig. 118.—Male, lateral view.
Fig. 119.—Head, male, ventral view, showing lobes of upper lip.

Maxillule as in *Centropages.* Epipod large, with 9 setæ, the two proximal small. Line dividing seg. 1 (gnathobase) from seg. 2 (with epipod and endite 2) faintly marked. Endites 2 and 3 relatively large ;

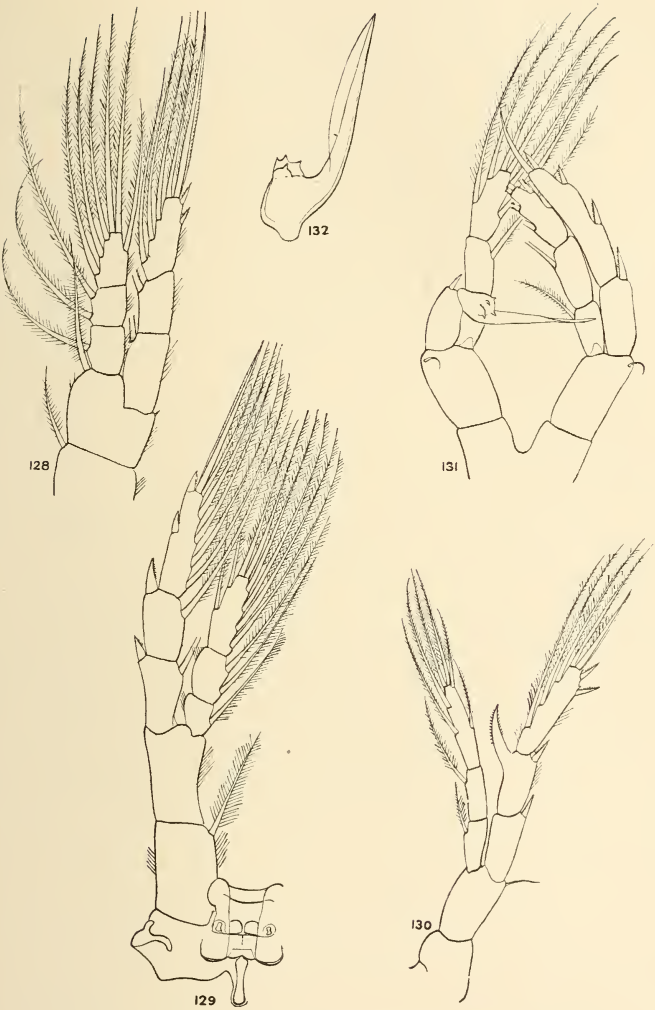
Figs. 120–123.—*Limnocalanus macrurus.*

Fig. 120.—Antennule of female ; segs. 1–8.
Fig. 121.—Antennule of female ; segs. 19–24.
Fig. 122.—Antennule of male, segs. 13–24.
Fig. 123.—Antenna.

seg. 3 with outer seta. Exopod with 7 long setæ. Endopod with small apical segment marked off. Maxilla with stout stem of 3 segments, with 5 small endites bearing 4, 3, 3, 3, 3 setæ. Terminal part very compressed, apparently consisting of 4 segments. This portion bears 5 exceedingly long, stout spines denticulated along the margin and with blunt hooked ends. Maxillipede long and slender, reaching forward in normal position to end of head. Stem of 3 segments, seg. 1



Figs. 124–127.—*Limnocalanus macrurus.*
Fig. 124.—Mandible.
Fig. 125.—Maxillule.
Fig. 126.—Maxilla.
Fig. 127.—Maxillipede.



Figs. 128–132.—*Limnocalanus macrurus.*

Fig. 128.—Leg 1.
Fig. 129.—Leg 3.
Fig. 130.—Leg 5, female.
Fig. 131.—Leg 5, male.
Fig. 132.—Leg 5, male; seg. 2 more magnified.

very small and without seta. Seg. 2 somewhat shorter than the long slender seg. 3, with 3 groups of 2, 3 and 4 setæ. Distal seta of group 2 very long. Seg. 1 of endopod entirely fused with sympod 3. Distal part of 5 segments, each with a long stiff seta and 1 or 2 small setæ. Legs 1–5 with both branches 3-segmented. In leg 1 coxa and basis not longer than wide. Endopod shorter than exopod. Exopod 1 and 2 without outer spines. In legs 2–4 coxa and basis very elongated, about 1½ times as long as broad. Exopod 1 and 2 each with outer spine; exopod 3 with 2 outer and an apical spine. Apical spine very long, slender, with an outer hyaline membrane faintly serrated. Endopod 3 bears 8 setæ in legs 2 and 3, and 7 in leg 4. Leg 5 differing very little from preceding legs. Coxa and basis not so elongated; no inner seta on coxa. Endopod 2 with 1 inner seta instead of 2. Exopod 1 without inner seta; exopod 2 with strong inner curved spine in place of inner seta. Exopod 3 with 4 inner setæ instead of 5.

Male.—Length 1·85–2·16 mm. (average 2·06).

Head and thorax as in female. Abdomen slender, of 5 somites; somites 2, 3, 4 with dorsal row of spinules. Furcal rami slender, covered with small spinules. Left antennule precisely as in female, with the same arrangement of setæ and æsthetes. Right antennule with segs. 13–18 scarcely at all swollen or modified. Seg. 17 with smooth hyaline membrane and a single small seta; seg. 18 with ribbed inner membrane and terminal æsthete; distal part of 3 segments. The first of these long and slender, representing segs. 19–21, with two inner membranes, or modified setæ, near base, the proximal one flattened and with a double row of transverse ribs. Segs. 22 and 23 fused, but with the pair of setæ of seg. 22 retained. Leg 5 biramous and natatory. Right leg: exopod of 2 segs; seg. 2 with large straight inner spine with smooth marginal hyaline membrane; seg. 3 represented by a terminal knob with 4 small points. Endopod of 3 segments, the 3rd with 6 setæ.

Left leg: exopod as long as endopod, of 2 segments, without inner setæ; seg. 2 very long, with 2 outer spines and a small terminal spine and seta. Endopod of 3 segments, the 3rd with 6 setæ.

Distribution in Britain.

Ennerdale Water, Cumberland. First taken by Dr. W. H. Pearsall on September 23rd, 1921. Subsequently found to be the most abundant species in the plankton in the deep eastern trough of the lake, but distributed all over it and at all depths.

Distribution Abroad.

The distribution of this species raises problems of extreme interest, but these can only be briefly dealt with here. (For full information see Ekman, 1913; Gurney, 1923.) The two forms *L. grimaldii* and *L. macrurus* so completely merge into one another, if all races are taken into account, that no clear distinction can be drawn. In inland waters the former occurs in the Caspian Sea, Greenland (Sälsöen) and Kolguev (Lake Pescanoje). Those races which can definitely be referred to *L. macrurus* are confined to two areas—the Baltic region, and the region of the Great Lakes of North America. In the former it occurs in a number of lakes in Norway, Sweden and Finland, all of which lie within the limits of the area once covered by the Baltic Sea. It is not found in any of the North German or Danish lakes. Ekman concluded that it is a relict of the Ancylus period, descended from the Arctic species *L. grimaldii*, which entered the Baltic during the Yoldia period and survived during the subsequent changes of level and salinity. The rising of the land cut off arms of the sea containing *L. grimaldii*, and each separate colony so isolated has developed independently into the "species" *L. macrurus*. The long-continued influence of the change to fresh water has caused these colonies to diverge from the parent form in shape of head in such a way that, on the whole, those longest isolated differ more than the younger populations. In the Baltic region, and in the lakes of North America, *L. macrurus* is certainly a marine-glacial relict in the true sense, and the question arises as to whether it owes its presence in Ennerdale Water to a similar sequence of changes. The lake surface lies at 308 ft. above sea-level, and it appears that no modern geologist would admit any post-glacial elevation of this extent.*

Charlesworth (1928) has adopted Högbom's " Stausee" theory to account for the presence of *Mysis relicta* in Lough Neagh, and Ekman (1930, p. 340) suggests that the same theory may account for the presence of *L. macrurus* in Ennerdale. According to Charlesworth's view the readvancing Scottish ice " converged upon the coastal tract of N.E. Ireland, on the north encroaching upon the lower part of the valley of the Bann, on the east sweeping up Belfast Lough and the lower reaches of the Lagan valley. It impounded the normal drainage of the country to form a vast lake whose surface lay roughly about 100 ft. above sea level." It is suggested that the advance of the ice drove the marine waters before it and introduced *M. relicta* with them into this new lake.

It is difficult for a zoologist to make himself conversant with geological facts, and impossible for him to criticize geological theory ; but I am unable to see any bearing of this theory on the facts in question. It must be remembered that the Lake District was itself a glaciated centre, and that Ennerdale was occupied by a westward-moving glacier. There could be no question of a shoreward thrust of ice from the sea impounding water in a drowned valley. It seems quite clear that *L. macrurus* reached Ennerdale after the retreat of the glaciers, and its presence points to physical changes of which geologists find no evidence.

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* On the other hand, Jukes-Browne (1911, p. 440) seems prepared to admit a submergence during the glacial period of at least 500 ft.

Ekman dismisses any possibility of transport or of active migration in the distribution of this species; but a form of it has been found living in the lower Dwina (Jaschnova, 1929) up to 15 km. from the sea. There are no lakes in this part of its course, and it appears that this is a case of active penetration from the sea. It is not, therefore, necessary to postulate direct connection of Ennerdale with the sea; it would be sufficient if such changes could be proved as would allow of access by a slow-flowing river.

Bionomics.

L. macrurus is only found in deep lakes, and usually only in the deeper layers. According to Ekman (1907) it is never found in the surface waters above 5 metres even when the temperature is low, and Marsh (1898, Green Lake) found it between 15 and 40 metres, with a maximum at 35–40 metres. It is, in fact, definitely a cold-water species. On the other hand, in Ennerdale (September) it is by no means confined to deep water, but was taken in abundance at the surface. It was, however, more abundant in the deep part of the lake and in the deeper layers. There was a distinct increase in numbers at the surface at night. This nocturnal rise was also noted by Marsh.

Reproduction in Sweden begins in October and continues throughout winter. Resting eggs only are laid, and these sink to the bottom and hatch out in March and April, the adults of the preceding year dying in the spring. The young become fully grown in about 2 months, but the gonads are not mature and reproduction is delayed until October or November, when the water has sunk to a temperature of about 7° C. There is thus one generation only in the year, and the individuals live for one year only. Such observations as have been made in Ennerdale indicate a similar life-history.

A striking feature of the living animal is the large fat-globules contained in the thorax. Birge and Juday (1922, p. 166) give analyses of certain Entomostraca, and note that in *L. macrurus* the fat-content amounts to 41·6% of the organic matter.

DIAPTOMIDÆ, Sars.

Somite of leg 1 distinct from head; somite of leg 5 distinctly marked off, generally more or less expanded in female. Abdomen of female of 2 or 3 somites (very rarely of 4—*Metadiaptomus chevreuxi*), that of male of 5 somites, sometimes rather asymmetrical. Furcal rami generally longer than broad, symmetrical in female, occasionally asymmetrical in male. Outer setæ on right branch sometimes modified in male. Genital somite of female rather dilated, sometimes greatly so, with a sensory spine on either side.

Labrum without lateral lobes. Frontal filaments small, sometimes reduced to small rounded papillæ. Antennule of 25 segments, the number of setæ reduced. Arrangement of these setæ often differing in allied species. Prehensile antenna of male with segs. 13–18 more or less swollen or modified; terminal part of 3 or 4 segments. Antenna with exopod generally longer than endopod, of 7 segments, the 3rd bearing 3 setæ. Mouth-parts as in Centropagidæ.

Leg 1 with endopod 2-segmented; exopod 2 with no outer spine. Legs 2–4 with endopod 3-segmented; exopod 3 with one outer spine only. In leg 2 endopod 2 may bear a cuticular lappet on its posterior face. Leg 5 not natatory, biramous in female, and generally so in male. Exopod 2 in female produced into a large inner spine; seg. 3 reduced, often absent, or represented by one or a pair of moveable spines. Leg 5 of male very asymmetrical, the left leg sometimes very much modified. Exopod 2 and 3 of right leg fused, the position of joint 2 marked by an outer spine. Seg. 3 bearing a long hinged terminal spine. Left leg with segs. 2 and 3 of exopod fused and variously modified, the fused segment usually with hairy inner pads, an inner spine, and a terminal finger-like process.

Eggs carried in a single sac. Reproduction often by resting eggs.

The following genera have been included in the family:

Diaptomus, Westwood.
Lovenula, Schmeil (= *Broteas*, Lovén).
Paradiaptomus, Sars.
Hemidiaptomus, Sars.
Adiaptomus, Cooper.
Metadiaptomus, Methuen.

Of these, *Adiaptomus* and *Lovenula* must be suppressed as synonyms of *Paradiaptomus* (see Gurney, 1929, Lowndes, 1930). The differences between the four remaining genera are so small that they might well be treated as subgenera of *Diaptomus*. There are, however, some practical disadvantages in so doing. They may be defined as follows:

1. *Diaptomus*, Westwood.

Female abdomen of 3 somites (occasionally of 2); furcal rami generally symmetrical in both sexes. Exopod of antenna longer than endopod; maxillipede slender, the 5 terminal segments well developed; exopod of leg 1 with one outer spine on seg. 3; leg 2 with cuticular lobe on posterior face of endopod 2; leg 5 of female usually with seg. 3 of exopod well defined.

Type.—*D. castor* (Jurine).

2. *Paradiaptomus*, Sars, 1895.

Female abdomen of 2 somites (3 in *P. greeni*); furcal rami of male more or less asymmetrical; prehensile antennule with finger- or hook-like process on last segment; exopod of antenna sometimes shorter than endopod; maxillipede with 2 terminal segments reduced, the whole appendage very stout; leg 1 with two outer spines on exopod 3; leg 2 without cuticular lobe;

leg 5 of female with exopod 3 reduced to a moveable spine ; leg 5 of male much modified in adult.

Type.—*P. falcifer* (Lovén).

South and East Africa (9 species), but with one species, *P. greeni* (Gurney) (= *P. similis*, van Douwe) found in Kalahari, Transvaal, Ceylon and India, and one, *P. biramata*, Lowndes, in Abyssinia.

Although it is impossible to draw any valid distinction between *Lovenula* and *Paradiaptomus*, these species may be provisionally arranged in two series corresponding to these two genera.

3. *Hemidiaptomus*, Sars, 1903.

Female abdomen of 2 or 3 somites ; furcal rami symmetrical in both sexes ; exopod of antenna slender, scarcely longer than endopod ; maxillipede very strong, with 5 segments in terminal part (Fig. 152) ; leg 1 with one outer spine on exopod 3 ; leg 2 without cuticular lobe ; leg 5 as in *Diaptomus*.

Type.—*H. ignatovi*, Sars.

Two species,* confined to Central Asia and Caucasus region.

4. *Metadiaptomus*, Methuen, 1910.

Female abdomen of 3 somites (4 in *M. chevreuxi*) ; furcal rami of male generally more or less asymmetrical ; prehensile antennule with finger- or hook-like process on last segment ; exopod of antenna longer than endopod ; maxillipede as in *Diaptomus ;* leg 1 with 2 outer spines on exopod 3 ; leg 2 with or without cuticular lobe ; leg 5 as in *Paradiaptomus*.

Type.—*M. transvaalensis*, Methuen.

The following species of *Diaptomus* should be referred to this genus :

- *æthiopicus*, Daday. East Africa.
- *asiaticus*, Ulj. Central Asia, Turkestan, China, S.E. Russia.

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* The description of the second species, *H. tarnogradskii*, Rylov, is in Russian, and the figures provide no evidence whatever for the reference of this species to *Hemidiaptomus*.

alluaudi, De G. and Rich. Spain, Portugal, Balkans, Galicia, Hungary, Canaries, Cyrenaica, Egypt.
capensis, Sars. Cape Town.
chevreuxi, De G. and Rich. Algeria, Cyrenaica, Mesopotamia.
colonialis, Van Douwe. Transvaal, S.W. Africa.
masculus, Brady. Orange Free State.
meridianus, Van Douwe. S. Africa (Kalahari).
purcelli, Sars. Cape Town.
rigidus, Sars. Orange Free State.
rehmanni, Grochm. E. Africa (Ussangu steppe).
transvaalensis, Methuen. Transvaal.

I originally included *D. tibetanus*, Daday, also (Gurney, 1929); but Smirnov (1930E) has redescribed it, and it is clear, from his account of leg 1, that it should remain in *Diaptomus*, though it is, in other respects, rather intermediate.

DIAPTOMUS, Westwood.

1836. *Diaptomus*, Westwood. In Partington. Cyclop. Nat. Hist. II, p. 227.
1838. *Omethia*, Templeton, Trans. Ent. Soc. Lond. II, p. 118.
1840. *Cyclopsina* (part), M. Edw. Hist. Nat. Crust. III, p. 427.
1850. *Diaptomus*, Baird, Nat. Hist. Brit. Entom., p. 219.
1896. ,, Schmeil, Bibl. Zool. XXI, p. 10.
1898. ,, Giesb. and Schmeil, Tierreich, Lief. 6, p. 66.
1902. ,, Sars, Crust. Norway IV, p. 84.
1929. ,, Gurney, Ann. Mag. Nat. Hist. (10), IV, p. 581.

Type.—*D. castor* (Jurine).

The number of species included in this genus has grown with astonishing rapidity. It is not possible to give an exact numerical census, owing to the differing views as to the validity of species, but the following are, roughly, the numbers dealt with at different revisions:

1889.	De Guerne and Richard .	40
1898.	Giesbrecht and Schmeil. .	67
1911.	Tollinger	117
1930.	. . . . . .	200*

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* Excluding species now referred to *Metadiaptomus*.

The flow of new species seems likely to continue in a steady, if diminishing, stream. Such an enormous group, in which species are often separated on differences which are scarcely appreciable, has become almost overwhelming, and any attempt to discover within it any well-defined sub-groups has become so formidable a task that it is altogether outside the scope of this work. Schmeil grouped the European species in 3 series, centering round the species *castor*, *salinus* and *vulgaris*.

Tollinger found it necessary to arrange the species of the world in 8 groups, but it is impossible to define them, and serious exception can be taken to some if they are to be regarded as evolutionary series. Krmpotic (1924) has discussed the grouping of some of the European forms, and concluded that it is impossible to separate the *castor* and *salinus* series of Schmeil. If it be admitted that transitional forms enforce the union of these two series of species, then all grouping will be impossible. But since it is a question of seeking for supposedly evolutionary series, and not for systematically definable groups, the existence of intermediates is not necessarily a difficulty. What does make grouping of the species so apparently futile is that the proportion of species which cannot satisfactorily be placed is so very large. Further, where distinctions are so small, and concerned with such trivial characters, speculations as to relationship must be mainly subjective, and may be most misleading. The zoogeographical speculations based upon a supposed relationship of *D. incrassatus* to certain North American species (Brehm, 1925) may be given as an example.

DISTRIBUTION OF DIAPTOMUS.

Tollinger (1911, p. 234) has dealt at length with the distribution of the genus, and only a general summary can be given here.

America.

North America has about 40 species, not one of which is found in South America. One American species only extends its range to Siberia, and one Asiatic species has crossed into America.*

South America has 28 species, all of which are confined to a region corresponding nearly to Wallace's Brazilian region. South and west of this it is completely replaced by *Boeckella*, *Pseudoboeckella* and *Parabroteas*, while these genera are entirely absent from the Brazilian region (Stillman Wright, 1927).

Africa.

Three regions may be distinguished :

(*a*) North Africa, with 11 species of *Diaptomus* and 2 of *Metadiaptomus* ; nearly all are species of transitory pools and of European or Asiatic affinity.

(*b*) Nile Valley and East and Central Africa, with 17 species of *Diaptomus* and 3 of *Metadiaptomus*.

(*c*) South Africa, with 8 species of *Diaptomus*, 7 of *Metadiaptomus* and 8 of *Paradiaptomus*.

Tollinger may be right in regarding the Nile Valley and great lakes as a region distinct from the "Central Girdle," but the distinction is not easy to press, and the main regional division seems to be between areas of perennial moisture and those of steppe-like character with temporary pools.

Australia.

Only two species, *D. lumholtzi*, Sars, and *D. orientalis*, Brady, are recorded from Australia, both of which extend to southern Asia (*e.g.* Ceylon), while the latter is found also in Natal. In the Australian region *Diaptomus* is almost wholly replaced by Centropagidæ of the genera *Boeckella*, *Brunella*, *Calamœcia* and *Gladioferens*.

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* *D. eiseni* is recorded from California and Nebraska, and also from Labrador and Eastern Siberia, while the European and Asiatic species, *D. bacillifer*, occurs also in Alaska.

Europe and Asia.

While the species of the Oriental region, of which about 16 have been described, are almost wholly distinct from those of Asia north of the Himalayas, there is some mingling of species eastwards in Japan and China.

The European and North Asiatic region is most difficult to deal with, since distribution has been affected by the glacial period and post-glacial changes. Europe and North Asia together have about 70 species, and of these a few, such as *D. bacillifer*, *D. denticornis* and *D. incrassatus*, have an enormous east and west range. It is possible to indicate, as Tollinger has done, some minor sub-areas characterized by certain species, but for the most part these are rather ecological subdivisions than divisions based upon geographical barriers. The south-east of Europe is particularly rich in *Diaptomus*, possibly owing to the survival in it of part of the Tertiary fauna.

STRUCTURE.

Schmeil gives a lengthy account of the structure of the genus, and it is not necessary to deal with it here. Attention may, however, be drawn to the structure of the antennule. Schmeil was the first to point out the systematic importance of the arrangement of the setæ on this appendage. While there is complete agreement throughout the family in the number and position of the æsthetes, and also in the number of setæ on segs. 1–10 and 12, there may be either 1 or 2 setæ on segs. 11 and 13–19. Within the species there appears to be no individual variation in this respect, and it is consequently of considerable importance that attention should be given to this point in descriptions of species. The following table shows the degree of difference that may be observed, and includes only certain species which I have examined myself. It illustrates the only exception known to me of the rule of invariability, namely the case of *D. similis.*

According to Kiefer there should be 1 seta only on segs. 13–19, and Smirnov (1928A) states that there may be either 1 or 2 on seg. 13, whereas I find 2 on segs. 13, 15, 17 in specimens from Palestine which should be typical.

Table Showing Number of Setæ on Segs. 11–19 of Female Antennule in Certain Species of Diaptomus *and Allied Genera.*

	Segments.								
	11	12	13	14	15	16	17	18	19
D. castor	2	1	2	2	2	2	2	2	2
,, *superbus*	2	1	1	2	2	2	2	2	2
,, *cyaneus*	2	1	2	2	2	2	2	2	2
,, *ingens*	2	1	1	2	1	2	1	2	2
,, *laciniatus*	2	1	1	1	1	2	1	1	1
,, *salinus*	2	1	1	1	1	1	1	1	1
,, *similis*	2	1	2	1	2	1	2	1	1
,, *bacillifer*	2	1	2	1	1	1	1	1	1
,, *wierzejskii*	2	1	1	1	1	1	1	1	1
,, *laticeps*	2	1	2	1	1	1	1	1	1
,, *acutilobatus*	2	1	2	1	2	1	2	1	1
,, *incrassatus*	2	1	1	2	2	2	2	2	2
,, *vulgaris*	1	1	1	1	1	1	1	1	1
,, *gracilis*	1	1	1	1	1	1	1	1	1
,, *graciloides*	1	1	1	1	1	1	1	1	1
,, *zachariasi*	1	1	1	1	1	1	1	1	1
,, *contortus*	1	1	1	1	1	1	1	1	1
,, *cinctus*	1	1	1	1	1	1	1	1	1
Metadiaptomus asiaticus	1	1	1	1	1	1	1	1	1
M. chevreuxi	2	1	1	1	1	1	1	1	1
Hemidiaptomus ignatovi	2	1	2	2	2	2	2	2	2
Paradiaptomus greeni	2	1	1	1	1	1	1	1	1

LARVAL DEVELOPMENT OF DIAPTOMUS.

D. castor.

The characteristic form of the nauplius of *Diaptomus* was first shown by Jurine in 1820, and good figures were given by Claus in more than one of his papers (*e. g.* 1858). The first to give a complete account of the development from stage to stage was Grandori (1912, *D. vulgaris*).

His figures are excellent. Dietrich (1915) also figured every stage of the nauplius in the same species, and gave an exact account of the changes in the appendages at each moult, but did not deal with the Copepodid stages. In *D. castor* development follows precisely the same course as in *D. vulgaris*, and it is no doubt the same for all species. In fact it does not seem possible to distinguish the nauplii of the three species which I have studied myself—*D. castor*, *D. vulgaris*, *D. gracilis*.

In *D. castor* the period during which the eggs are carried seems to vary greatly. In one case they were hatched on the fifth day, but I have known them to be carried for more than 12 days. Lowndes (1930B, p. 102) finds that maturity is reached at a temperature of 22° C. in 20 days. Walter (1922) found that *D. vulgaris* reaches maturity in about 25 days, and lives for 10–13 months.

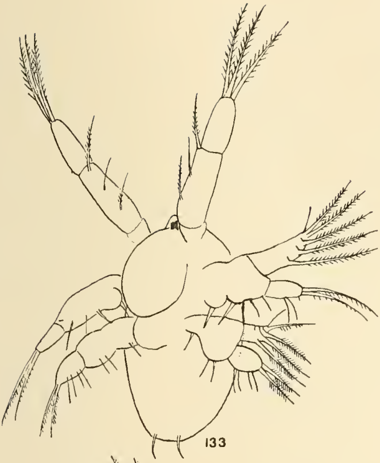
The number of eggs in a single sac may be as many as 100, and their diameter about ·07 mm. As hatching approaches the inner membrane swells up to a diameter of about ·2 mm, breaking the outer membrane. The nauplius is at first inert but soon begins to move, ruptures the membrane and becomes free, having a length of about ·09 mm. Ziegelmayer has described the same process of hatching in Cyclops, and it may also be seen in *Estheria*. The cause of the swelling of the inner membrane is unknown. The nauplius changes its shape after hatching, becoming more elongated. There are 6 nauplius stages, most easily distinguished by the number of setæ on the antennule.

Nauplius I.

(Fig. 133.)

Length ·19–·20 mm.

Colour a rich orange red. Body very opaque. Eye red. General form oval, without indication of dorsal shield or hind body. Two very small furcal setæ. Upper lip very large, smooth. Behind it a large swelling,



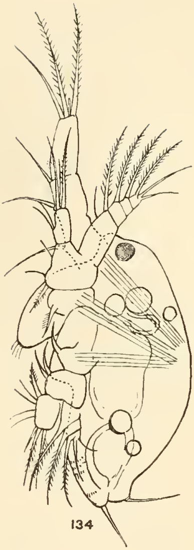


FIG. 133.—*Diaptomus castor*; Nauplius I, ventral.

FIG. 134.—*D. castor*; Nauplius II, lateral.

FIG. 135.—*D. gracilis*; Nauplius V.

perhaps representing future paragnaths. Antennule of 3 segs.; seg. 1 without seta; seg. 2 with 3 setæ of nearly the same length; seg. 3 with 3 feathered setæ, but no æsthete. Segs. 1 and 2 remain unchanged throughout development. Antenna: Coxa and basis not clearly separated; coxal lobe with one short spine; basis with a spine and 2 outwardly directed small setæ. Endopod unsegmented, with 2 terminal and a pair of small lateral setæ. Exopod not distinctly segmented, with 5 long feathered setæ and a small terminal smooth seta. Mandible without masticatory process, but with a small seta on coxal lobe and 2 on basis. Endopod unsegmented, broad, with 4 small inner setæ and 2 distal feathered setæ. The animal apparently does not feed at this stage.

Nauplius II.

(Fig. 134.)

Length ·2–·249 mm.

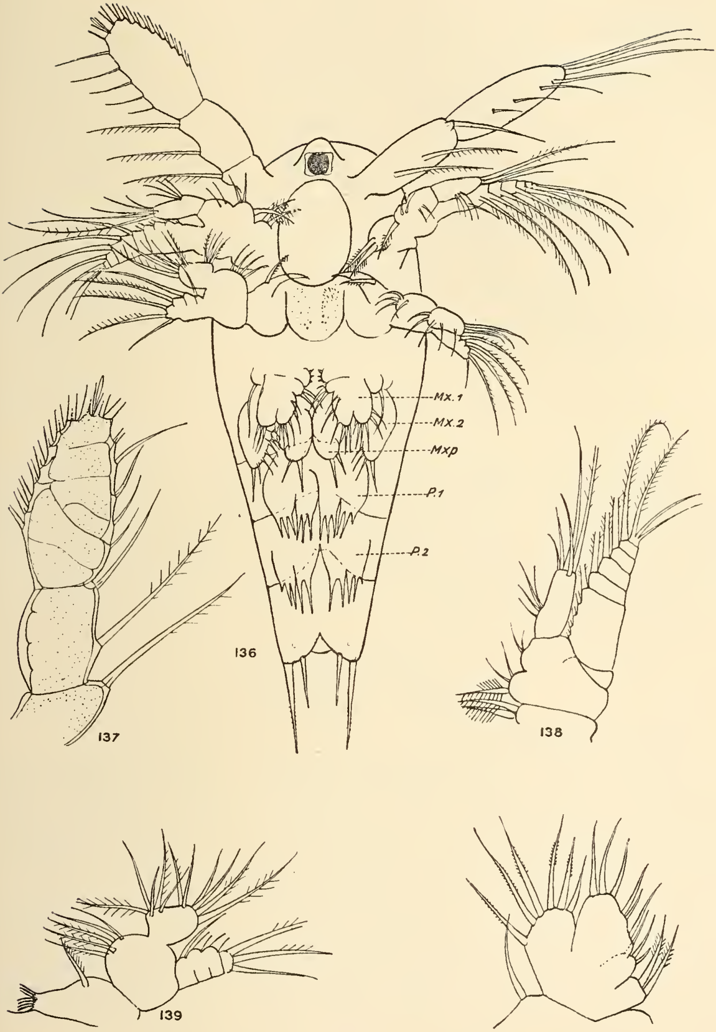
Body more elongated and narrowed behind. Furcal region cleft. Each lobe with one small seta, that on the right bent upwards. Antennule: Seg. 3 with 3 terminal setæ, of which the anterior one is not feathered, or has feathering which is most difficult to see. Dietrich figures 4 setæ at this stage, but I have not found more than 3 in any species. At this stage a delicate æsthete may sometimes be seen between the middle and posterior apical setæ. This æsthete is found in all later stages and in the adult. It is not mentioned by Dietrich or Grandori, but is probably found in all Calanoida.

Posterior end of body with transverse rows of hairs. Labrum with a fringe of hairs. Antenna and mandible much as before, but exopod of antenna of 5 distinct segments, with 7 setæ in all. Intestine now functional.

Nauplius III.

Length ·28–·31 mm.

Body much more elongated. Furcal lobes each with a straight terminal spine and a dorsal slender seta,



Figs. 136–140.—*Diaptomus castor*; Nauplius.

Fig. 136.—Nauplius VI.
Fig. 137.—Antennule, nauplius VI, about to moult.
Fig. 138.—Antenna, nauplius VI.
Fig. 139.—Mandible, nauplius VI.
Fig. 140.—Maxillule, nauplius VI.

bifurcate at end. The right seta directed upwards. Antennule: Seg. 3 with 1 small anterior marginal seta, and 2 (feathered) on dorsal margin. Maxillule represented by a stout feathered seta.

Nauplius IV.

Length ·34–·37 mm.

Antennule: Seg. 3 with 4 anterior and 2 posterior marginal setæ. Mandible with strong coxal mandibular process. Maxillule a bilobed plate bearing short setæ. Antennal gland well developed.

Nauplius V.

(Fig. 135.)

Antennule: Seg. 3 with 6 anterior and 3 posterior marginal setæ. Maxillule a bilobed plate with numerous setæ. Maxilla represented by a small lobe with 2 setæ. Furcal lobes as before, but with an additional pair of very small inner setæ.

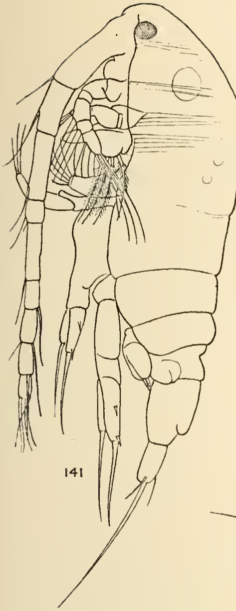
Nauplius VI.

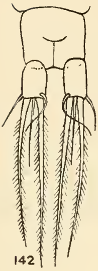
(Figs. 136–140.)

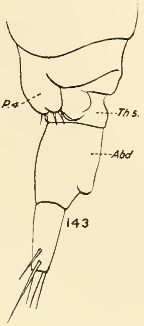
Length ·48–·52 mm.

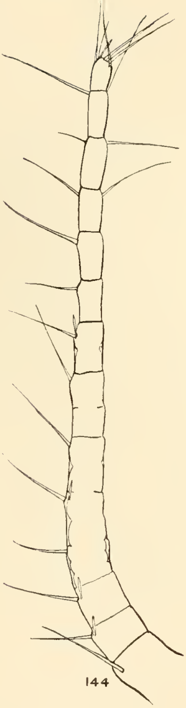
Length about 2½ times the width. Furcal lobes with 2 pairs of terminal and a pair of cleft dorsal setæ. Antennule seg. 3 with 5 anterior and 8 posterior marginal setæ. Mandible with strong coxal process bearing a seta at its base. Maxillule a large bilobed appendage, with well-defined coxal and basal inner lobes. Maxilla and maxillipede springing close together and uniramous, with setæ. Legs 1 and 2 are bilobed rudiments, the exopod with 3 and the endopod with 2 spines.

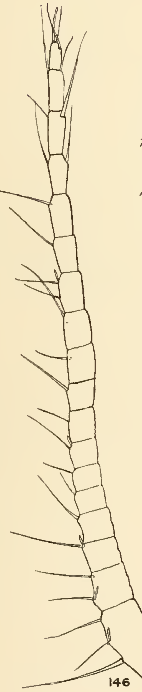
The nauplii of *Diaptomus*, as compared with those of *Cyclops*, are distinguished by their rich colour, their gliding motion, narrow and rather laterally compressed bodies in later stages, and by the slender dorsal bifurcated furcal setæ. There are also considerable differences in detail in the appendages.

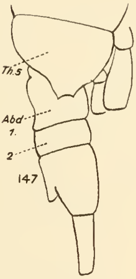


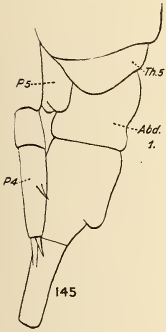


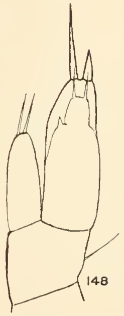












Figs. 141–148.—*Diaptomus castor*; Copepodid stages.
Fig. 141.—Stage I, side view.
Fig. 142.—Stage I, furcal rami, dorsal view.
Fig. 143.—Stage II, soms. 3–5 of th. and abdomen, side view.
Fig. 144.—Stage II, antennule.
Fig. 145.—Stage III, th. som. 5 and abdomen, side view.
Fig. 146.—Stage III, antennule.
Fig. 147.—Stage IV, female, th. 5 and abdomen, side view.
Fig. 148.—Stage IV, female; leg 5 about to moult.

COPEPODID STAGES.

Stage I.

(Figs. 141, 142.)

Length ·62–·76 mm. (average ·69 mm.).

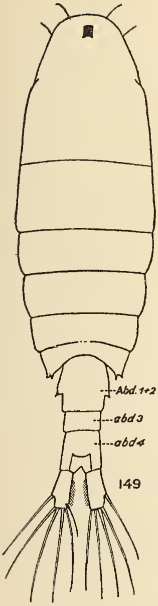
Head without rostral filaments. Thorax of 4 free somites, followed by a single somite representing th. som. 5 and abdomen. Furcal rami with 5 setæ. The 4 terminal setæ are quite different from those of the adult, the 2nd (from outside) and the innermost being very long and feathered, while 1 and 3 are short and smooth. Antennule of 10 segments, but joints ill defined. The six terminal segments are quite distinct, but the 5th is long and represents 2 segments undivided. The next segment bears an æsthete and corresponds to seg. 19. Antenna and mouth-parts nearly of adult form, but not fully developed. Epipod of maxillule with 4 setæ only. Legs 1 and 2 functional, the rami unsegmented. Legs 3 and 4 represented by bilobed rudiments.

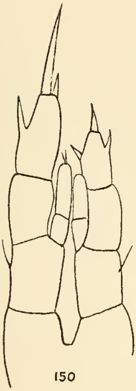
Stage II.

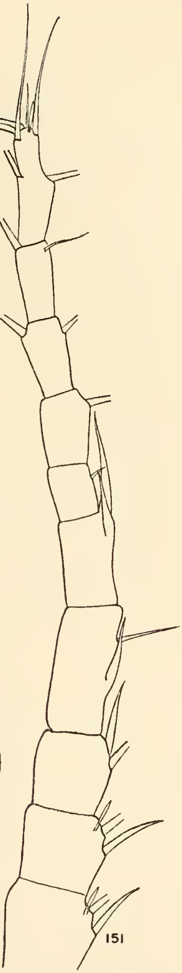
(Figs. 143, 144.)

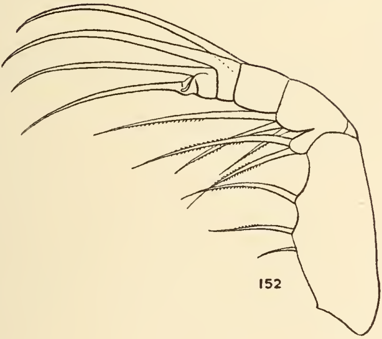
Length ·9–·97 mm. (average ·93 mm.).

Frontal filaments present. Th. som. 5 distinct, followed by undivided abdomen. Furcal rami with 6 setæ, the outer lateral seta having appeared. Number of setæ now as in adult, but outer two not feathered. Antennule with proximal segments not clearly marked, the terminal 7 (19–25) distinct. Indications of 18 segments in all can sometimes be seen. It is clear that the 7 terminal segments correspond to the terminal 6 of stage I; but it is out of the question to speculate as to how the proximal segments of stage I have divided. Oberg has found no difficulty in stating quite precisely the fate of each segment in *Centropages* and other genera, but I am unable either to follow his reasoning or to apply it to *Diaptomus*. There are, at this stage, 4 æsthetes and 8 setæ in the region of segs. 1–19. Maxillule with 6 setæ on epipod. Legs 1 and 2 with rami









Figs. 149–151.—*Diaptomus castor*; Copepodid stages. Fig. 152.—*Hemidiaptomus ignatovi*, Sars. Maxillipede.

Fig. 149.—Stage V, female, dorsal view.
Fig. 150.—Stage V, male, leg 5.
Fig. 151.—R. antennule of male.
Fig. 152.—*Hemidiaptomus ignatovi*, Sars. Maxillipede.

2-segmented; rami of leg 3 unsegmented. Legs 4 and 5 rudimentary.

Stage III.

(Figs. 145, 146.)

Length 1·13–1·2 mm.

Th. somites all distinct, and abdomen of 2 somites. Furcal rami as in adult, all setæ feathered. Rami smooth on outer margin. Antennule with segments not distinct, apparently of 23 segments. Segments 10–25 are distinct, but the basal part consists of 6 imperfectly divided segments. There are æsthetes on segs. 9, 14 and 19, and 2 on the basal part. Seg. 19 alone has 2 setæ. Although, therefore, the adult segmentation is very nearly reached, the number of setæ is by no means complete. Exopod of maxillule with 7 setæ. Maxillipede with setæ on basis as in adult, but endopod of 4 segments only.

Leg 1–3 rami 2-segmented; unsegmented in leg 4.

Leg 5 a bilobed rudiment.

The sexes are not distinguishable.

Stage IV.

(Figs. 147, 148.)

Length: Female, 1·52–1·67 mm.; male, 1·35–1·47 mm.

Abdomen of 3 somites in both sexes. Th. som. 5 of female a little expanded and with two points. Antennule of 25 segments, with setæ and æsthetes as in the adult. In the male the right antennule is not swollen, and all the segments are distinct; but setæ on segs. 18 and 19 show incipient modification to spines. Epipod of maxillule with 9 setæ. Rami of legs 1–4 2-segmented. Leg 5 almost alike in the two sexes, with unsegmented rami. In the female each exopod bears two terminal spines, of which the inner one is more than twice the length of the outer. In the male the left leg is as in female, but the right a little the larger and the inner spine a little shorter than the outer.

Gonads visible.

Stage V.

(Figs. 149–151.)

Length: Female, 1·83–2·1 mm.; male, 1·71–1·87 mm. Differing very little from the adult. Th. som. 5 not so expanded, and genital somite with small lateral points. Abdomen of 3 somites in female. Somites 1 and 2 of Stage IV have fused, and a new somite has been separated. Abdomen in male of 4 somites—*i. e.* as in female, but without fusion of 1 and 2. Prehensile antennule of 25 segments, not hinged. In seg. 18 the proximal seta and in seg. 19 both setæ are transformed into spinous processes. Leg 5, female: exopod 2-segmented, seg. 2 with strong inner spine and small outer spine. The portion beyond these spines corresponds to seg. 3, and bears two apical spines, of which the outer is much the shorter. In the male right leg is distinctly larger than left. Left leg as in female, but inner spine of seg. 2 smaller, and only one apical spine. Left leg has no inner spine, but has two apical spines, of which the outer is much the longer. In retaining two apical spines at this stage *D. castor* differs from *D. vulgaris* and *D. gracilis*, which have lost the inner spine. The retention of the spine may perhaps be regarded as a primitive character. In *Paradiaptomus greeni* there are two spines on each leg in stage V. In *D. doriai* there are two on the left leg and one on the right.

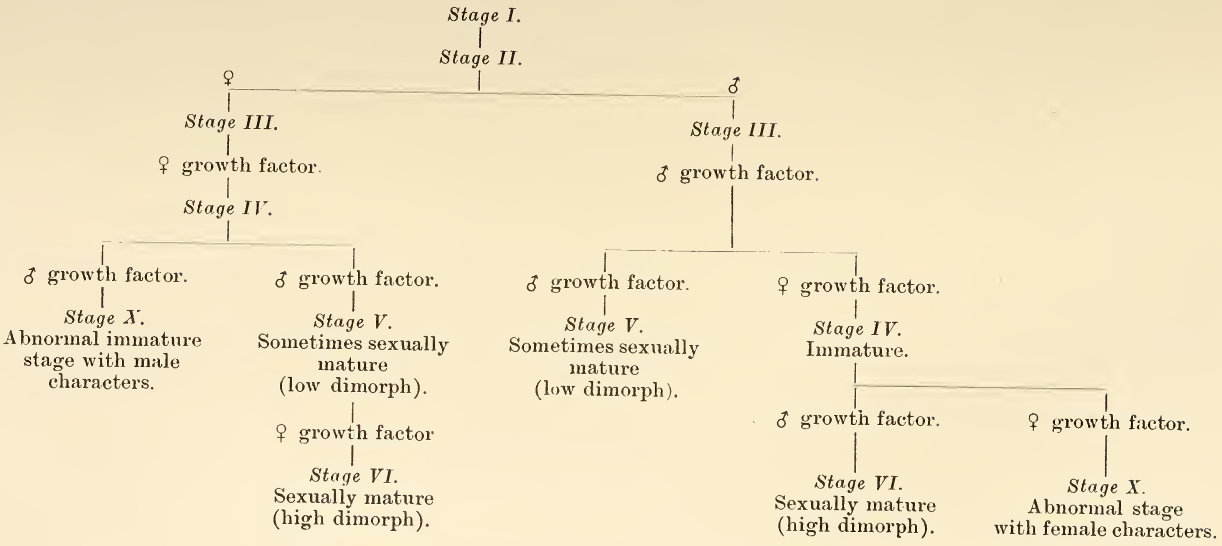
RATE OF GROWTH.

It has been claimed by Sewell (1912) that the rate of growth of marine Copepods is in accordance with "Brooks's law," namely, "during early growth each stage increases at each moult by a fixed percentage of its length, which is approximately constant for the species and sex" (Fowler, 1909). If this were exactly true, we should have a valuable means for distinguishing the larval stages of allied species; but I have attempted to apply Sewell's methods to certain fresh-water species, and have not found that the growth-rate was sufficiently specific or uniform to conform strictly to this law (Gurney, 1929A). Rammner for Cladocera (1928) and Calvert for certain insects (1929) have both found that the growth increment from moult to moult is most irregular. The following table shows the measurements and the growth factors for nauplius and copepodid of *Diaptomus vulgaris*. In this case the growth factor was about the same for both sexes, and shows a decrease from stage to stage. The growth factor in this and other cases does not much exceed 1·3, except for the moult from nauplius VI to copepodid I, which is abnormally high owing to the change in shape at this moult. The normal ratio of increase was assumed by Brooks to be by a factor of 1·25, and the figure 1·26 was calculated by Przibram and Megusar (1912) on the basis of observations on *Sphodromantis bioculata*. This rate may be much exceeded in certain insects—Calvert gives rates varying from 1·14 to 1·83 for *Anax imperator*, and even a rate of 2 for *A. junius*. Nevertheless a rate exceeding 1·4, in the case of a Copepod, seems to suggest a possibility of error.

Diaptomus vulgaris, Norfolk.

	Number measured.	Average length.	Growth factor.
Nauplius 1 . .	1	·175	..
,, 2 . .	5	·205	1·17
,, 3 . .	7	·230	1·09
,, 4 . .	9	·280	1·25
,, 5 . .	16	·322	1·15
,, 6 . .	5	·370	1·15
Copepodid I . .	2	·52	1·40
,, II . .	9	·69	1·33
,, III . .	16	·89	1·29
,, IV ♀ . .	35	1·15	1·29
,, IV ♂ . .	28	1·06	1·19
,, V ♀ . .	21	1·44	1·25
,, V ♂ . .	19	1·32	1·24
Adult ♀ . . .	91	1·72	1·19
,, ♂ . .	96	1·55	1·17

TABLE SHOWING POSSIBLE LINES OF CALANOID DEVELOPMENT.*



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* Copy of Sewell's table, 'Mem. Ind. Mus.,' x, p. 7.

So far as I am aware, no direct observations have been made on the moulting of post-naupliar stages in Calanoida, and indeed it is doubtful if such observations on individuals in artificial surroundings would be of value. Consequently the assumption that each individual as a rule goes through 6 stages is founded upon probability, and a reasonably close agreement between the observed sizes of the stages. The correctness of this assumption has been questioned by Sewell, who maintains that there are entirely different growth factors in female and male, but that one sex may increase in size at one moult by the factor of the opposite sex, to revert again to its own factor at the next moult. In this way alternative possibilities of development are arrived at, as shown in the diagram taken from his latest work. This diagram applies more particularly to the genera *Paracalanus* and *Acrocalanus*, but expresses his views of the probable course of development in other genera also. Sewell has shown that, in many marine Calanoida, there are two forms of the adult, usually distinguished only by difference in size, though occasionally also by small differences in structure—*e. g. Labidocera euchæta*; and it is to account for the existence of these dimorphic forms that he has postulated this complicated type of ontogeny. His new table differs markedly from that in his previous scheme (1912, p. 329), in which he accepted 6 stages in normal development, while the " high form " represented an additional stage VII.

Space cannot be given here to detailed examination of Sewell's evidence. While occasional abnormalities in development may be readily admitted, there seems to be no reason whatever to doubt that, in fresh-water Copepods, growth is a straightforward affair, similar in both sexes, and proceeding at a diminishing rate.

I have tried to follow the development of isolated individual copepodids of *D. castor*, but the results are unsatisfactory owing to the difficulty of accurate measurement of living specimens and of reproducing natural conditions. All that can be said at present is that every moult observed followed the expected course from stage to stage, and provided no evidence for Sewell's theory.

In fresh-water Copepods no similar distinction between two adult size groups has previously been observed, but it appeared, from examination of material of *D. laticeps* and *D. wierzejskii*, that they may occasionally be recognized. This was particularly the case in a sample of the latter from Tunisia, where a considerable proportion of the adults were so strikingly larger than the rest that they could easily be picked out under a lens, and appeared at first to represent a different species. Similarly, in a sample of *D. laticeps* from the Orkneys and of *D. wierzejskii* from the Shetlands, a small proportion of both sexes in the former and of females in the latter were strikingly larger than the majority. In order to explain the existence of the larger size-group it is necessary to suppose, either that copepodids of stage V moulted with an abnormally high growth factor, or that there may be an additional moult from the normal "low form" to the "high form."

Diaptomus wierzejskii.

	Tunisian specimens.			Shetlands.
	Number measured.	Average length.	Growth factor.	Average length.
Copepodid II . . .	1	·760	. .	. .
,, III . . .	26	·818	1·07	. .
,, IV ♀ . .	15	1·090	1·3	·97
,, IV ♂ . .	13	·960	1·17	·92
,, V ♀ . .	29	1·303	1·2	1·26
,, V ♂ . .	22	1·160	1·2	1·18
Adult VI ♀ . .	10	1·590	1·2	1·50
,, VI ♂ . .	18	1·338	1·15	1·35
,, VII ♀ . .	9	2·150	1·3	1·73
,, VII ♂ . .	18	1·635	1·2	. .

The average sizes of the age-groups are shown in the table, and it will be seen that, in the case of *D. wierzejskii* from Tunisia, the increase in size is fully accounted for by the continuance of a quite normal growth factor, if we assume a linear succession of stages. Direct evidence of such a moult in the adult is not available. I have shown that, in *D. laticeps* from Loch Hundland, some adult specimens appeared to be sexually immature, and showed signs of withdrawal of tissues for a moult, but no moulted skins were seen. Grandori, however, states that he has seen moulted skins of *Acartia clausi* in the adult form (1912, p. 437). Moulting in the adult in Copepods has never actually been observed, and it must be admitted that the question is still open. The existence of two distinct size-groups in the adult is certainly a fact in the two species mentioned, but it is a rare phenomenon in fresh-water species, and I have found no evidence of it in other species.

KEY TO BRITISH SPECIES OF DIAPTOMUS.

I. *Females.*

1. Genital somite with large triangular lateral processes. Antennule segs. 14, 15 with 2 setæ . . . . *D. castor.*
   Genital somite without processes. These segments with 1 seta each . . . . 2.
2. Th. som. 4 and 5 each with wing-like lateral processes *D. laciniatus.*
   Som. 4 without process . . . . 3.
3. Thorax narrowing behind; posterior expansions of th. som. 5 rounded . . . . 4.
   Thorax scarcely narrowed; expansions of th. som. 5 large, angular . . . . 5.
4. Antennule seg. 13 with 2 setæ . . . . . *D. laticeps.*
   This segment with 1 seta . . . . . *D. wierzejskii.*
5. Lateral spines of genital somite long and slender; antennules longer than body . . . . . . *D. gracilis.*
   These spines short and stout; antennules generally shorter than body . . . . *D. vulgaris.*

II. *Males.*

1. Prehensile antennule, seg. 23 without process of any kind 2.
   This segment with straight or hook-like process . . . 3.

2. Leg 5, right, endopod unsegmented, large, pointed at end . . . . *D. laciniatus.*
   Endopod cylindrical, segmented, blunt . . *D. castor.*
3. Leg 5, right, exopod 1 with long, acutely-pointed angle; endopod unsegmented, conical. . . . . . 4.
   This angle rounded or simply acute; endopod cylindrical or dilated in middle . . . . . . 5.
4. Prehensile antennule, seg. 23 with straight toothed process . . . . *D. wierzejskii.*
   Seg. 23 with short, hooked process . . . *D. laticeps.*
5. Leg 5, right, endopod unsegmented, very large, swollen; longer than exopod 1 . . . . *D. gracilis.*
   Endopod slender, small, usually not longer than exopod 1 *D. vulgaris.*

Diaptomus castor (Jurine).

(Figs. 153–169.)

1820. *Monoculus castor*, Jurine, Hist. des Monocles, p. 50, figs.
1850. *Diaptomus castor*, Baird, Nat. Hist. Brit. Entom. p. 219, pl. xxvi.
1878. ,, ,, (in part), Brady, Mon. Brit. Cop. I, p. 59.
1863. ,, ,, Lubbock, Trans. Linn. Soc. XXIV, p. 205, pl. xxxi.
1892. ,, ,, Brady, Trans. N.H.S. Northd. XI, p. 192, figs.
1896. ,, ,, Schmeil, Bibl. Zool. XXI, p. 35, pl. i.
1902. ,, ,, Sars, Crust. Norway, p. 85, pls. lvii, lviii.

Female.—Length 1·8–2·5 mm.

The average length differs much in different colonies, *e.g.*:

South Devon (April) female 2·05; male 1·86 mm.
Oxford ,, ,, 2·46; ,, 2·25 ,,

General form stout, thorax about $2\frac{1}{2}$ times as long as broad, greatest width between th. soms. 2 and 3, but very little narrowed behind. Th. som. 5 indistinctly marked off and expanded laterally into large wings, each of which is cleft into two pointed lobes. Abdomen of 3 somites, som. 2 very small. Genital somite very broad, with a large triangular lappet on either side, ending in a small sensory spine; the right lappet much the larger. Furcal rami about twice as long as broad, with hairs along both sides. Setæ long and slender, the dorsal seta about half length of inner apical seta.

Upper lip with very long hairs, attached anteriorly and reaching backwards nearly to its posterior margin.

Antennule relatively short, reaching scarcely beyond thorax. Seg. 1 with very long seta ; segs. 11 and 13–19 each with 2 setæ. The following table shows arrangement of setæ and æsthetes. Except for the number of setæ on segs. 11 and 13–19, this table holds good for the genus, and probably for the whole family. Exopod of antenna slender ; seg. 2 with 3 setæ of equal length.

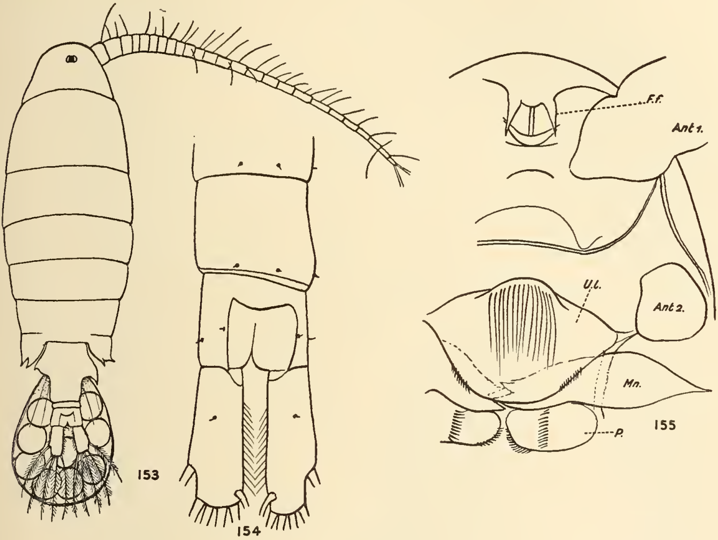
Antennule of Diaptomus castor, *female* (*and on left side in male*). *Arrangement of Setæ and Æsthetes.*

1	2	3	4	5	6	7	8
s., a.	3 s., a.	s., a.	s.	s., a.	s.	s., a.	s., sp.
9	10	11	12	13	14	15	16
2 s., a.	s.	2 s.	s., a., sp.	2 s.	2 s., a.	2 s.	2 s., a.
17	18	19	20	21	22	23	24 & 25
2 s.	2 s.	2 s., a.	s.	s.	s. + s.	s. + s.	s. + s. 5 s., a.

s. = seta ; a. = æsthete ; sp. = spine.

The mandible and maxillæ do not seem to show any specific differences. Schmeil notes that 2 setæ on lacinia 3 of the maxillule are much longer in *D. castor* than in *D. vulgaris*, but I do not find any such difference. Maxillipede : Seg. 2 of sympod generally a little longer than seg. 3 ; seg. 2 with 4 inner lobes bearing 1, 2, 3, 4 setæ ; on lobes 2–4 the distal seta very much longer than the proximal seta. Seg. 3 rather broad, the length about twice breadth ; the 3 marginal setæ of lengths—23, 13, 44. Endopod shorter than seg. 3 of sympod ; of 5 distinct segments, seg. 1 being suppressed and represented only by its spine.

Leg 5: Coxa with large, broad, sensory spine; exopod 1 slender (58 : 23); exopod 2 longer than seg. 1 (72 : 58), straight, with hairs on inner margin; exopod 3 a distinct segment, bearing a stout seta which reaches about halfway along seg. 2, and a small spine. Endopod 2-segmented, reaching about two-thirds the length of exopod 1, with 2 unequal terminal setæ and a minute spine on inner angle.



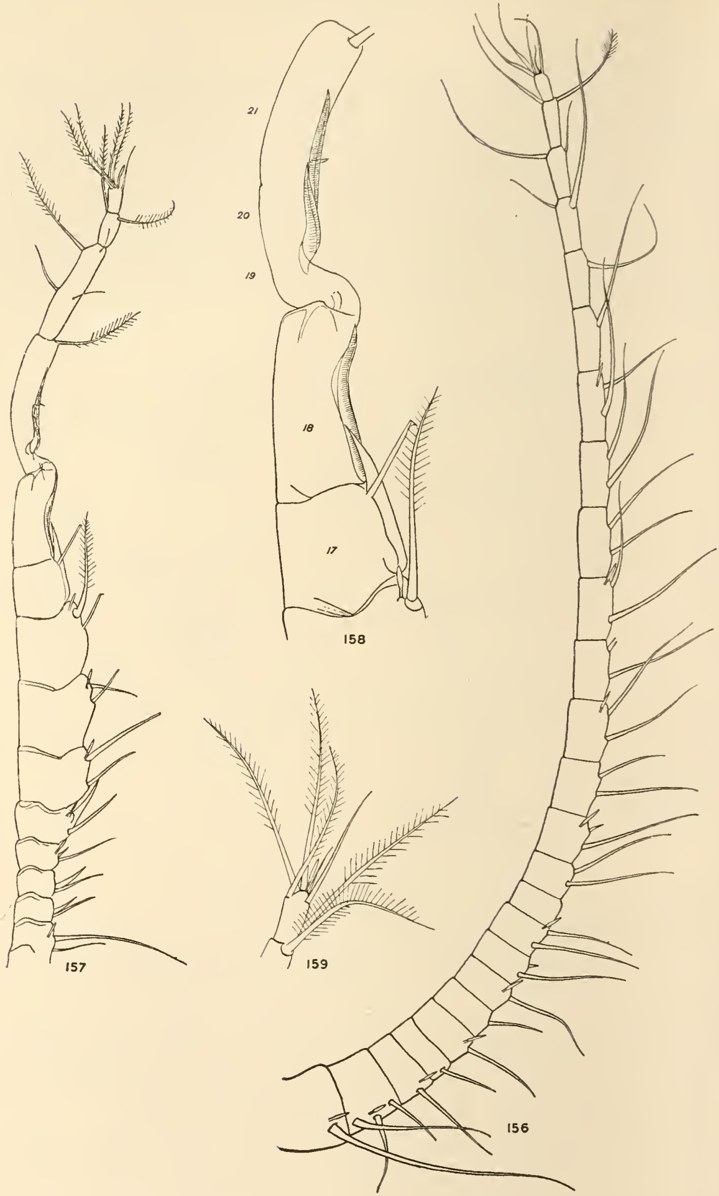
FIGS. 153–155.—*Diaptomus castor.*
FIG. 153.—Female, dorsal view, bearing resting eggs.
FIG. 154.—Male, soms. 3–5 of abdomen.
FIG. 155.—Ventral view of head, showing upper lip and paragnaths. *F.f.*, frontal filament; *U.l.*, upper lip; *P.*, paragnath.

Egg-sac very large, generally with many small eggs, but sometimes with few eggs of larger size (Fig. 153). In these cases the sac is very strong and the egg membrane conspicuously thick. Perhaps resting eggs (?).

Colour variable. Commonly dark red, but often brown-green with blue margins to segments.

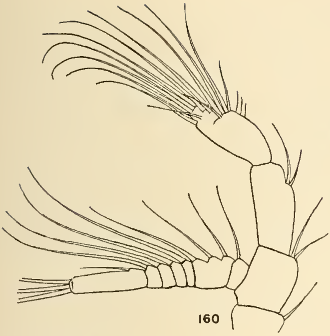
Male.—Length 1·75–2·3 mm.

General form slightly more slender than in female. Th. som. 5 slightly produced on either side, and



Figs. 156–159.—*Diaptomus castor.*

Fig. 156.—Antennule, female.
Fig. 157.—Prehensile antennule of male.
Fig. 158.—The same, segs. 16–21, more enlarged.
Fig. 159.—Antennule of male, seg. 25.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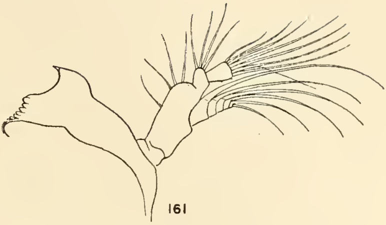
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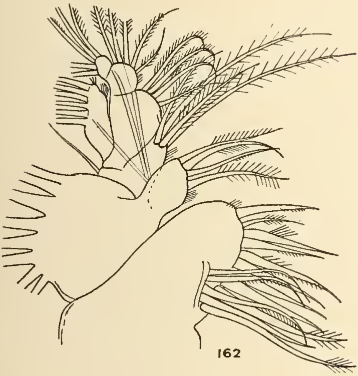
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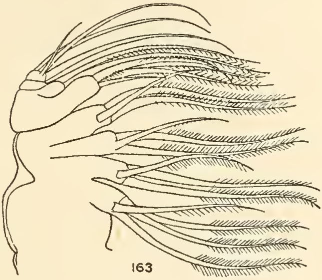
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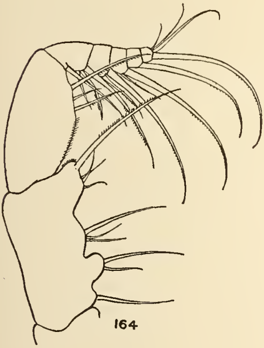
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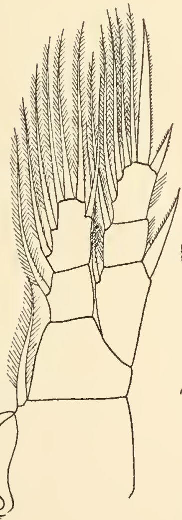
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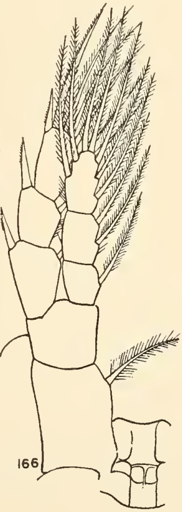
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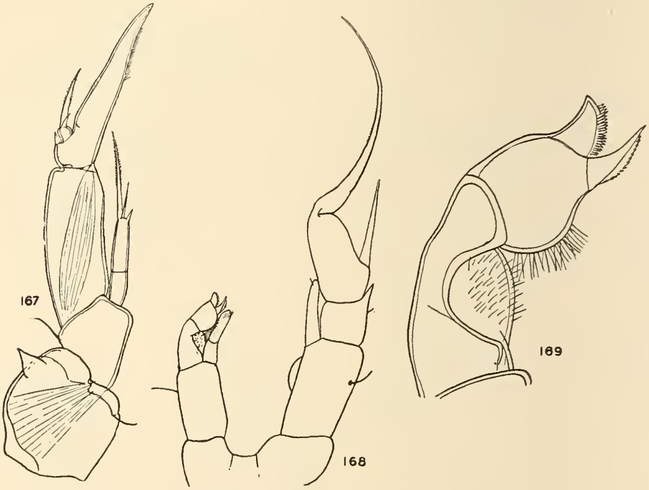
Figs. 160–166.—*Diaptomus castor.*

Fig. 160.—Antenna.
Fig. 161.—Mandible.
Fig. 162.—Maxillule.
Fig. 163.—Maxilla.
Fig. 164.—Maxillipede.
Fig. 165.—Leg 1.
Fig. 166.—Leg 4.

notched as in female. Abdomen of 5 somites, som. 4 and 5 slightly asymmetrical; minute sensory hairs on these somites disposed as in Fig. 154. Furcal rami about 3 times as long as broad, symmetrical, with hairs on inner margin only. Prehensile antennule without spinous process on segs. 14–16. Proximal seta of seg. 14 not modified. Those of segs. 15–17 are "Hakenborsten" (Schmeil)—straight rods with an apparently soft pointed extremity bent backwards as a small hook. Seg. 20 (segs. 22 and 23) has a narrow inner hyaline membrane, not produced into a terminal hook. Leg 5: Coxa with very small sensory spine, that of left leg sometimes absent. Right leg—basis long and slender (40 : 22), with oval hyaline lamella on inner margin. Exopod 1 generally with outer angle produced into a sharp point, rarely rounded. Exopod 2 long, slender and tapering, nearly twice as long as wide. Outer spine inserted near base (14 : 25).* Terminal claw more than



Figs. 167–169.—*Diaptomus castor.*
Fig. 167.—Leg 5, female.
Fig. 168.—Leg 5, male.
Fig. 169.—Leg 5, male, left exopod.

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* In this and following species the figures given are distance from spine to base and apex of segment respectively.

twice length of exopod 2, not greatly curved. Endopod unsegmented or divided into 2 segments, longer than exopod 1.

Left leg: Basis without hyaline membrane, rather narrow (35 : 22). Exopod 1 and 2 with inner hairy pads. Terminal process short, curving outwards, with a double row of short stiff hairs on inner margin ; inner process short and broad ; fringed with a jagged membrane. Endopod longer than exopod 1, 2-segmented.

All British specimens agree with Schmeil's excellent description with the exception of the form of leg 5, male. Schmeil's figure shows the basis in both legs much shorter and broader than I find it. The difference, in fact, is as great as that between certain races of *D. vulgaris*, which have been described as distinct. The slender form of leg seems to be much the most usual, since it is so figured by De Guerne and Richard, Sars, Brady, Lubbock and Rylov. Lubbock's figures of this species and of *D. gracilis* (1863) are accurate, and show the differences between the species quite clearly. It is remarkable that Brady, having this paper before him, should still have regarded the two species as identical in 1878. His description and figures of "*D. castor*" are mainly taken from *D. gracilis*.

DISTRIBUTION IN BRITAIN.

Widely distributed and not uncommon in the east and south of England. It is probably commoner in other parts than the records indicate, since the small ditches and pools in which it occurs are likely to receive less attention than larger waters, and also most collecting has been done in summer, when it has largely disappeared. In Devon and Cornwall it occurs in a large proportion of roadside ponds.* Mr. Scourfield found it in a number of small ponds in the Epping District, and it is common in Norfolk. On the other hand there are at present no records for Wales, and very

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* I have to thank Mr. R. A. Todd for collections from about 200 ponds and ditches in these and adjacent counties.

few from Scotland. It was taken by Scott (1898) in a small pool near Helliers Water in the Isle of Unst (Shetlands); in Braid Pond, near Edinburgh; and in a pond near Aberdeen. Mr. Scourfield records it from Nerston quarry near Glasgow, and from Ireland.

Distribution Abroad.

Widely spread in the lowlands of western and central Europe and in Sweden and south Norway. While it appears to be absent from the extreme north and from northern Russia, it is recorded by Haberbosch from Greenland, and there are specimens in the Norman collection labelled "Greenland." Towards the south and east it becomes rare, but is recorded from Spain (Burckhardt), Côte d'Or (Roy) and Corsica (Richard). Eastward it is found in the Austrian plain (Spandl), in Croatia and Slavonia (Krmpotic) and in south-west Russia (Skorikow).

Bionomics.

Unlike the majority of *Diaptomus*, *D. castor* lives only in small shallow ponds or in ditches. Apart from size and depth of water it seems to be tolerant of a rather wide range of conditions, being found in small peat pools with yellow water, ditches nearly full of decaying leaves, muddy ponds, or ponds with weeds and clear water. It is most commonly associated with *Daphnia pulex*, and is a characteristic species of pools which dry up in summer.

Throughout the greater part of its range *D. castor* is found most commonly or exclusively in the colder months. In Norfolk, and near Oxford, it makes its appearance generally in October or November, and dies out again about March. It may also be found occasionally in other months, but it is very rare indeed in May, June and July. In Greenland Haberbosch found it in July, but here, of course, climatic influences would be entirely different.

Wolf (1905) states that it is monocyclic, producing only resting eggs, and that these eggs endure desiccation, but can develop without it. In a pond which has been dry all summer the appearance of multitudes of nauplii of *D. castor* as soon as the water returns proves the existence of resting eggs, but I have isolated females from such a pond and have found in all cases that the eggs hatched after about 4 days. No difference was noticed in the eggs produced in this pond throughout the cycle of the species. It seems possible that the same egg may either develop directly or "rest." On the other hand, in some colonies the females are found bearing few and large eggs with thick membranes, which are no doubt resting eggs.

Diaptomus laciniatus, Lilljeborg.

(Figs. 170–182.)

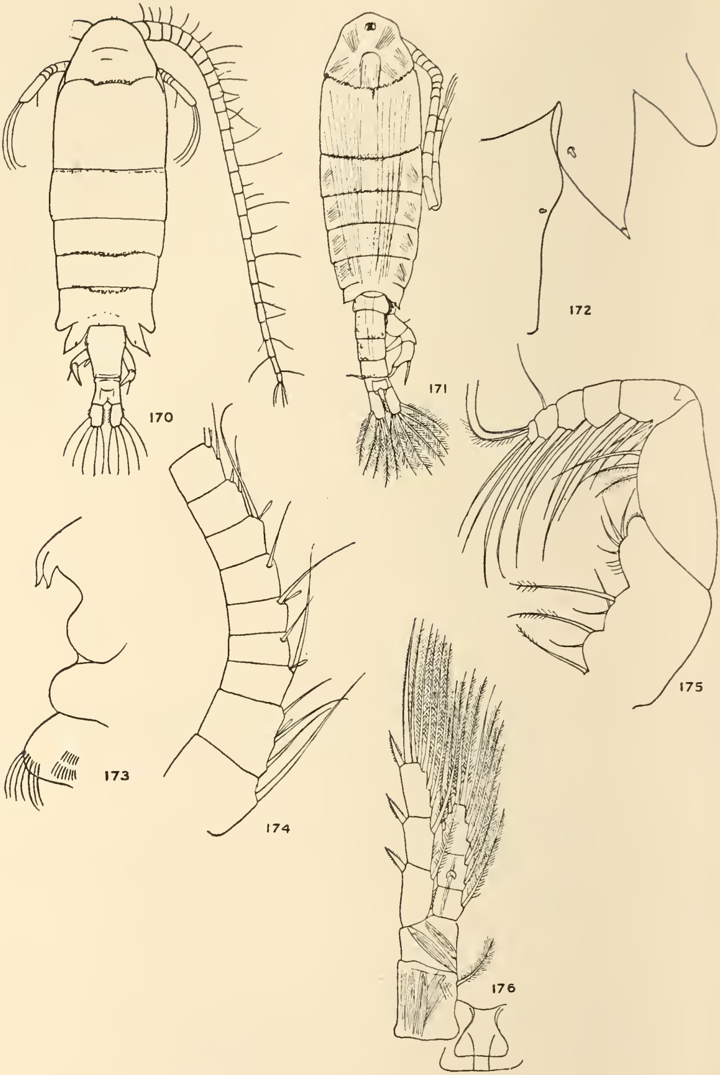
1889. *D. laciniatus*, Lilljeborg, in Guerne & Richard, Mem. Soc. Zool. Fr. II, p. 99, figs.
1897. ,, Scott, T. & A., Ann. Mag. Nat. Hist. (6), XX, p. 493, pl. xii.
1896. ,, Schmeil, Bibl. Zool. XXI, p. 167, figs.
1899. ,, Scott, T., Rep. Fish. Bd. Scot. XVII, p. 187, pl. xiii.
1900. ,, Burckhardt, Rev. Suisse Zool. VII, p. 653, pl. xxi.
1902. ,, Sars, Crust. Norway, IV, p. 91, pl. lxii.
1928. ,, var. *migoti*, Monard, Bull. Soc. Zool. France, LIII, p. 257.

Female.—Length 1·05–1·2 mm.

The size varies greatly in different localities, and it is generally larger in its northern habitats than in the south. Examples :

Norway, 1·6–1·8 mm.
Switzerland, 1·43–1·6 mm.
Black Forest, 1·05–1·2 mm.
Scotland—Loch Shiel, 1·65–1·74 mm.
Loch Eilt, 1·58–1·62 mm.

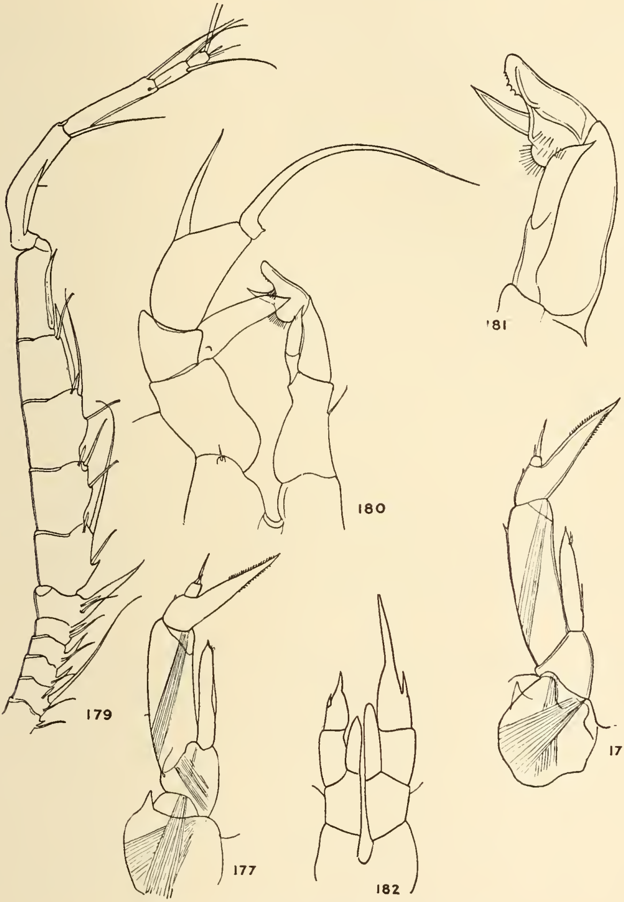
General form stout, thorax more or less parallel-sided, the width about one-third the length. Last two somites generally fused dorsally, but sometimes showing a faint line of division. Each somite expanded laterally into conspicuous lobes, those of the 4th somite being



Figs. 170–176.—*Diaptomus laciniatus.*

Fig. 170.—Female, dorsal view.
Fig. 171.—Male, dorsal view.
Fig. 172.—Th. som. 5 and genital somite female.
Fig. 173.—Head of female, side view, showing labrum.
Fig. 174.—Antennule, female, segs. 1–8.
Fig. 175.—Maxillipede.
Fig. 176.—Leg 2 from behind, showing lamella on R.I. 2.

rounded, and those of the 5th sharply pointed, and with a very small sensory papilla near the base. Abdomen generally of 2 somites only, the 2nd being partly or wholly fused with the 3rd. Genital somite a little longer than wide, expanded anteriorly. Lateral spines



Figs. 177–182.—*Diaptomus laciniatus.*

Fig. 177.—Leg 5, female.
Fig. 178.—Leg 5, female, abnormal.
Fig. 179.—Antennule of male.
Fig. 180.—Leg 5, male.
Fig. 181.—Leg 5, male, left leg more magnified.
Fig. 182.—Leg 5, male, Cyclopid stage V.

represented by minute sensory papillæ, only visible with difficulty. Furcal rami about twice as long as broad, with both margins hairy.

Upper lip with an anterior group of very long hairs, and lateral groups of short hairs.

Antennule reaching just beyond genital somite. Segs. 13–20 have 1 seta only, with the exception of the 16th, which has 2. Maxillipede with a group of 4 short setæ on the 3rd lobe of the basis, the distal seta a little the longest. Leg 5: Coxopod with a large triangular sensory process. Seg. 1 of exopod long and slender, the width less than one-third of its length. There may sometimes be a small spine on the outer edge, near the end. This segment seems to be stouter in specimens from Scandinavia than in those from Switzerland or Scotland. Seg. 2 of exopod a strong, slightly sinuate claw; seg. 3 distinctly marked off, and bearing 2 spines, the inner of which is about three times as long as the outer. Endopod long, slender, and pointed at the end, reaching nearly to the end of seg. 1 of exopod. In one specimen one of the legs had a small seta near base of endopod (Fig. 178).

Male.—Length (Loch Eilt) 1·4–1·55 mm.

Rather more slender than the female, and with the last thoracic somites not expanded. The 5th somite produced backwards a little on the right side and with a terminal sensory spine.

Antennule: Seg. 13 with a very long spine; seg. 14 with a very small tooth, but segs. 15 and 16 without teeth; seg. 23 with a very narrow hyaline membrane, but without any distal process.

Leg 5: Basal segment of each leg with a very minute sensory spine, but that of the left leg reduced to a minute hair which is very difficult to see, and may be absent. Basis of right leg without a hyaline lamella, or occasionally with a very small marginal lamella. Seg. 1 of exopod with a small blunt outer projection; seg. 2 tapering towards the end, the lateral spine inserted about the middle of the outer margin. Terminal spine sickle-shaped, rather slender, and with a peculiar notch at the base. This notch is easily seen, and is an excellent means of distinguishing the male among other species in the plankton. Endopod long, reaching nearly to end of exopod 2, and acutely pointed at the end.

Left leg: Basis without hyaline membrane. Terminal claw short and blunt, with a serrated edge. Inner spine stout and nearly straight. Endopod generally closely apposed to the exopod, as long as first segment of latter, rather twisted, and sharply pointed at the end.

Colour: All the Scottish specimens that I have seen have been dark blue, the colour most marked along the lines between the thoracic somites. Ekman states that it is generally orange red, more rarely blue, in the Swedish highlands. Sars found it generally blue, rarely reddish orange.

DISTRIBUTION IN BRITAIN.

In the island of Lewis *D. laciniatus* was the only species of *Diaptomus* found by the Scottish Lake Survey. It occurs also in the lochs of Skye, but is apparently absent from Uist, Jura and the other western islands.

On the mainland of Scotland it is most frequently found in Sutherland and Caithness. Further south it seems to be confined to lochs of the west, but has been taken in some small lochs in the extreme west of Aberdeenshire.* Murray states that, in the Great Glen, it occupies the hill lochs, while *D. laticeps* takes its place at lower levels. South of the Glen I have found in in Loch Ossian, one of the highest lochs investigated (1268 ft.). Curiously enough, it does not seem to have been taken there by the Survey, since it is not mentioned by Murray. Murray records it from Loch Lomond, but it must be very rare and unevenly distributed there, since it was not taken there by Scott, neither have I been able to find it myself. Outside the Highlands it

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* Lochs Vrotachan and Phadruig, Scott, 1901.

has been found by Scott in Loch Doon in Ayrshire. The accompanying table is taken from Murray's summary of the results of the Survey :

Table of Distribution of Scottish Diaptomus *from Murray,* 1905.

	Orkneys and Shetlands.	Outer Hebrides.	Sutherland and Caithness.	Ross-shire.	Inverness.	Perthshire and W. Aberdeenshire.	Argyll.	Ayr and Galloway.	Mid-East Scotland.	S.E. Scotland.
D. gracilis .	1	..	23	40	54	25	34	24	9	6
,, *laciniatus* .	..	12	9	7	6	..	2	1	..	..
,, *laticeps* .	4	11	8	2	13	4	2	..	..	..
,, *wierzejskii*	21	5	4	1	..	..	..	..	..	..

It is unfortunate that it is impossible to recover from Murray's scattered notes the exact distribution of the Scottish *Diaptomus.* I have re-examined all the Survey collections from the north and west that are now available, and give the list of the lochs in which *D. laciniatus* occurs, since it is of importance that the distribution should be established as accurately as possible.

If *D. laciniatus* is monocyclic and only reaches maturity in autumn in Scotland as it does in Switzerland, it is likely to escape notice when plankton samples are taken in summer. The survey collections from Sutherland and Caithness were made in September and October, and as a rule contain adult *Diaptomus*, but much of the work was done in July and earlier in the year, and many samples contain only immature individuals which cannot be identified with certainty. Most of the samples also were taken at the surface, and any species inhabiting deep strata would tend to escape notice. This source of error is probably not serious for, except in Loch Shin, I have found *D. laciniatus* common at the surface.

List of Lochs on Mainland of Scotland Containing Diaptomus laciniatus.

Lake.	County.	Basin.	Area in square miles.	Maximum depth (feet).	Mean depth.	Height above sea-level (feet).	Accompanied by—*
Shin . . .	Sutherland	Shin	8·7	162	51	270	G.
Merkland . .	,,	,,	·69	85	30	360	Alone.
A'Ghriama . .	,,	,,	·4	64	28	303	G., L.
Ailsh . . .	,,	,,	·38	24	8·3	498	L.
Craggie . . .	,,	,,	·07	40	15·3	505	Alone.
An Daimh . .	,,	,,	·27	52	27	671	L.
Kinaskink . .	,,	Assynt	2·09	216	60	245	G.
Owskeich . .	,,	,,	·65	153	47	72	G.
Leum a'Chlamhain .	,,	Helmsdale	·55	51	19·5	770	G., L., W.
Nan Cuinne . .	,,	,,	1·15	28	12·4	395	G., W.
A'Chlair . . .	,,	,,	1·17	32	13·7	394	G., W.
Baddanloch . .	,,	,,	·99	42	17·3	394	G., W.
Bhaid Daraich .	,,	Scourie	·17	121	55·6	48	Alone.
Na Meide . .	,,	Naver	·87	63	20·6	. .	L.
Stack . . .	,,	Laxford	·99	108	36	117	?
Achall . . .	Ross	Broom	·52	70	27·8	263	Alone.
An Eilean . .	,,	Gairloch	·14	34	14	. .	Alone.
Doon . . .	Ayr	Doon	2·04	100	26·7	673	G.
Eilt . . .	Inverness	Shiel	·66	119	37	96	G.
Shiel . . .	,,	,,	7·56	420	81·6	11	G.
Ossian . . .	,,	Lochy	1·03	132	42·7	1269	Alone.

G. = *D. gracilis*; L. = *D. laticeps*; W. = *D. wierzejskii*. With the exception of Loch na Meide and Stack, the records have been confirmed by re-examination of the original plankton samples.

Distribution Abroad.

D. laciniatus is confined to two widely separated areas in Europe.

North Europe : As far north as the Murman coast. It is found both in lakes and in small pools in lowland and in mountains of Norway and Sweden, but it does not appear to be very common in the lakes of Norway. Huitfelt-Kaas only records it from two—Kallandsvand and Lundevand. Sars found it in Finmark in company with *Heterocope borealis* and *Polyartemia forcipata*. Smirnov (1930E) records it from the North Ural Mountains.

South European Mountain Region : It is recorded from the Black Forest—Titisee (Schmeil), Pyrenees (Monard), Auvergne (Guerne and Richard), Cevennes (Pelosse)—and from a number of lakes in Switzerland. In the region of the Swiss Alps the lakes in which it occurs are rarely above 500 m. and are usually deep. While, therefore, common in the western mountain region, it is rare in the eastern Alps, and only recorded from Attersee, Bodensee and Mondsee. It is not found in the Tatra, but is recorded by Jungmayer from Hungary. Its most southern habitat is in the Moroccan Atlas mountains at 2000 m. (Kiefer, 1928).

It is generally recognized as a typical " Arctic-Alpine " species, of northern origin ; but its limited range to the east is not easily explained, having regard to the distribution of *D. denticornis*. The wider eastern range of *D. denticornis* and *D. bacillifer*, both of which are found in Scandinavia but are absent from Scotland, seems to show that these two are comparatively recent immigrants from the east, while *D. laciniatus*, *D. laticeps* and *D. wierzejskii* may be ancient northern species.

D. laciniatus is most closely related to *D. tatricus*, *D. kupelwieseri* and *D. appenninicus*, Brian, and it is replaced by the former in the eastern mountain region.

D. appenninicus, Brian, from Liguria, differs from *D. laciniatus* only in some minute details, and should be regarded rather as a variety of it than as a distinct species. The interest of its occurrence and of its difference from the type is concealed by giving it a separate specific name.

D. tatricus is widely distributed in the eastern highlands, generally at high altitudes, and is always found in small muddy pools, commonly associated with *Daphnia pulex*. It is considered by Brehm to be an eastern immigrant like *D. zachariæ*.

Bionomics.

Nothing is known of the life-cycle of the species in Scotland, since no continuous observations have been made on any loch in which it occurs. The only reference to it is that of Scott (1899, p. 187), who noted that it was not to be found in Loch Doon in winter.

A good deal of information is, however, available from other sources, and has been summarized by Tollinger (1911, p. 15). The reproductive cycle varies greatly with the locality. In the Swedish highlands (Ekman, 1904) only resting eggs are produced. The young appear about the end of June after the melting of the ice, and attain maturity towards the end of August, when reproduction begins.

Its biology has been closely followed in Lake Lucerne by Burckhardt (1914, 1920). The duration of life is about 12 months. In spring only young are found, and they become adult by the end of August. The maximum of adults is in mid-October. Egg-laying does not, however, begin till December. There is, therefore, a pause of 3–4 months after maturity as there is in *Limnocalanus macrurus*. Egg-laying takes place when the autumn circulation brings the temperature at about 50 m. to about 7° C. The period of reproduction will, therefore, depend to a considerable extent on the time at which this circulation occurs. In Lake Maggiore the maximum of egg production falls in April and May and the adults die off in July. The young of the next generation are adult by October–December, but do not produce eggs till spring. The cycle is much the same in Titisee (Häcker, 1902).

The evidence shows that it is a monocyclic species, but it is not clear to what extent it produces resting eggs in its southern habitats.

In Scandinavia it inhabits not only lakes, but also small tarns and pools. In the southern area, on the other hand, it is only found in lakes and is always a deep-water form, but with pronounced diurnal migration (Burckhardt).

In Scotland it appears to be confined to lakes of considerable size, but not much is known of its depth-range. In Loch Shin (August, 1928) it was found in very small numbers and only at depths of 50 ft. or more. On the other hand, in Lochs Shiel, Eilt and Ossian (July, 1923) it was abundant at the surface. The plankton collections of the Scottish Lake Survey were usually taken at the surface, and the species was often taken in considerable numbers.

Diaptomus gracilis, Sars.

(Figs. 183–200.)

1863. *D. gracilis*, Sars, Forh. Vidensk. Selsk, Christ. p. 218.
1863. *D. westwoodi*, Lubbock, Trans. Linn. Soc. XXIV, p. 203, figs.
1878. *D. castor* (in part), Brady, Mon. Brit. Cop. I, p. 51, pl. vi, figs. 7, 9, 10, 12, 13.
1890. *D. gracilis* var. *carnicus*, Senna, Boll. Soc. Ent. Ital. XXII, p. 104.
1892. *D. gracilis*, Brady, Trans. H.N. Soc. Northd. XI, p. 94, figs.
1892. *D. sanctipatricii*, Brady, *ibid.* XI, p. 99, figs.
1896. *D. gracilis*, Schmeil, Bibl. Zool. XXI, p. 67, figs.
1902. ,, Sars, Crust. Norway, IV, p. 92, pl. lxiii.
1913. *D. pusillus*, Brady, Proc. Zool. Soc. Lond. p. 231, figs.
1914. *D. sanctipatricii*, Brady, Trans. N.H. Soc. Northd. N.S. IV, p. 168, figs.

Female.—Length ·99–1·65 mm.

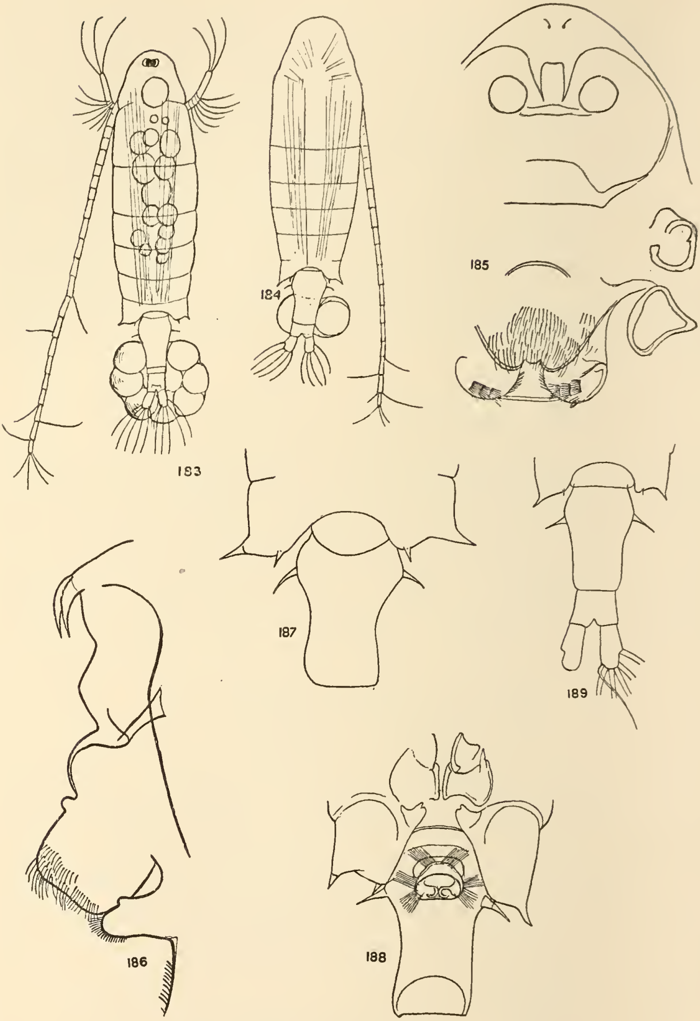
General form slender; thorax in dorsal view more or less parallel-sided, not markedly widened at any point. Th. som. 5 faintly marked off from som. 4, not greatly expanded, and nearly symmetrical. Outer angle on each side produced into a large spine directed outwards, or often outwards on one side and backwards on the other. A small spine on posterior edge, rather distant from outer spine. Abdomen of 3 somites, som. 2 very small and sometimes not separated. Genital somite widened anteriorly, about $1\frac{1}{2}$ times as long as 2 succeeding somites together, and bearing on each side a slender spine. Furcal rami symmetrical, with hairs on inner margin, not twice as long as wide (40 : 23). Upper lip thickly covered with hairs ; posterior margin deeply notched. Antennule very long, usually reaching beyond end of furcal setæ, but in some localities not reaching to end of rami. Relative lengths of setæ on segs. 1–4 :

Seg. 1.		Seg. 2.		Seg. 3.		Seg. 4.
21	.	16, 23, 17	.	41	.	17

Segs. 13–21 bear one seta each. Feathered setæ on segs. 22–25. Maxillipede slender, the endopod much longer than basis (42 : 33). Setæ of 4th coxal lobe all relatively short, the proximal one the longest. The 3 setæ of basis increasing in length from proximal to distal. Inner setæ of endopod slender. Outer seta of seg. 5 and 3 terminal setæ of seg. 6 very long and feathered. Leg 5, coxa with very large hyaline spine. Endopod much shorter than exopod 1, either unsegmented or 2-segmented ; apex with 1 or 2 small setæ and some delicate hairs. Exopod 1 about $2\frac{1}{2}$ times as long as wide ; exopod 2 longer than seg. 1, slightly curved and tapering to a fine point ; seg. 3 distinct, bearing a spine and a seta. The relative length of these is variable, but generally the spine is about $\frac{1}{3}$ the length of the seta, which generally extends to end of seg. 2.

Male.—Length ·98–1·5 mm.

Thorax gently tapering posteriorly, som. 5 not expanded but pointed on either side, the right side rather more produced than left. Soms. 1 and 4 of abdomen slightly asymmetrical, a little dilated on right side. Furcal rami longer than in female (24 : 10). Prehensile antennule with spines on segs. 14, 15, 16, rather variable in size, but always present. Spine of



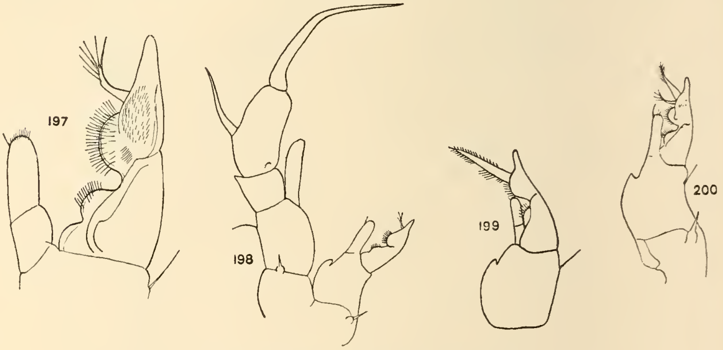
Figs. 183–189.—*Diaptomus gracilis.*

Fig. 183.—Female, dorsal view. Ormesby.
Fig. 184.—Female, dorsal view. Loch Ness.
Fig. 185.—Head and labrum, ventral view, female.
Fig. 186.—Head and labrum, lateral view.
Fig. 187.—Th. som. 5, female, dorsal view, typical form. Scotland, L. Lait.
Fig. 188.—Th. som. 5 and genital somite, ventral view, showing genital operculum.
Fig. 189.—Th. som. 5. Ennerdale. Wings reduced.

FIGS. 190–196.—*Diaptomus gracilis.*

FIG. 190.—Abdomen of male.
FIG. 191.—Antennule, female, Norfolk.
FIG. 192.—Antennule, male, segs. 13–25. Small form from Loch Ness (*D. pusillus*, Brady).
FIG. 193.—Antennule, male, typical; seg. 23.
FIG. 194.—Maxillipede.
FIG. 195.—Leg 5, female.
FIG. 196.—Leg 5, male. Loch Awe.

seg. 15 generally the largest. Seg. 23 generally with a hook-like process, very variable in size, and often absent. The presence or absence of the hook generally characterizes all the individuals in a population, but there may be some individual variation also. Leg 5—coxa of each leg with a papilla bearing a slender sensory spine. Right leg—basis about $1\frac{1}{2}$ times as long as broad, without hyaline lamella; exopod 1 as broad as long, outer angle very slightly produced, and either acutely pointed or bluntly rounded; exopod 2 rather narrow, the greatest width not much exceeding half the length (24 : 43); lateral spine inserted nearer base than end (24–27), rather short and strongly curved. Terminal claw long and slender, not evenly curved, but sharply bent inwards a little beyond the middle. Endopod unsegmented, swollen and reaching about to insertion of lateral spine of seg. 2. Left leg: Basis very broad, with a small inner hyaline lamella in the form of a hook. Exopods 1 and 2 fused, each with hairy inner pad; seg. 2 with short, blunt finger-like process and hairy pad on posterior face (Fig. 197). Inner spine curved, and bearing at end a brush-like group of long hairs. Endopod about as long as exopod 1.



Figs. 197–200.—*Diaptomus gracilis.*
Fig. 197.—Leg 5, left, showing hairy pads. Loch Lait.
Fig. 198.—Leg 5. Loch Ness. Small form (*D. pusillus*).
Fig. 199.—Leg 5, abnormal. Loch Chlair.
Fig. 200.—Leg 5, abnormal. Leeds.

VARIATION.

Although *D. gracilis* is so widely distributed, and occurs in such a variety of waters, it does not vary to any marked extent. There is variation in size and colour, but in structure it is very constant. Such variation as there is in the form of th. som. 5 is small, and concerns generally the direction in which the outer spines point. This somite is always much more expanded than in *D. graciloides* * (Fig. 219).

In Loch Ness a race of *D. gracilis* is found which differs from the ordinary type in its small size, delicacy and transparency. In some of the samples taken by the Scottish Lake Survey two distinct races were present together, and the difference in size was very striking:

	Female.	Male.
Small form . .	·99–1·2 mm. .	·98–1·17 mm.
Large form . .	1·4 mm. .	1·26–1·35 mm.

The females carried egg-sacs containing only one or two eggs of relatively large size (Fig. 184). There is, however, no appreciable difference in structure between the two forms, except with regard to the process on seg. 23 of the prehensile antennule, which is small and not hooked in the small form. The endopod of the male right leg is rather less swollen. It is certainly this race which was described by Brady as *D. pusillus*. I have examined a type slide prepared by him, and find the specimen to be *D. gracilis*. Brady's drawings of the 5th leg are not correct. Brady (1893, p. 32) states that he has seen specimens lacking the brush-like termination of the inner spine in the male left leg, mentioning, among other localities, Floutern Tarn. I have collected in this tarn myself, but have not seen any such specimens. On the other hand, abnormalities in the structure of the left leg are occasionally met with, involving a transformation of this spine and disappearance of the

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* This is true for North European races, but may not hold good in the Mediterranean region, where transitional forms have been described. These races will be referred to below when dealing with *D. vulgaris*.

terminal brush (Fig. 199). A specimen from a pond near Leeds had 2 inner spines (Fig. 200).

A curious case of abnormality is recorded by Nordquist (1889), this specimen, having the general form of a female as regards th. som. 5 and abdomen, and also apparently functioning as a female, since it bore spermatophores, yet had a prehensile antennule and leg 5 of the male form. This leg was not, however, normal. Instead of the usual terminal claw there was a small 3rd segment bearing 2 long spines.

Colour Variation.

The colour is extraordinarily variable, without apparent reason. In Scotland it is possible to find the *Diaptomus* of lochs apparently similar and adjacent of quite different colour. In large clear lakes the animal is commonly colourless, or faintly tinged with blue; but in smaller lakes and shallow waters it may be dark brown, blue or red. Murray, in his notes on the Scottish Lake Survey, gives a number of observations on colour. The most striking colour variety which I have met with was found in a small tarn at 2000 ft. on Ben Dubchraig (Tyndrum). Here the animals were of so dark a red that they looked black to the naked eye.

Distribution in Britain.

Throughout the British Isles *D. gracilis* is the characteristic *Diaptomus* of lakes, both large and small. It may even be found in ponds, but has a distinct preference for open water. In eastern England it is largely replaced by *D. vulgaris* in ponds or where water plants reach the surface, but both species may occur together in the weedy waters of the Broads.

In Scotland it is almost universal, and I have found it even in small peat pools, *e. g.* on the moor at Corrour. It is, however, entirely absent from the Orkneys* and

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* Murray states that it has been found in two lochs in the Orkneys. I have examined all the Survey collections from Orkneys and Shetlands which are preserved without finding it. Murray does not give the names of the lochs.

Shetlands and the islands of Uist and Barra, but is found commonly in Lewis and in almost every loch in Jura. Scott found this the only species in Mull.

In the Norfolk Broads its distribution is peculiar. It is abundant in the closed Broads, such as Ormesby, and also in South Walsham and Ranworth, two adjacent Broads connected with the River Bure; but above Ranworth it seems to disappear, and is not found in Salhouse and Wroxham Broads, where *Eurytemora velox* is the only Calanoid. In other respects the plankton of all these waters seems very much the same. In Sutton and Barton Broads, where there is practically no true plankton, it is again common, and it is occasionally taken even in Hickling, where the water is of high salinity.

A similar example of inexplicable distribution is found in Jura. In 20 lochs in the centre of the island *D. gracilis* was present in 16 at all levels to 800 ft. It was absent from three high tarns at 700–800 ft., possibly owing to elevation and exposure; but there was no apparent reason for the absence of any *Diaptomus* in Loch an Arcill, which lies low and seems perfectly well suited to it.

DISTRIBUTION ABROAD.

This is perhaps the commonest European species, with its centre of abundance in central Europe. South of the Alps it is almost entirely replaced by the so-called *vulgaris-graciloides* forms, but is recorded by Roy for the Côte d'Or. In Scandinavia it is confined to the south of Sweden and Norway, but it extends on the east of the Baltic northwards through Finland to Kolguev, its most northerly habitat (Zykoff, 1904). It is not recorded from Spain, and in France it is very rare. In the south-east it is widely distributed in the eastern Alps to a height of 2300 m., and is found in many places in Austria and Hungary, but not south of the Danube. Eastward it ranges over Russia to Omsk and Tobolsk.

ASSOCIATION WITH OTHER SPECIES.

D. gracilis is frequently found associated with other species (*e. g. D. laticeps*) in the Scottish lochs; and in Norfolk it is sometimes found with *D. vulgaris*. I have found it with *D. vulgaris* also in the Naardermeer in Holland. It is not, however, found as a rule in company with the closely allied species *D. graciloides*. These two species do, however, occasionally live together, for Levander and Wuorentaus (1918) give four records of samples from Finnish lakes containing both species.

BIONOMICS.

Tollinger gives a full summary of the facts regarding the reproductive cycle. The species generally persists throughout the year, and reproduction continues in some cases in winter. On the other hand, it may either cease in November, or the eggs produced in winter may be carried unhatched until spring. The actual course of the seasonal cycle varies a great deal with the locality and the facts are sometimes difficult to interpret. Wolf (1905) found two well-marked-periods of intenser reproduction, one in May–July, and the other in December–April. The sudden rise in numbers in May was due to hatching of retarded winter eggs. In the Danish lakes (Wesenberg Lund, 1904) there seems to be no well-marked sexual period, but females with eggs were most numerous in May. In the majority of cases there is evidence of two maxima, in spring and autumn. According to Haempel (1918) the *Diaptomus* maximum in Hallstattersee is preceded by a maximum of *Cyclotella* and *Asterionella*, and the oil-globules found in the bodies of the Copepods are derived from the Diatoms.

The number of eggs varies partly with the season and partly with the size of the water, being least in large lakes and in summer. Thus the small form of Loch Ness has at most 4 eggs, and usually two. Rzoska (1925) found 22–28 in May, but only 4–6 in July, when the greatest number of females were breeding.

Spandl (1926c, p. 14) gives an account of the life-cycle of two colonies in neighbouring ponds. In one of these, which was relatively deep and weedless, the *Diaptomus* was perennial, with a slight maximum at end of June. In the shallower pond the maximum in June was followed by a rapid fall and disappearance in August. The disappearance was caused by the spreading of weeds over the open water. The pond was recolonized each year from the neighbouring pond by flooding, and, in a particularly dry year, when communication was not established, no *Diaptomus* appeared. This seems to be proof not only of the absence of resting eggs, but also of limited power of dispersal.

In the English lakes the evidence is rather contradictory. In some cases there is a definite summer minimum, and a great maximum in spring. Thus in Coniston it was dominant in January–April, rare June–August, but abundant and in full breeding in September. The same in Crummock. On the other hand, in Ennerdale it was abundant in all collections with the exception of February, and no fluctuations were observed. In Windermere there was a marked minimum in May and June, great abundance July–October, and a decline in November. It was abundant in the following March, so that there appear to have been two maxima, both earlier than in Coniston. Windermere is a lake of more evolved type, and may warm up earlier. Southern and Gardiner (1926) give the results from observations in the Shannon and Lough Derg. They found two maxima, one in winter (December–January) and the other in June–July. They noted remarkably uneven distribution in the lake. Thus in one day at seven stations the numbers varied from 410 to 18,440 per cubic metre. Dakin (1913) found in Lough Neagh a maximum in spring and another in autumn; but in this case the numbers were large throughout the year, whereas they were small in Lough Derg except at the maxima. In Ormesby Broad in Norfolk I find two rather ill-defined maxima in February–April and September, but numbers are always rather large.

SEASONAL VARIATION.

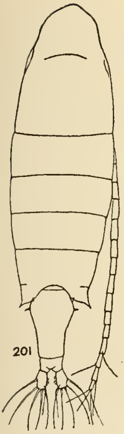
Brehm and Zederbauer (1906, p. 26) found that, in summer, the process on seg. 23 of the prehensile antennule is longer than in winter, and Haempel (1918, p. 284) found a process present in summer but absent in winter. I have been unable to trace any such seasonal change in this country. In Ormesby Broad there is individual variation in the size of this hook which is quite unconnected with the season. On the other hand there is a definite relation of size to season. The maximum size is reached in April—average, female 1·5 mm., male 1·41 mm. The size decreases to a minimum in September—female 1·25, male 1·14 mm.

Diaptomus vulgaris, Schmeil.

(Figs. 201–218.)

1853. (?) *Cyclopsina cœrulea*, Fischer, Bull. Soc. Moscou, XXVI, p. 75, figs.
1889. *D. cœruleus*, De Guerne & Richard, Mem. Soc. Zool. Fr. II, p. 65, figs.
1896. ,, Schmeil, Bibl. Zool. XXI, p. 59, figs.
1897. *D. vulgaris*, Schmeil, *ibid.* Nachtrag, p. 168.
1903. *D. cœruleus*, Sars, Ann. Mus. St. Petersb. VIII, p. 210, figs.
1911. *D. vulgaris*, Tollinger, Zool. Jahrb. Syst. XXX, p. 97.
1929. ,, Gurney, Int. Rev. Hydrobiol. Leipzig, XXII, p. 353, figs.
1930. *D. cœruleus*, Rylov, Zool. Anz. LXXXVIII, p. 111, figs.

It is unfortunate that the correct name of this species remains in doubt. Fischer's species is not recognizable from his description and figures except by inference; but that he actually was dealing with the species in question is rendered almost certain by the discovery by Rylov of a form of *D. vulgaris* in waters round St. Petersburg which Fischer himself mentioned. But if, for this reason, we accept Fischer's species as adequately described or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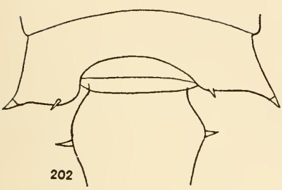
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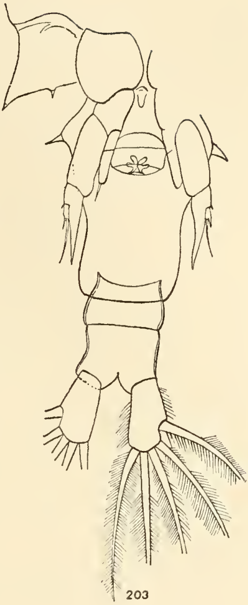
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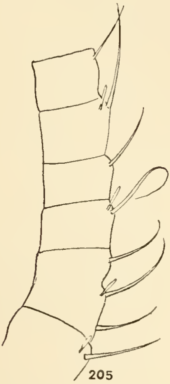
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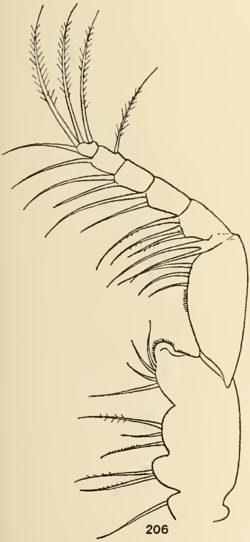
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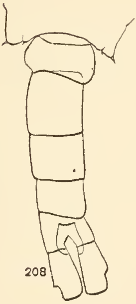
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FIGS. 201–209.—*Diaptomus vulgaris.*

(All figures from Norfolk specimens.)

FIG. 201.—Female, dorsal view.
FIG. 202.—Th. som. 5, dorsal view.
FIG. 203.—Abdomen, ventral view.
FIG. 204.—Upper lip, side view.
FIG. 205.—Antennule, female, segs. 1–6.
FIG. 206.—Maxillipede.
FIG. 207.—Leg 5, female.
FIG. 208.—Th. som. 5 and abdomen, male.
FIG. 209.—Antennule, male.

at least determined, the name is still, according to Schmeil, invalid on the ground that Fischer erroneously supposed his species to be identical with Müller's *Cyclops cœruleus*. Article 31 of the International Rules lays down that "a specific name which undoubtedly rests upon an error of identification can not be retained . . . ." On the other hand, it might be urged that Fischer's name should be retained on the ground that, while it is impossible to recognize Müller's species, it is equally impossible to deny the identity. We should then be in the absurd position of having to call this form *D. cœruleus* (O.F.M.), although it is only now, after Rylov's redescription, that it is possible to recognize it with certainty. There is no rule which permits Fischer to be regarded as author of the name. Schmeil's name is therefore used here, as no ambiguity whatever attaches to it, and it has been generally accepted.

Female.—Length about 1·5 to 2 mm.

In dorsal view the thorax is rather slender, the greatest width in the 1st or 2nd free somite, and narrowing slightly behind. Last somite partly fused with the 4th, and with posterior projections or wings not very prominent. The exact form of this somite is rather variable, but it is usually nearly symmetrical, with an apical point on either side; but the projection on the right side is a little more pointed than that of the left. Abdomen about one-third the length of the thorax, of 3 or 2 somites. The 2nd somite is generally present, but so much reduced as to be sometimes invisible from above. Genital somite little dilated, with a short thick hyaline spine on either side. Antennule reaching just beyond the end of the furca. Segs. 10 to 21 have each one seta, and the relative length of them is as follows (specimen from Sutton Broad):

1	2	3	4	5	6	7	8	9	10	11	12	13
13·5	15·5 23 18	35	19·5	25	12	38	21	22 39	20	51	24	29

14	15	16	17	18	19	20	21	22	23	24
52	31	16	23	50	18	22	56	8+29	12+64	54+58

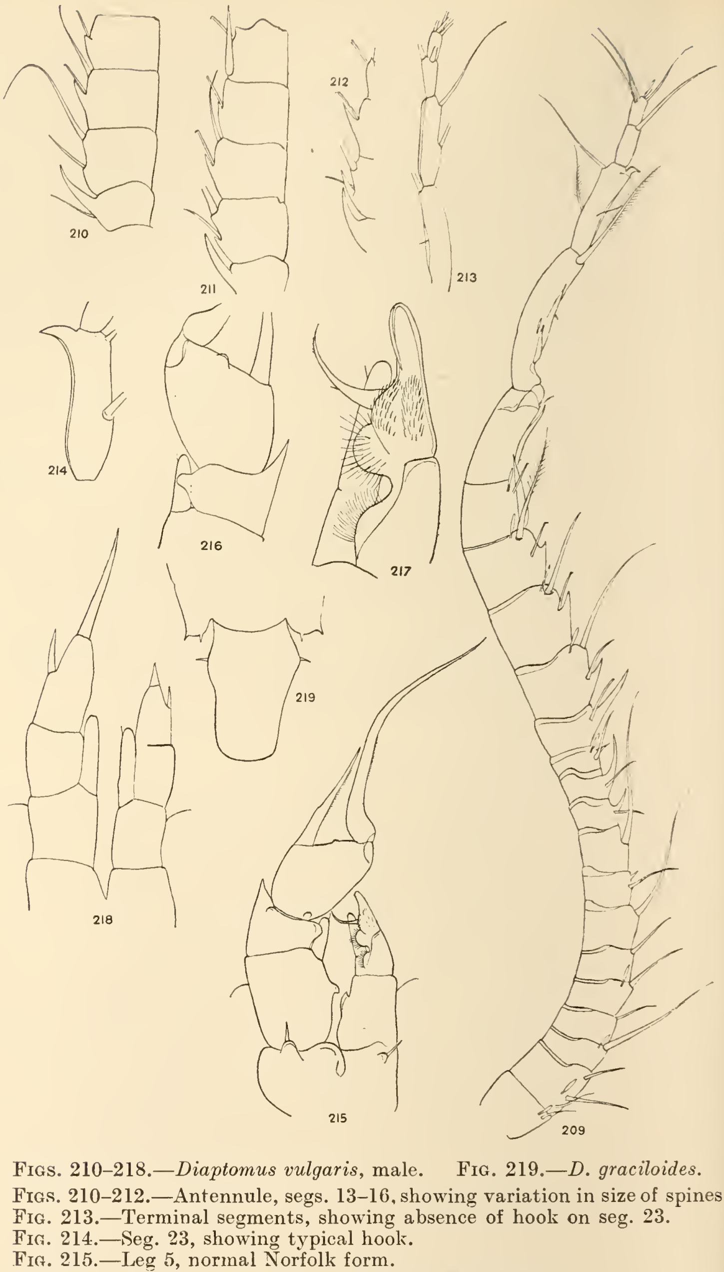
The length of a seta is not always precisely measureable, but the figures given are, I think, as accurate as possible, and characteristic for Norfolk specimens. Maxillipede with endopod about equal to coxa. The lengths of the setæ on the basal joints are not greatly dissimilar, but there is some variation even among specimens from the same neighbourhood. The relative lengths of the setæ in the first three groups in a female from Langmere were :

Group 1.	Group 2.	Group 3.
16–23 .	21–11·5–20 .	18·5–7–9–8·5

Leg 5 with a large hyaline spine on basal segment. Endopod 1- or 2-segmented, shorter than seg. 1 of exopod. Its end falls short of the end of this joint usually by about one-fourth of the latter. It is slender, with one or two terminal setæ and a ring of small hairs. Second segment of exopod a strong sinuate claw ; seg. 3 well developed and bearing a spine and seta, of which the relative lengths are about 4 and 12.

Male.—Length 1·3–1·8 mm.

Antennule : Segs. 14, 15, 16 each have a spine, that of 15 being the largest ; the spine of 16 very small, sometimes almost obsolete. Seg. 23 may have a simple, rather broad hyaline membrane, but usually this membrane is very narrow or absent, and the joint itself is produced into a short hook-like process. The presence or absence of this hook is, as Schmeil has pointed out, an individual variation, both forms of antenna being found in a single population. Leg 5 : Coxa of each leg with a very slender hyaline spine on the posterior face. That of the right leg generally stouter than that of the left. Basis in both legs with a small process on inner margin. In the right leg this is in the form of a rounded knob. In the left leg it may be a forwardly directed hook-like process, or it may take the form of a rounded hyaline lamella, or again it may even



FIGS. 210–218.—*Diaptomus vulgaris*, male. FIG. 219.—*D. graciloides*.

FIGS. 210–212.—Antennule, segs. 13–16, showing variation in size of spines

FIG. 213.—Terminal segments, showing absence of hook on seg. 23.

FIG. 214.—Seg. 23, showing typical hook.

FIG. 215.—Leg 5, normal Norfolk form.

FIG. 216.—Right leg, with very acutely pointed exopod 1.

FIG. 217.—Left leg, showing hairy pads on posterior face.

FIG. 218.—Leg 5, copepodid stage V.

FIG. 219.—*Diaptomus graciloides*, th. som. 5 and genital somite. Co-type from Sweden. (Norman Collection.)

be absent. These differences do not apparently characterize populations. In the right leg exopod 1 is produced on the outer side into a strong spinous projection, and, on the inner side (posterior face), it bears a round hyaline process. Exopod 2 is very broad. The relation of width to length varies within a single population from 1·05 to 1·45. Outer spine, which is inserted about the middle of the segment, very strong, nearly straight, and about the same length as the segment. It may be a little shorter or, more rarely, a little longer. Generally, but not always, the spine narrows rather suddenly, giving a characteristic notched outline to its posterior face. Between the outer spine and the terminal claw there is commonly a small chitinous knob. This knob may be present in the majority of the individuals of a population, but never in all. Endopod small, unsegmented, extending slightly beyond exopod 1. Terminal claw not greatly swollen at base, nor greatly curved. It is about 2½ times as long as the outer spine. The curvature is variable. Left leg with terminal process rather short and blunt. Inner seta curved, generally smooth, but sometimes with very minute hairs along posterior edge. Exopod 2 with a hairy ridge on posterior face.

The following figures show the rate of growth and average size of the adult. Locality: Ringmere, Norfolk, April 12th, 1928.

Nauplius stages.		Copepodid stages.			
I.	·175 mm.	I.		·52 mm.	
II.	·205 ,,	II.		·69 ,,	
III.	·224 ,,	III.		·89 ,,	
IV.	·28 ,,	IV.	Male	1·06 ,,	
V.	·322 ,,		Female	1·15 ,,	
VI.	·37 ,,	V.	Male	1·32 ,,	
			Female	1·44 ,,	
		VI.	Adult:		
			Male	1·5 ,,	(1·38–1·73)
			Female	1·7 ,,	(1·45–1·93)

Distribution in Britain.

D. vulgaris is very common in Norfolk, both in the Broads district and throughout the county. In the Broads district it may occur in company with *D. gracilis*, but is usually confined to weedy ditches and not found in plankton. In the Breckland near Thetford it occurs in the meres without *D. gracilis*. Outside Norfolk I have found it in ponds in Suffolk, Cambridgeshire (near Wicken), at Ross in Herefordshire and in the New Forest. Mr. Scourfield records it from Epping and Richmond. It seems to be characteristic of the eastern counties, from which it is in process of spreading, and may be a recent immigrant of the "Germanic" type.

Distribution Abroad.

Sweden (DeGuerne and Richard, p. 66), but absent from Norway.

Denmark: Rare (Jensen, 1905).

France: Generally distributed, and ranging south to Côte d'Or (Roy, 1922).

Germany: Common in south and west.

Holland: Haarlemmermeer, etc. (Van Breemen), Nardermeer (*transylvanicus*-form), Haren (Gurney).

Switzerland: In lowland of Rhine valley (Graeter), up to 1595 m. (Thiébaud, 1915).

Austria and Hungary: Bohemia, Tirol, Carinthia (up to 1800 m., Steuer, 1897). Croatia (Krmpotic). In Eastern Alps only in Veldeme (Pesta, 1924).

Balkans.

Russia: Moscow, North Russia (Rylov, etc.).

Siberia and Central Asia (Sars).

Mesopotamia (Gurney).

Italy: Astronisee (Brehm).

North Africa (*D. ziegelmayeri*, *D. chappuisi*, *D. numidicus*).

VARIATION.

Steuer (1900) was the first to draw attention to the minute differences which may be found between certain races of this species, and subsequent intensive study has shown that there exist in Europe south of the Alps a number of races which, while resembling *D. vulgaris* in most respects, may also have some of the characters of *D. graciloides.* Indeed the relation of some of these forms is still obscure.

The following list of varieties or of species which seem to come within this "*graciloides-vulgaris*" group shows not only how rich the south European and north African region is in these forms, but also the difficulty which has been found in placing them :

1891. *D. transylvanicus*, Daday, Termes. Fuz. XIII, p. 122, figs.
1897. *D. intermedius*, Steuer, Verh. zool. bot. Ges. Wien, XLVII, p. 621, figs.
1900. *D. graciloides* var. *padana*, Burckhardt, Rev. Suisse Zool. VII, p. 646, figs.
1900. *D. vulgaris* vars. *intermedius*, *scutariensis*, *transylvanicus*, Steuer, Verh. zool. bot. Ges. Wien, CIX, pp. 316–332, figs.
1902. *D. etruscus*, Losito, Boll. Soc. Zool. Ital. X, p. 150.
1904. *D. steueri*, Brehm and Zederbauer, Verh. zool. bot. Ges. Wien, LIV, p. 637, figs.
1909. *D. numidicus*, Gurney, J. R. Mic. Soc. Lond. p. 295, figs.
1911. *D. v.* var. *verrucosa*, Brehm and Ruttner, Arch. Hydrob. Plankt. VI, p. 95, figs.
1924. *D. ziegelmayeri*, Brehm, Zool. Anz. LIX, p. 310, figs.
1926. *D. chappuisi*, Kiefer, Zool. Anz. LXVI, p. 263, figs.
1928. *D. gracilis* vars. *æmiliana* and *ligustica*, Brian, Mem. Soc. Entom. Ital. VI, pp. 31, 34, figs.

It is impossible to enter here into a discussion of the problem in detail,* but certain points may be dealt with. In the first place, it has not been sufficiently realized that even in north Europe the species is variable. The form described by Rylov, which he claims as typical for the species, is, in respect of the 5th th. somite of the female, almost indistinguishable from *D. graciloides*, while leg 5, male, is practically identical with that of the *transylvanicus* form. A race which has all the characters of *transylvanicus*

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* For fuller discussion see Gurney, 1929. Baldi (1931) has now restated the whole case most fully, but concludes that no final judgment is at present possible. *D. larianus*, Baldi (1925), is not included in the list above as I have been unable to find the description of it.

also lives in Holland (Naardermeer), and the same form is recorded from Basel. Lepeschkin's var. *sibirica* seems also to be identical with it. No real distinction can be drawn between *intermedius* and *transylvanicus*, and *scutariensis* is linked up with the type by forms described by Krmpotic and another found in Mesopotamia. Probably *D. chappuisi* and *D. ziegelmayeri* are slight modifications of the *scutariensis* form. Finally I must refer to a form described by Brehm (1906, p. 227) from Karlsbad and later (1911) from Grenoble, which differs from the type only in the presence of a small knob between the outer spine and terminal claw in leg 5, male. The same form also occurs in Central Asia (Sars, 1903), and Brehm speculates on the possibility that this is another case of the westward migration of Asiatic forms. He states (1920) that the same form is found in the Balkans, and that the knob characterizes local races. As stated above, I find this knob to be characteristic of Norfolk specimens, but by no means always present. I find it also in specimens kindly sent to me by Dr. Kiefer from Villingen and Constanz. This small but very definite character seems to be of sporadic appearance and to have no zoogeographical interest. It seems that we are dealing with a species which is variable throughout a very wide range, giving rise to independent races with the same characters, but without genetic connection or geographical significance. On the other hand, it is possible that *D. vulgaris* is a preglacial species of the lowlands which survived the glacial period in two separate centres—the south of France and the Balkan region—and that the eastern survivors have spread west and north, and have become adapted to life in large lakes with consequent modification in the direction of the limnetic *D. graciloides*.

VARIATION IN COLOUR.

Red, blue and white races have been recorded, but all that I have seen myself have been either blue or orange red.

Wolf (1905) found a red and a blue race of which the life-cycles were distinctly different. Blaas (1924) describes two races, one very red and the other chalk-white. These were very large forms (in both cases over 3 mm.), but the red one was the larger and lived in richer conditions (with *Daphnia pulex*, etc.). The two sexes may differ in colour : I have seen the male orange red while the female was pale blue.

Bionomics.

In Norfolk, and indeed apparently generally, the species survives the winter and is polycyclic, reproducing even in winter. On the other hand Wolf has recorded a monocyclic form. Roy (1927) found eggs all the year round, but a maximum in May to August and minimum November to January. Hartwig (1901) found it in temporary pools, and in these pools of larger size than in perennial waters.

Diaptomus laticeps, Sars.

(Figs. 220–234.)

1863. *D. laticeps*, Sars, Forh. Vidensk. Selsk. Christ. p. 219.
1889. ,, De Guerne & Richard, Mem. Soc. Zool. Fr. II, p. 117.
1892. *D. bacillifer*, Brady, Trans. N.H. Soc. Northd. Durh. XI, p. 98, pl. xiv, figs. 9, 11, 12.
1892. *D. hircus*, Brady, *ibid.* p. 100, figs.
1897. *D. laticeps*, Schmeil, Bibl. Zool. XXI, Nachtrag, p. 174, figs.
1899. *D. hircus*, Scott, Rep. Fish. Bd. Scot. XVII, p. 188, pl. xiii.
1902. *D. laticeps*, Sars, Crust. Norway, IV, p. 90, pl. lxi.

Some doubt has been expressed as to the identity of the British form, *D. hircus*, Brady, with *D. laticeps*, Sars, but no doubt remains. I have examined specimens from Lesje Vand (one of the Norwegian type localities given by Sars in 1863) and find complete agreement, with the exception that the form of the process on seg. 23 of the male antennule differs slightly from that usual in Scottish specimens. I have also seen Brady's types of *D. hircus*, and have collected specimens from Goat's Water, from which his types were taken. The specimens from Loch Earn* referred by Brady to *D. bacillifer* are actually *D. laticeps*; *D. bacillifer* has not been found in this country.

Female.—Length 1·15–1·6 mm.

General form rather robust; dorsal outline in side view sloping rather steeply upwards from the front to a point about middle of cephalothorax, where there is rather a distinct angle. Outline from that point continues straight to end of 1st free somite, then sloping in gentle curve to end of thorax. Seen dorsally, greatest width about the mandibular region of the head; width to length about as 26 to 74. Fifth th. somite not at all expanded laterally, but projecting backwards on either side as a pair of small lobes, each bearing 2 small spines. Abdomen apparently of 2 somites only. In some cases soms. 2 and 3 may be indistinctly separated, but there is usually no line of division. Genital somite scarcely dilated anteriorly, bearing on either side a small blunt spine. Furcal rami rather long and narrow (about 16 : 33). Antennule variable in length, usually not reaching to the furca, but sometimes extending beyond it. Segs. 11 and 13 with 2 setæ; segs. 14–19 with 1 each. Maxillipede slender, the lengths of setæ on basis as shown in Fig. 234. Leg 5: Basis with small spine; endopod usually about half length of exopod 1, but sometimes about two-thirds of its length; generally rather thick and constricted near base as if imperfectly 2-segmented, in some cases distinctly divided. Exopod 3 distinct, bearing 2 spines, of which the outer is about one-third the length of the inner one. Terminal claw stout, with fine marginal denticulation.

Male.—Length 1·05–1·4 mm.

General form of head and thorax as in female. Th. som. 5 scarcely at all produced backwards. Abdomen almost symmetrical, som. 1 with a spine on right side. Prehensile antennule with large spine on seg. 14, but

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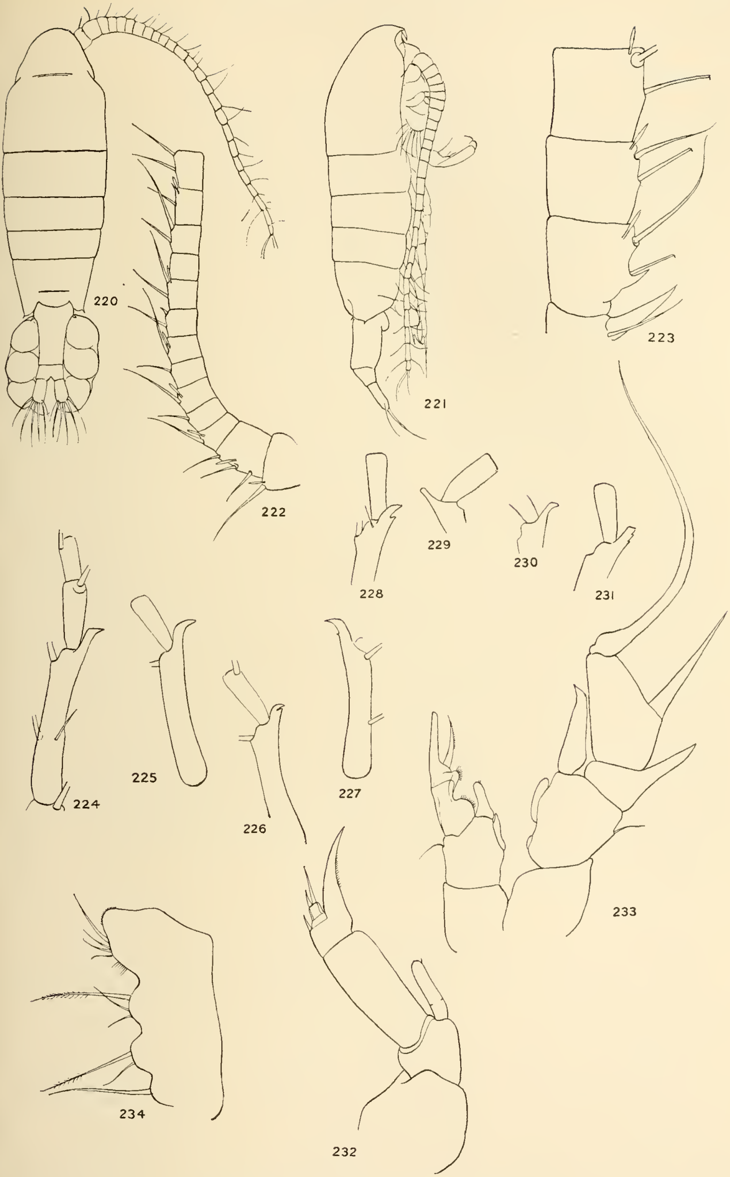
* The Scottish Lake Survey found *D. gracilis* only in Loch Earn (Murray, 1904, p. 57).



Figs. 220–234.—*Diaptomus laticeps.*

Fig. 220.—Female, dorsal view.
Fig. 221.—Female, lateral view.
Fig. 222.—Antennule, female, segs. 1–13.
Fig. 223.—Antennule, male, segs. 13–16.
Fig. 224.—Antennule, male, segs. 22–25. Loch Hundland.
Figs. 225–227.—Seg. 23. Loch Kirbister, Orkney.
Fig. 228.—Seg. 23. Loch Moracha (Uist).
Figs. 229, 230.—Loch Ness.
Fig. 231.—Gorm Loch Mor.
Fig. 232.—Leg 5, female.
Fig. 233.—Leg 5, male.
Fig. 234.—Maxillipede.

none on segs. 15 and 16. In some cases the spine on seg. 14 may be very small (some specimens from North Uist). Seg. 23 with a process of very variable form. Typically it has the shape of a bill-hook, about one-third as long as seg. 24. It may, however, be perfectly straight, bifid at the end, or with a small tooth on the margin. Various forms are shown in Figs. 225–231. In no case, either in Scottish specimens, in specimens from the Lake District or in Brady's types, have I seen any trace of the crenulated margin described by him. Leg 5: Coxa of right leg with a small protuberance bearing a spine, but no spine on left leg. Basis of both legs with inner hyaline lamella which may be entire, or may be deeply indented or bilobed. Exopod 1 of right leg produced outwards into strong spinous process. Exopod 2 constricted distally, and bearing a long spine about middle of outer margin. There is a small hyaline lamella on the posterior face at base of outer spine. Terminal claw very long and conspicuously curved. Endopod unsegmented, rather swollen at base, and slightly curved outwards, pointed distally. In left leg endopod extends to near end of exopod, conical in shape. Exopod with 2 inner hairy pads and terminating in a long finger-like process, at the base of which is a long slender spine directed almost parallel to it.

Colour: Either blue or red.

Variation in Size.

The length is extremely variable, as the following figures show:

Orkneys :—	Female.	Male.
Loch Hundland	1·12–1·6 mm. (av. 1·34)	1·05–1·4 (av. 1·19)
Loch Harray	1·15–1·44 „ (av. 1·27)	1·05–1·29 (av. 1·16)
North Uist	1·27–1·5 „ (av. 1·4)	Av. 1·29
Loch Ness	About 1·18 mm.	

The range in size in Loch Hundland is so great that it seems necessary to suppose that in some cases there is a moult in the adult to a "high form," or stage VII, which is not distinguished by structural change (see above, p. 129).

DISTRIBUTION IN BRITAIN.

Orkney Islands: The lochs of Pomona or Mainland are all shallow and low-lying. Loch Harray is even subject to influx from the sea, and the highest loch is Hundland, at 89·7 ft. The only species of *Diaptomus* found is *D. laticeps*. In the island of Rousay, just north of Mainland, *D. wierzejskii* alone is found. The lochs here lie at about 300 ft., and are narrow, rocky lochs unlike those of Mainland.

North Uist: The Scottish Survey collections were made at end of May or beginning of June, and adult *Diaptomus* were generally few. In many lochs no adults were taken, and in some of these the species was not identified. In 20 lochs in which the species were identified* *D. laticeps* occurred in 12 and *D. wierzejskii* in 11. The two species were found together in Lochs Scadavay, Caravat and Moracha. All these lochs are near sea-level, the highest being 35 ft. above it; all are shallow, and some are influenced by the tide. It is worth noting that *D. laticeps* was found only in lochs containing *Holopedium*, while *Holopedium* was generally absent from those in which *D. wierzejskii* occurred alone.

Skye: Loch Lonachan; Loch an Eilein (Lowndes, 1930).

Lewis: In 10 lochs (Murray).

It has not been found in the islands of Jura or Mull.

Scotland—the mainland: The Scottish Lake Survey has 46 records of it from Perthshire, Inverness, Sutherland, Caithness, Ross-shire, Argyll and Edinburgh, at all elevations up to 2500 ft. (in Perthshire). It is found, in company with *D. gracilis*, in all the lochs of the Caledonian Canal system, and in some of those on the south side of the Glen, but not on the north side (Murray). It is to be regretted that it is impossible to recover, from Murray's short published notes, the exact distribution, and his records appear to be lost.

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* My own determination.

From the Shin Basin in Sutherland collections from 9 lochs are preserved and contain the following species :

Lochs.	*D. gracilis.*	*D. laciniatus.*	*D. laticeps.*	*D. wierzejskii.*
Shin	+	+	..	..
Merkland	..	+	..	..
a'Ghriama . . .	+	+	+	..
Fiog	*	..	+	..
Ailsh	*	+	+	..
Craggie	..	+	..	..
An Daimh . . .	..	+	+	..
Gorm Loch Mor . .	*	..	+	+
An Lagain . . .	+	..	..	..

* Recorded by Murray. Not now in the samples.

Ireland : Lough Mask ; Lough Corrib ; The Rosses, Sligo (Kane) ; Lough Erne (R.G.).

Wales : Llyn Padarn and Llyn Idwal (Scourfield).

England, Lake District : Goat's Water, a small tarn at a height of 1646 ft., above Coniston. Hawes Water, the highest of the lakes, 694 ft. (Gurney).

Distribution Abroad.

Norway : In a number of lakes up to 1500 m. (Sars, Huitfeldt-Kaas).

Sweden : Not found in the south. Found, but not very commonly, in the conifer and birch region of the north Swedish highlands up to 700 m. (Ekman).

Carniola : Wocheiner See, Julian Alps (Langhans).

Herzegovina : In a lake at 250 m. (Brehm and Ruttner).

Serbia : Balkans (Gjorjewic).

Croatia and Slavonia : Srjem and Kupmovo (Krmpotic).

It is a distinctively northern species, and its occurrence in the Julian Alps and Balkans and not in the western Alps is difficult to explain. Gjorgjewic suggests transport by birds, but this explanation is not very convincing.

Diaptomus wierzejskii, Richard.

(Figs. 235–247.)

1888. *D. wierzejskii*, Richard, Bull. Soc. Zool. Fr. XIII, p. 45.
1888. *D. serricornis*, Lilljeborg, Bull. Soc. Zool. Fr. XIII, p. 156.
1889. *D. wierzejskii* and *D. serricornis*, De Guerne and Richard, Mem. Soc. Zool. Fr. II, pp. 35, 37.
1892. *D. serricornis*, Brady, Trans. N.H. Soc. Northd. XI, p. 101, figs.
1896. *D. wierzejskii*, Schmeil, Bibl. Zool. XXI, p. 54, figs.
1903. ,, Sars, Ann. Mus. St. Petersb. VIII, p. 205, fig.
1931. *D. w. palæstinensis*, Keifer, Zool. Anz. XCII, p. 242, 1 fig.

Female.—Length 1·44–1·8 mm.

General form closely resembling that of *D. laticeps*, the dorsal outline sloping upwards from the head to a more or less definite angle ; but in dorsal view there is not quite the same widening of the head region, the greatest width falling in the first free th. somite, or the whole thorax slender and parallel-sided. The difference is too small to afford a ready means of recognition. Th. som. 5 exactly as in *D. laticeps*, produced slightly backwards on either side, but not expanded laterally, and with 2 very small spines on either side. Abdomen of 2 somites, the genital somite symmetrical, little dilated anteriorly, and with a pair of very small spines. Antennule reaching usually to, or just beyond, end of furcal rami, but sometimes barely reaching their base. Arrangement of setæ as in *D. laticeps*, except that seg. 13 bears only one seta. This is invariable. Leg 5 : Coxa with small spine ; exopod 1 sometimes with a minute seta on outer edge ; exopod 3 distinct, bearing 2 spines, of which one is about half the length of the other. Relative length variable. Endopod reaching scarcely midway along exopod 1, unsegmented. It is usually more slender than in *D. laticeps*, and may have a slight constriction or incipient division into 2 segments.

Male.—Length 1·2–1·45 mm.

General form as in female, but dorsal outline with less definite angle. Th. som. 5 not expanded, and but slightly produced backwards ; very slightly asymmetrical, with 2 spines on right side and 1 on left.

Abd. soms. 1 and 5 slightly asymmetrical. Antennule as in *D. laticeps*, but the spine on seg. 14 always large and process of seg. 23 straight, with a toothed, saw-like, edge. Distal teeth of this saw large; proximal teeth very small; number variable. Generally 5 or 6 larger teeth are distinguishable from the proximal group of small teeth. Leg 5 indistinguishable from that of *D. laticeps*.

Colour: Murray states that the colour may be blue, red and blue, or blood-red. Specimens taken in Jura were brick-red in life, turning bright blue in spirit or formol.

These two species are not easy to distinguish. There is no difference in the form of th. somite 5, or in leg 5 of either sex, and the only differences which can be relied upon are:

(1) Shape of head in dorsal view: Difference very small.

(2) Number of setæ on seg. 13 of antennule in female, and structure of process on seg. 23 in male. Although *D. laticeps* sometimes has teeth on this process, there is never any close resemblance.

The adult characters of the antennule are acquired in the female in copepodid stage V, so that the species can be separated at this stage.

When the two species occur together, as in Loch Moracha, there is a small difference in size:

D. wierzejskii.		*D. laticeps.*	
Female.	Male.	Female.	Male.
1·53 mm.	1·4 mm.	1·43 mm.	1·3 mm.

(average measurements).

Size is, however, no criterion in separating specimens from different localities.

It should be pointed out that the Scottish specimens differ in some respects from the descriptions of Schmeil, Richard and Sars. Sars shows th. som. 5 of the female distinctly produced outwards on the right side, but this is not so in Schmeil's figure, and Richard states that it is rounded on either side. Specimens from Algeria and

Tunisia have the right lobe of this somite distinctly bent outwards (Fig. 238), exactly as in Sars's figure, so that the north African race resembles in this respect the race from Central Asia, and differs from that of northern Europe. This is rather an interesting fact, having regard to the occurrence in North Africa of certain Asiatic species, *e. g. D. incrassatus*. The latter has also been found in Spain (Brehm, 1925, *D. pontifex*), and it will perhaps be found that Richard's types of *D. wierzejskii* really resemble the north African form.

Schmeil shows 2 setæ on seg. 19 of the antennule, whereas there is only 1 in Scottish and Tunisian specimens. On the other hand, he states (p. 56), "Die Glieder 13–19 tragen nur je eine." Probably there is an error in the figure (taf. VI, Fig. 1).

There appears to be some difference in the form of the process of seg. 23 of the prehensile antennule, which in De Guerne and Richard's figure (pl. ii, fig. 22) is armed with a row of short, more or less equal teeth, whereas Schmeil and Sars show it, as in Scottish specimens, with larger teeth distally, Schmeil's figure being somewhat intermediate. The difference is probably not important, since specimens from Algeria have the process of the same type as that of the Scottish form (Figs. 243, 244).

Kiefer states that his *D. w. palæstinensis* differs from the typical form only in having the process of seg. 23 without teeth.

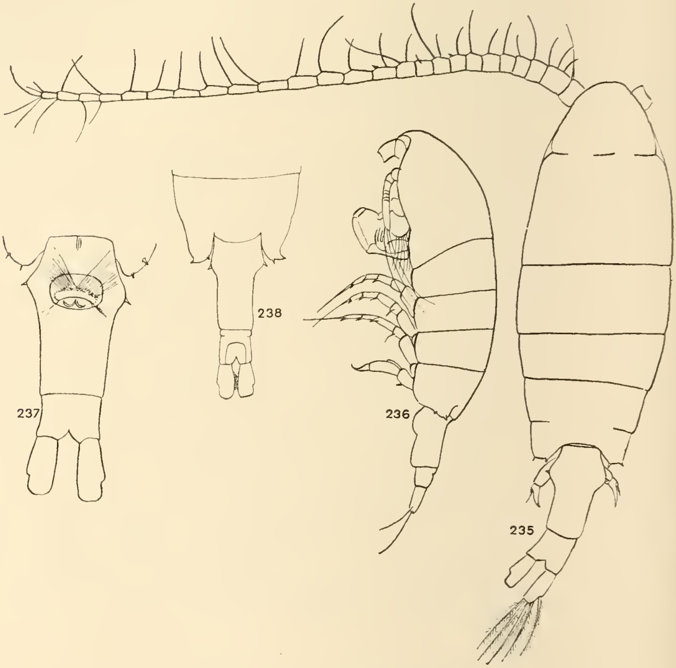
The measurements given by different authors differ greatly :

	Female.	Male.
Schmeil	2·5 mm.	2·0 mm.
Richard	2·75 ,,	2·4 ,,
Daday	2·3 ,,	1·9 ,,
Lilljeborg	1·8 ,,	1·5 ,,
Sars	1·8 ,,	1·45 ,,

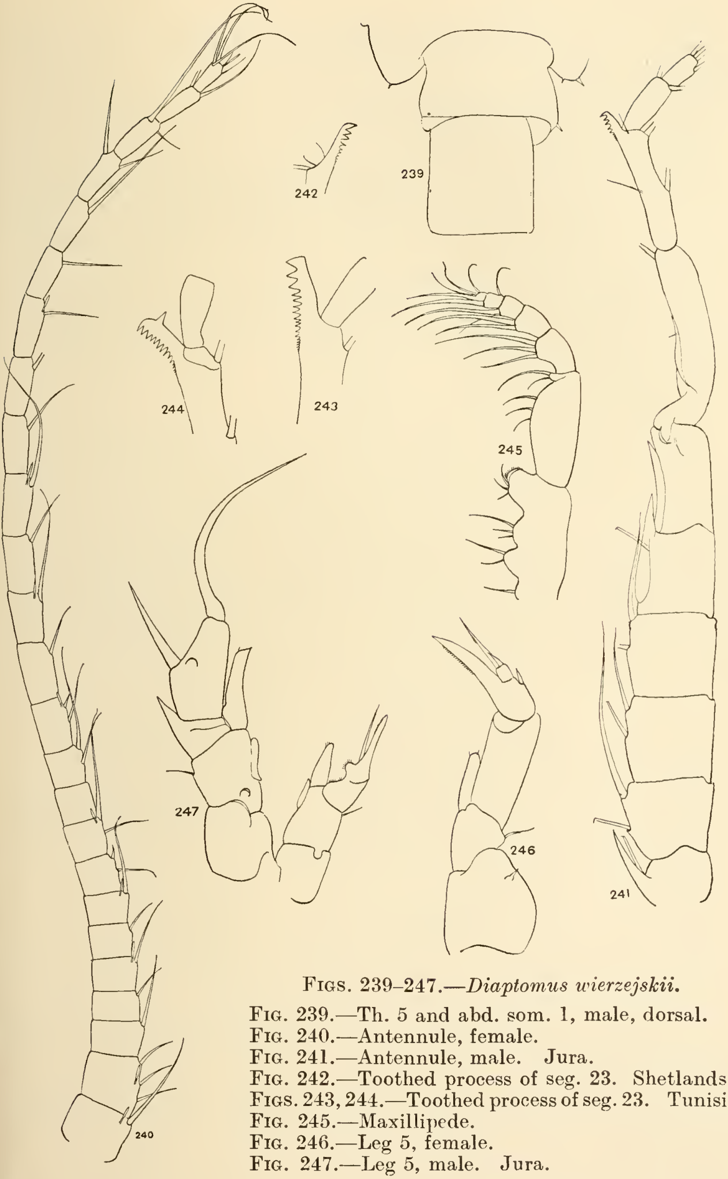
The Scottish form does not approach the largest sizes given here, but the range of size in a single population is so great that, as in the case of *D. laticeps*, it seems necessary to postulate an occasional moult of the adult.

Distribution in Britain.

Shetland Islands: This species, and no other, was present in each of 27 lochs investigated by the Scottish Survey. It is entirely replaced in the Orkneys by *D. laticeps*, except in the island of Rousay, where it was taken in 2 lochs. There is a distinct difference between the lochs of the two groups of islands, since the race of *Daphnia* found in the Orkneys is quite different from that of the Shetlands.



Figs. 235–238.—*Diaptomus wierzejskii.*
Fig. 235.—Female, dorsal view.
Fig. 236.—Female, lateral view.
Fig. 237.—Th. 5 and abdomen female, ventral view.
Fig. 238.—Th. 5 and abdomen, female, dorsal view. Tunisia.



Figs. 239–247.—*Diaptomus wierzejskii.*

Fig. 239.—Th. 5 and abd. som. 1, male, dorsal.
Fig. 240.—Antennule, female.
Fig. 241.—Antennule, male. Jura.
Fig. 242.—Toothed process of seg. 23. Shetlands.
Figs. 243, 244.—Toothed process of seg. 23. Tunisia.
Fig. 245.—Maxillipede.
Fig. 246.—Leg 5, female.
Fig. 247.—Leg 5, male. Jura.

Western Islands:

North Uist: Found alone in 11 lochs, and with *D. laticeps* in 3.

Lewis: Two lochs (Murray).

Mull and Barra (Scott).

Jura: Of 22 lochs examined by me, one only contained *D. wierzejskii*. This was Loch Braigha Choire, a small tarn at 750 ft. above Tarbert Lodge. In all others *D. gracilis* occurred alone.

Scotland—mainland. Sutherlandshire: Lochs Maol a Choire, Awe, Na-Cuin, a' Chlair, Badenloch, Leum a' Chlamhain, na Moine.

Caithness: St. John's Loch.

Perthshire (Tay Basin): Lochs Hoil, Kennard, Tay.

It is therefore a species of the north and west, the only record of its occurrence in the south being that of Scott from Loch Achray (southern Perthshire). Here it was not found in the plankton (in which only *D. gracilis* occurred) but in one of the hand-net gatherings on November 27th, 1897. It is desirable that this southern record should be confirmed.

DISTRIBUTION ABROAD.

Germany: Small pools near Halle (Schmeil).

Spain: Madrid and Valladolid (Richard).

Russia: Samara River (tributary of Volga) (Behning).

Croatia and Slavonia: (Krmpotic).

Hungary: (Daday).

Bulgaria: (Van Douwe).

Kola Peninsula: In Tundra pools: (Lilljeborg).

Mongolia (Sars).

Turkestan: River plankton: (Meissner).

Algeria: Biskra (Gurney). High Plateau of Aïn Beida (Gauthier).

Tunisia: Common in north-eastern plain (Gurney, Gauthier).

Palestine: (Kiefer).

Azores: (De Guerne and Richard, 1889, p. 163).

Borneo: (Spandl).

Bionomics.

While in this country this is a species confined to the north and to lakes of the oligotrophic type, its range elsewhere shows an astounding adaptability. Without appreciable structural change, it is found in tundra pools of the extreme north of Europe and in hot shallow pools in Algeria, some of which dry up early in summer and may be of rather high salinity. Outside Britain it seems to be found generally in small pools rather than in lakes, but is given also, in more than one case, as a member of the river plankton.

D. laticeps and D. wierzejskii.

Seasonal Cycle.

No systematic series of collections has been made in any lake in which either *D. laticeps* or *D. wierzejskii* occurs, and it is therefore impossible to determine with any certainty their cycle of reproduction. At the same time the facts permit some speculation. The Scottish Survey collected widely in North Uist in May and June, and in the Orkneys and Shetlands in July and August, while there are scattered records for other months from other parts of Scotland. It is, of course, to be expected that the cycle will vary with different localities, but in Uist and the Shetlands there is fairly close agreement between the different lakes. In the former it is quite clear that the *Diaptomus* population is very rich in May and June, but that it consists entirely of young in stages older than the nauplius. It seems almost certain that this is the spring brood from resting eggs laid the preceding autumn, and that these young mature and breed in July and August. In some lochs, such as Veirgavat, many adults were found early in May, and on May 11th in Loch Moracha many of them had eggs, so there is some variation. Both species seem to have the same breeding period.

In July, August and September in the Shetlands and other places adults usually preponderate, and nauplii are often abundant. So far as the evidence goes it seems to point to a single reproductive cycle between July and September. Probably resting eggs are largely produced in autumn, but it is certain that there is also active production of young.

The only published information regarding the reproductive period of *D. wierzejskii* is Schmeil's statement that he found the species at Halle in thousands in midwinter under thick ice, that the numbers decreased in succeeding months, to increase again at the approach of winter. My own collections in Tunisia were made in March, when there were great numbers of young with relatively few adults, some of which bore eggs. It is impossible from the limited information to establish any conclusion.

Allied Species.

Schmeil (1897, p. 173) pointed out the very close relationship between the species *D. salinus*, *D. bacillifer*, *D. similis*, *D. laticeps*, *D. wierzejskii* and *D. pectinicornis*, and concluded that, while *D. salinus* and *D. wierzejskii* are quite distinct species, it was doubtful if the others could be maintained. In this "*D. salinus*-group" should also be included *D. acutilobatus*, Sars, *D. dentifer*, Smirnov, and *D. steindachneri*, Rich., while *D. paulseni*, Sars, and certain related species seem to be at least derivatives of the group.

In all these species the resemblance, especially in the form of leg 5, is so close that any differences that there are generally concern the smallest details. *D. acutilobatus* differs considerably both in the form of th. som. 5 and in the number of setæ on the antennule; but the remaining species of the *salinus*-group resemble each other so closely that identification is often most difficult (*e.g. D. similis* and *D. bacillifer*). In no other group of *Diaptomus* can direct relationship be so confidently assumed. It is a group also containing species of unusually wide range and adaptability, and *D. bacillifer* has the widest distribution of any species. It is found in Siberia and islands north of it, and extends westwards through Central Asia to Norway, and south and west through Chitral, Turkestan and Armenia to Bulgaria and the eastern and western Alps. It is also recorded by Marsh from Alaska and arctic Canada, being the only species, except *D. eiseni*, found both in Asia and North America. Just as is the case with *D. wierzejskii*, *D. bacillifer* is equally at home in high mountain lakes and in rain pools of the lowlands, and even in water of high salinity. It seems reasonable to suppose that it may be the oldest species of this group from which the others have originated; but its absence from Scotland is difficult to explain.

TEMORIDÆ, Sars.

Somite of leg 1 marked off from cephalothorax; th. som. 5 either fused with som. 4 (*Temora*) or more or less free (*Eurytemora*). Abdomen of female of 3 somites. Frontal filaments absent or very small. Antennule of female of 24 or 25 segments, segs. 24 and 25 generally fused. Right antennule of male prehensile. Endopods of legs 1–4 with less than 3 segments; with slight sexual differences in *Heterocope* and *Eurytemora*. Leg 5 of female with 3 distinct segments, but no trace of endopod in adult. This leg in male much modified, the right leg without endopod, the left with endopod either absent, or modified into a claw-like process of 2nd basal segment. Eggs generally not carried in egg-sac.

The family contains the following genera:

Marine: *Temora*, Baird; *Temoropia*, Scott; *Temorites*, Sars.

Brackish and fresh water: *Eurytemora*, Giesbrecht.

Fresh water: *Epischura*, Forbes; *Heterocope*, Sars; *Lamellipodia*, Schmeil.

Of these fresh-water genera *Epischura* has 4 species confined to North America and 2 in Asia. Of these two, *E. baikalensis*, Sars, forms the bulk of the plankton in Lake Baikal, while the other, *E. chankensis*, Rylov (1928), is found in Chanka Lake in lat. 45° N., long. 132° E. *Heterocope* is a genus with 5 species in northern Europe and Asia, and one species (*H. septentrionalis*, Juday) in arctic North America. The distribution of the European species appears to have been greatly influenced by the glacial period. *H. caspia*, Sars, which is found in the Caspian Sea, in Anatolia, and the Black Sea region, appears to be a derivative of the northern *H. appendiculata*.

The family is represented in British fresh and brackish waters only by *Eurytemora*.

EURYTEMORA, Giesbrecht.

1853. *Cyclopsina* (part), Fischer, Bull. Soc. Nat. Moscou, XXVI, p. 86.
1853. *Temora* (part), Lilljeborg, Crust. Ord. trib. p. 177.
1881. *Eurytemora*, Giesbrecht, Zool. Anz. IV, p. 258.
1881. *Temorella*, Claus, Sitzber. Ak. Wiss. Wien, LXXXIII, p. 488.
1896. *Eurytemora*, Schmeil, Bibl. Zool. XXI, p. 100.
1902. ,, Sars, Crust. Norway, IV, p. 99.

Cephalothorax usually with a small dorsal protuberance; th. som. 5 distinct from som. 4 and usually produced in female into posteriorly directed wings. Genital somite of female sometimes markedly dilated. Furcal rami slender, sometimes conspicuously hairy or covered with spinules. Furcal setæ relatively short, longer in male than in female. Frontal filaments present, very small. Upper lip with median and lateral lobes. Antennule shorter than thorax, of 24 segments except in *E. grimmi*, which has 25. Right antennule of male with peculiar ribbed modified setæ on segs. 17–19. Maxillipede shorter and stouter than in *Temora*, seg. 2 dilated. Endopod of leg 1 unsegmented; 2-segmented in legs 2–4. Exopod 3 of legs 2–4 with 3 spines, the terminal spine serrated. Leg 5, female, of 3 segments, seg. 2 with strong inner spine. Leg 5, male, uniramous, asymmetrical, curved inwards, the right leg ending in a claw, the left expanded at end. Egg-sacs carried.

Type: *E. velox* (Lilljeborg).

Table showing Distribution of Setæ and Æsthetes on the Antennule of Certain Temoridæ.

	Eurytemora.						*Temora longicornis.*						*Epischura lacustris.*			*Heterocope borealis.*		
	Female.			Male (left).			Female.			Male (left).			Female.			Female.		
	S.	A.	SP.	S.	A.	SP.	S.	A.	SP.	S.	A.	SP.	S.	A.	SP.	S.	A.	SP.
1	3	1	..	3	1	..	2	1	..	2	1	..	2	1	..	3	1	..
2	3	1	..	3	1	..	2	2	..	2	2	..	3	1	..	3	1	..
3	2	1	..	2	1	..	1	1	..	1	1	..	2	1	..	2	1	..
4	1	..	..	1	..	..	2	1	..	2	1	..	1	..	..	1	..	..
5	2	1	..	2	1	..	1	1	..	1	1	..	2	1	..	2	1	..
6	1	..	..	1	1	..	1	1	..	1	1	..	1	..	..	1	..	..
7	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..
8	..	..	1	..	1	1	..	1	1	..	1	..	..	..	1	..	..	1
9	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..
10	..	..	1	..	1	1	1	..	..	1	..	..	1	..	..	..	..	..
11	2	1	..	1 or 2	1	..	2	1	..	2	1	..	1	1	..	1	1	1
12	1	1	1	1	1	1	1	1	..	1	1	..	2	1	..	2	1	..
13	2	..	..	2	1	..	1	1	..	1	1	..	1	1	..	1	1	..
14	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..
15	2	..	..	2	1	..	1	1	..	1	1	..	2	1	..	2	1	..
16	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..	2	1	..
17	2	..	..	2	1	..	1	..	..	1	1	..	2	1	..	2	1	..
18	2	..	..	2	1	..	1	1	..	1	1	..	2	1	..	2	1	..
19	2	1	..	2	1	..	1	1	..	1	1	..	2	1	..	2	1	..
20	1	..	..	1	..	..	1	..	..	1	..	..	1	..	..	1	..	..
21	1	..	..	1	..	..	1	..	..	1	..	..	1	..	..	1	..	..
22	1+1	..	..	1+1	..	..	1+1	..	..	1+1	..	..	1+1	..	..	1+1	..	..
23	1+1	1	..	1+1	1	..	1+1	1	..	1+1	1	..	1+1	1	..	1+1	1	..
24 25 }	6	1	..	6	1	..	6	1	..	6	1	..	5	1	..	1+4 1	1	..

S. = seta; A. = æsthete; SP. = spine.

The antennule of *Eurytemora* is fully described by Schmeil, and differs from that of *Diaptomus* in the greater number of æsthetes and their larger size. While the arrangement and number of setæ and æsthetes appear to be constant for the genus, there are marked specific differences in the length of both. The left antennule of the male differs from that of the female in having more æsthetes. Schmeil notes that, on seg. 11, the female usually has one seta, but may occasionally have 2, whereas the male always has one only (*E. velox*). I find in *E. velox* always 2 in the female, and occasionally 2 also in the male.

Within the family there are great differences in the arrangement of setæ and æsthetes. For example, while *Eurytemora* (female) has 13 æsthetes, there are 17 in *Epischura lacustris* and 19 in *Temora longicornis*. There is less difference between the sexes in the latter than in *Eurytemora* (see table, p. 183).

The number of æsthetes appears to be constant throughout the Diaptomidæ, and in the genera *Eurytemora* and *Heterocope*. It is not known if this is the case for *Epischura*, but it is certainly not true for *Temora*. The arrangement shown in above table for *T. longicornis* differs much from that given by Giesbrecht for *T. stylifera* (1892, p. 332, taf. 17, fig. 1). In this genus the æsthetes are only distinguishable from the setæ by their blunter ends.

Key to the Genus Eurytemora.*

1. Leg 5, female, seg. 2 with 1 outer spine . . . . 2.
Leg 5, female, seg. 2 with 2 outer spines. . . . 3.
2. Th. somite 5, female, rounded, not expanded
1. *E. grimmi*, Sars.
(Caspian Sea.)
Th. somite 5, female, with broad lateral expansions
2. *E. velox*, Lillj.
3. Exopod of right leg 5, male, 3-segmented . . . 4.
Exopod of right leg 5, male, 2-segmented . . . 6.

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* The species *E. johanseni*, Willey, and *E. thompsoni*, Willey, are omitted.

4. Th. somite 5, female, rounded . 3. *E. canadensis*, Marsh.
Th. somite 5, female, pointed . . . . . . 5.
5. Leg 5, female, seg. 3 with long subequal setæ
4. *E. americana*, Williams.
Leg 5, female, seg. 3; these setæ very unequal
5. *E. herdmani*, Scott.
(N. America.)
6. Th. somite 5, female, rounded . 6. *E. lacustris*, Poppe.
Th. somite 5, expanded, wing-like . . . . 7.
7. Genital somite, female, markedly dilated, constricted in middle . . . . 8.
Genital somite dilated anteriorly, narrowing behind . 9.
8. Furcal rami, female, short (about 1 : 4) 7. *E. raboti*, Richard.
(Spitzbergen, etc.)
Furcal rami, female, long, at least 1 : 5
8. *E. composita*, Keiser.
(Issyk Kul, Tashkend.)
9. Leg 5, male, right. Exopod 3 slender, not dilated at base . . . . 9. *E. gracilis*, Sars.
(N. Asia, N. Canada.)
This segment dilated at base . . . . . . 10.
10. Leg 5, male, left. Exopod 2 very broad, nearly half as wide as long, with strong outer spine. Furcal rami smooth dorsally . . . . 10. *E. tolli*, Rylov.
(Siberia.)
This segment slender. Furcal rami hairy dorsally . 11.
11. Th. somite 5, female, produced into long pointed wings
11. *E. affinis*, Poppe.
These prolongations short, rounded at end
12. *E. hirundo*, Giesb.

The genus contains 14 species,* but of these, 2, *E. johanseni*, Willey, and *E. thompsoni*, Willey, are not sufficiently described, while *E. hirundoides* (Nordquist) is certainly, and *E. hirundo*, Giesb., probably, to be regarded as within the range of variation of *E. affinis*, Poppe.

The genus is of definitely northern distribution in the Old World, though in America *E. affinis* is recorded by Marsh and by Foster from Louisiana (Gulf of Mexico).

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* To these must be added *E. Kieferi*, Smirnov (1931 B) from Kamchatka, and *E. pacifica*, Sato, from Japan. The latter, of which I have not been able to see the description, is considered by Smirnov to be perhaps identical with *E. johanseni*, Willey.

The species are mainly confined to coastal regions and to waters in direct connexion with rivers, but some, such as *E. herdmani*, are purely marine. Species, such as *E. affinis* and *E. velox*, may be found both in brackish and in fresh water, while *E. lacustris* is confined to fresh-water lakes. The genus seems to be most closely related to the marine genus *Temora*, with which it was formerly united, and may, perhaps, be regarded as having originated from it in the arctic sea of glacial times. The occurrence of *E. affinis* and related species on the east coast of North America and its abundance, together with varietal forms, in the Baltic region, show some correspondence with the distribution of *Limnocalanus* and of *Mysis relicta*. *E. affinis* and *E. velox*, together with an endemic species, *E. grimmi*, Sars, are found in the Caspian Sea, and Keiser (1929) has described another species, *E. composita*, from Issyk Kul in the heart of eastern Turkestan. This lake is now entirely isolated, and it seems necessary to suppose that this species is of recent origin from one of the species of the Caspian region, although it more closely resembles *E. raboti*—a species of fresh and brackish water in Spitzbergen, Novaya Zemlya, Waigatz and the White Sea coast. The distribution of the species of this genus cannot be accounted for by transport by birds, as Spandl (1926) suggests for *E. velox*, and is of the greatest interest.

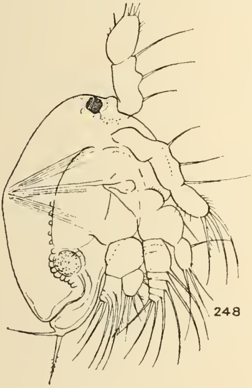
DEVELOPMENT OF EURYTEMORA (*E. velox*).

Nauplius I (Fig. 248).

Length ·12 mm.

Body oval, not much compressed. In front of eye a small knob, which persists throughout nauplius stages, and may represent a frontal organ. Body narrowing behind and bearing a pair of stout furcal setæ, of which that on right is directed upwards. In front of anus, on ventral side, a few short hairs in transverse rows. Antennule of 3 indistinctly separated segments. Seg. 1 with 1 seta ; seg. 2 with 2, of which the distal is longer ;

seg. 3 with 3 strong setæ and a very delicate seta which eventually becomes the æsthete of the adult. Antenna: Coxa with 1 strong spine; basis with 1 spine and 2 setæ; endopod unsegmented, with 3 terminal setæ; exopod of 5 segments with 7 long setæ. Mandible: Basis with 2 strong spines; endopod unsegmented, broad, with a proximal group of 3 setæ and terminal group of 5. Exopod 4-segmented, with 5 setæ.



Figs. 248–254.—Development of *Eurytemora velox*.

Fig. 248.—Nauplius I.
Fig. 249.—Nauplius VI.

This stage lasts a very short time, and is rarely found in the plankton.

Nauplius II.

Length ·15–·17 mm.

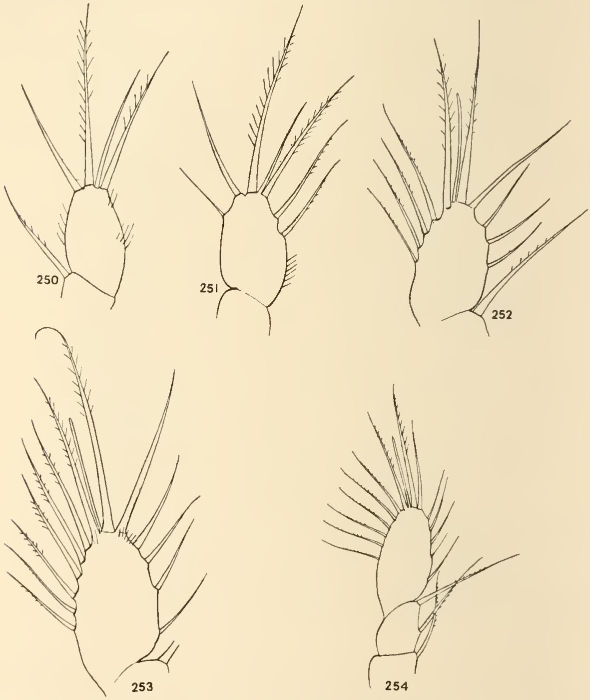
Differs little from stage I. Body more elongated. Antennule unchanged, without marginal setæ on seg. 3. Exopod of mandible with 5 setæ.

Colour brownish-yellow. Eye blue-black.

Nauplius III.

Length ·2–·23 mm. (average, ·21 mm.).

Rudiment of maxillule present in form of a long seta. Body with faint line of division behind maxillule. Furcal region with an outer pair of spines in addition to the two furcal setæ. Antennule with 2 setæ on anterior edge of seg. 3, and 1 on posterior edge. Exopod of antenna with 9 setæ. Mandible unchanged.



Figs. 250–254.—Development of antennule of *Eurytemora velox* in nauplius stages II–VI, showing successive additions of setæ to the distal segment. Segs. 1–3 remain the same as shown in VI, which is drawn to a smaller scale than the others.

Nauplius IV.

Length ·24–·25 mm.

Maxillule a small bilobed appendage with 3 setæ on outer lobe. Furcal region as in III. Antennule seg. 3

with 3 inner and 4 outer setæ. Maxilla may in some cases be traceable as an elevation behind maxillule.

Nauplius V.

Length ·26–·29 mm.

Furcal region with an additional pair of small spines. Antennule seg. 3 with 4 inner and 6 outer setæ. Antenna exopod with 10 setæ. Maxillule a large biramous appendage with 4 inner lobes. Maxilla a distinct uniramous rudiment without setæ.

Nauplius VI (Fig. 249).

Length ·3–·35 mm.

Body elongated, but not laterally compressed. Antennule seg. 3 with 5 inner and 6 outer setæ. Antenna exopod with 11 setæ. Maxillule and maxilla well developed and approaching adult form, the latter with 6 lobes. Maxillipede a large rudiment bearing 2 terminal setæ. Legs 1 and 2 bilobed rudiments, each lobe bearing terminal setæ. In one case I have seen a perfectly distinct rudiment of leg 3 under the skin, showing that this specimen would have moulted to copepodid stage II, omitting stage I.

Copepodid I (Figs. 261–266).

Length, ·40–·58 mm. (Average of 74 specimens: Female, ·56 mm.; male, ·49 mm.)

Body now definitely of Calanoid form and appendages of adult structure. Cephalothorax with dorsal hump as in adult. No trace of rostral filaments. Th. somites 1–4 distinct: th. som. 5 not separated from abdomen. This condition may be compared with that of the adult "Podoplea." Furcal rami short, with full number of adult setæ, but outer terminal seta very slender, and lateral seta small. Antennule of 8 or 9 segments. Seg. 1, which bears 3 setæ, succeeded by a very long segment with 2 setæ about middle, and 1 distal; seg. 3 with æsthete and seta; seg. 4 with 1 distal seta. This segment may be divided into two. Last 3 segments well defined. Last segment as in adult, with 6 setæ and æsthete. It is, in my opinion, impossible to interpret these segments in terms of the adult antennule (see above, p. 43). Swimming-legs with rami unsegmented. Leg 3 a small bilobed rudiment.

Although it is impossible to distinguish the sexes by any structural details in this, or in the next two stages, measurement of numbers of specimens show that they fall into two size-groups which no doubt actually correspond to the two sexes (see Gurney, 1928).

Copepodid III.—Arrangement of Antennular Setæ.

1	2	3	4	5	6	7
3 S.	2 S., A.	S., A.	—	S.	S., A.	—
8	9	10	11	12	13	14
S.	S.	S.	S., A.	S.	S.	S.
15	16	17	18	19	20	1
S.	2 S., A.	S.	S.	S. + S.	S. + S., A.	6 S., A.

Copepodid II (Fig. 267).

Length: Female, ·7–·78 mm.; male, ·63–·68 mm.

Legs 1–3 with exopod 2-segmented. Leg 4 a bilobed rudiment. Somites 4 and 5 still appear to form part of abdomen, which is still unsegmented, but may show traces of division into two. Furcal rami smooth; setæ as in adult. Antennule of 15 segments.

Copepodid III.

Length (average): Female, ·95 mm.; male, ·90 mm.

Th. som. 5 distinct, and abdomen of 2 segments, distinct from thorax. Legs 1–4 developed; endopod of 1–3 of 2 segments, unsegmented in leg 4. Leg 5 a

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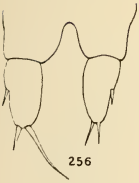

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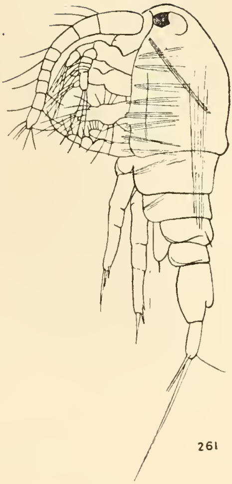

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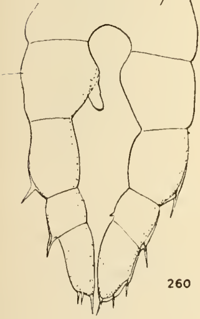

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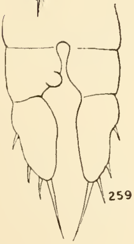

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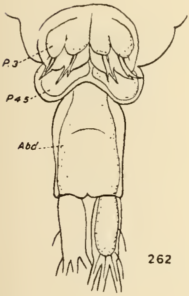

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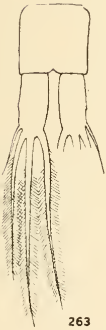

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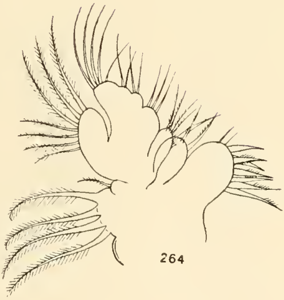

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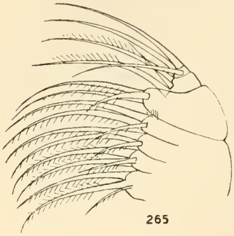
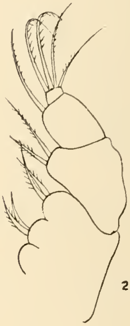
FIGS. 255–264.—DEVELOPMENT OF *Eurytemora velox*.

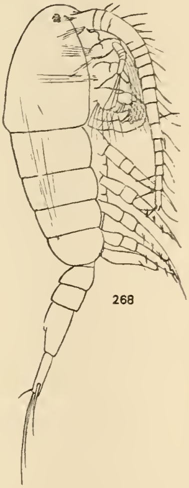
(Figs. 255–260, development of leg 5 in male and female.)

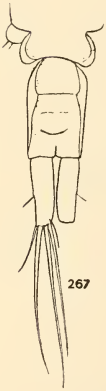
FIG. 255.—Stage III, undifferentiated.
FIG. 256.—Stage IV, female.
FIG. 257.—Stage V, female.
FIG. 258.—Adult female.
FIG. 259.—Stage IV, male.
FIG. 260.—Stage V, male.
FIG. 261.—Copepodid I, side view.
FIG. 262.—Copepodid I, abdomen, ventral, before moult.
FIG. 263.—Copepodid I, furcal rami.
FIG. 264.—Copepodid I, maxillule.

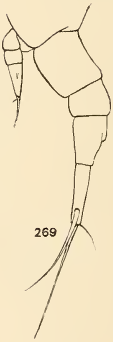
small knob without sexual differences. Antennule of 21 segments, with setæ as shown in table. It should be noted that two of the setæ on segment 1 are feathered, whereas none are feathered in the adult.











Figs. 265–269.—Development of *Eurytemora velox.*

Fig. 265.—Copepodid I, maxilla.
Fig. 266.—Copepodid I, maxillipede.
Fig. 267.—Stage II, th. soms. 4 and 5 and abdomen.
Fig. 268.—Stage IV, male, side view.
Fig. 269.—Stage V, female, abdomen, side view.

Copepodid IV (Fig. 268).

Length (average): Female, 1·24 mm.; male, 1·07 mm.

The sexes can now be distinguished by differences in the antennule and leg 5. Abdomen of 3 somites in both sexes, of which som. 3 is longest. Antennule of

24 segments. The right antennule of male distinguished from that of female by having distal seta of segment 19 modified as a long spine. Segs. 20–24 are distinct, and not fused as in adult.* Swimming-legs usually with exopods 2-segmented, but occasionally with 3 segments. Leg 5, female, with coxa and basis, and exopod segs. 1 and 2, not separated. Exopod with outer spine and two apical spines. The two appendages may be asymmetrical, the right leg a little the larger, and with the apical spines of very unequal length (Fig. 256). Leg 5, male : basis separated from coxa, the former with a small papilla in right leg representing vestigial endopod. Exopod nearly or quite symmetrical, with 2 outer and 2 apical spines.

Copepodid V (Fig. 269).

Length (average) : Female, 1·52 mm. ; male, 1·33 mm. In female th. som. 5 shows incipient lateral outgrowths. Abdomen of female of 3 somites of relative length 17 : 8 : 12. Som. 1 represents som. 1 and 2 of preceding stage fused, while a new somite has been separated behind. Abdomen of male of 4 somites. Furcal rami hairy on inner side, and about as long as genital somite. Swimming-legs with exopods of 3 segments. Antennule of 23 or 24 segments, segs. 8 and 9 being sometimes not separated (as is the case in the adult of *E. lacustris*). Right antennule of male with 5 terminal segments still distinct, and with setæ and æsthetes as in female. In seg. 19 the two setæ are modified into spines, and in segs. 17 and 18 one seta is so modified and these represent the combed scales of the adult. Seg. 15 has 2 setæ, and lacks the æsthete present in the adult. Leg 5, female, of the same form as in adult, but seg. 2 not separated. Leg 5, male, nearly symmetrical. Right leg with vestigial endopod on basis. Exopod of 3 segments, with outer spine on segs. 1 and 2 and 3 small terminal spines on seg. 3.

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* In *E. grimmi*, Sars, the four terminal segments remain separate in the adult.

Rylov (1928c) describes the development of leg 5 in *Epischura chankensis.* In this species there is a vestigial endopod in stage IV on both legs, and it is clear that in the adult the long, sickle-shaped process of the basis in the left leg and the inwardly-directed process of the right leg are both modified endopods.

Eurytemora velox (Lilljeborg).

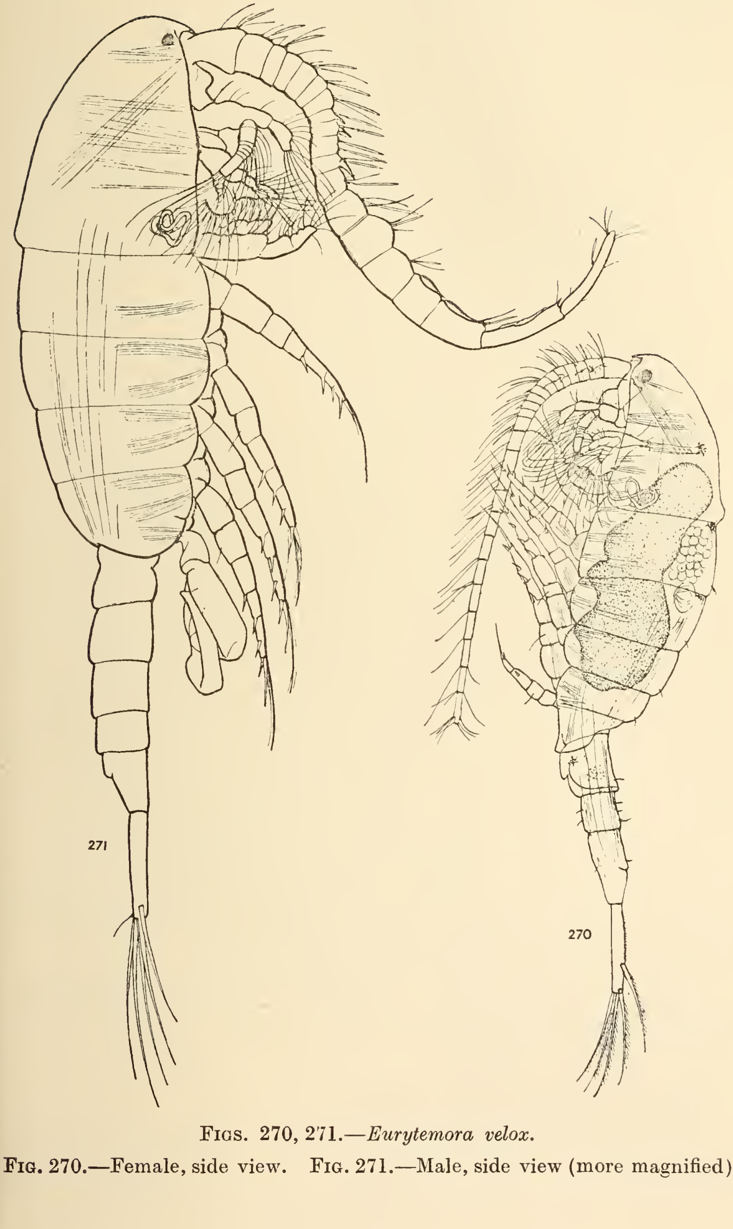
(Figs. 270–284.)

1853. *Cyclopsina lacinulata*, Fischer, Bull. Soc. Moscou, XXVI, p. 86, figs.
1853. *Temora velox*, Lilljeborg, Crust. Ord. Trib. p. 177, pl. xx, figs. 2–9.
1878. *T. clausii*, Hoek, Tijdschr. ned. dierk. Ver. III, p. 23, figs.
1881. *Temorella clausii*, Claus, Sitzber. Akad. Wiss. Wien, LXXXIII, p. 490, figs.
1889. *Eurytemora lacinulata*, De Guerne & Richard, Mem. Soc. zool. Fr. II, p. 82, figs.
1892. *E. clausi*, Brady, Trans. N.H. Soc. Northd. VI, p. 105, figs.
1896. *E. lacinulata*, Schmeil, Bibl. Zool. XXI, p. 109, figs.
1898. *E. velox*, Giesbrecht & Schmeil, Thierreich. Lief. 6, p. 102.
1902. ,, Sars, Crust. Norway, IV, p. 100, pls. lxvii, lxviii.
1931. *E. adleri*, Schiklejew, Zool. Anz. XCI, p. 22, figs.

Although Fischer's name is the earliest given, it has been superseded, under the rules of nomenclature, on the ground that he wrongly identified his species with *Cyclops lacinulatus*, O. F. Müller. Müller's species is unrecognizable, but it is impossible to say that his figure does not represent *E. velox*, and the abandonment of Fischer's name does not seem to be strictly in accordance with the rules. On the other hand, the name *E. velox* has now become established, and is therefore used here.

Female.—Length 1·6–1·95 mm.

Body robust, almost parallel-sided, and not contracted posteriorly. Cephalothorax broad, with a small median dorsal prominence posteriorly. This prominence is sometimes absent, and is not so conspicuous as in *E. lacustris*. Th. som. 5 distinctly marked off, very narrow in middle line, but greatly expanded on either side. Lateral expansions of characteristic shape, with a rather S-shaped outline in dorsal view, the posterior ends being turned outwards. Outer margin with about 5 small marginal hairs. Abdomen of 3 somites.



Figs. 270, 271.—*Eurytemora velox.*

Fig. 270.—Female, side view. Fig. 271.—Male, side view (more magnified).

Genital somite slightly dilated in front, with a shallow constriction in the middle. Genital operculum rounded at end. Furcal rami not much longer than abd. som. 3, about four times as long as wide, rather divergent; inner margins hairy, and hairy also on dorsal face along both margins. Lateral seta inserted near end (1 : 3). Terminal setæ rather short and stout. Rostral filaments very small and blunt. Upper lip trilobed, the margin fringed with delicate hairs. Antennule reaching nearly to end of thorax, with æsthetes and setæ as in table (p. 183). None of the setæ are feathered, and none very markedly longer than the others, but both æsthetes and setæ are generally longer than in *E. affinis*. Cutting edge of mandible with 7 teeth, a wide gap separating the large anterior tooth from the next one. Maxillipede with basis broad, with 3 large inner lobes bearing 2, 2, 3 setæ. Endopod of 5 distinct segments, shorter than basis. Exopod 3 of swimming-legs about 2½ times as long as wide. Basis of legs 1 and 2 without outer seta; this seta present on legs 3 and 4. Leg 5: Exopod 1 about 1½ times as long as wide, with a single outer spine. The strong inner spinous process with a few spinules on distal edge, and scarcely longer than seg. 2. Seg. 2 about half the length of seg. 1, with 2 distal setæ, of which the outer is about one-third the length of the inner. Abnormal fifth legs are shown in Figs. 272, 283. In the one case there are 2 outer spines on exopod 1, as in *E. affinis*,* while the other has the inner spinous process strongly toothed. There is also some variation in the relative length of the apical setæ, the outer one being sometimes reduced to a small spine.

Colour.—Often almost colourless, except for the dark-coloured ovaries and for small patches of blue. Occasionally red, or brown.

Male.—Length 1·3–1·65 mm.

Form more slender than in female; th. som. 5 without lateral wings, simply rounded. Abdomen of 5 somites.

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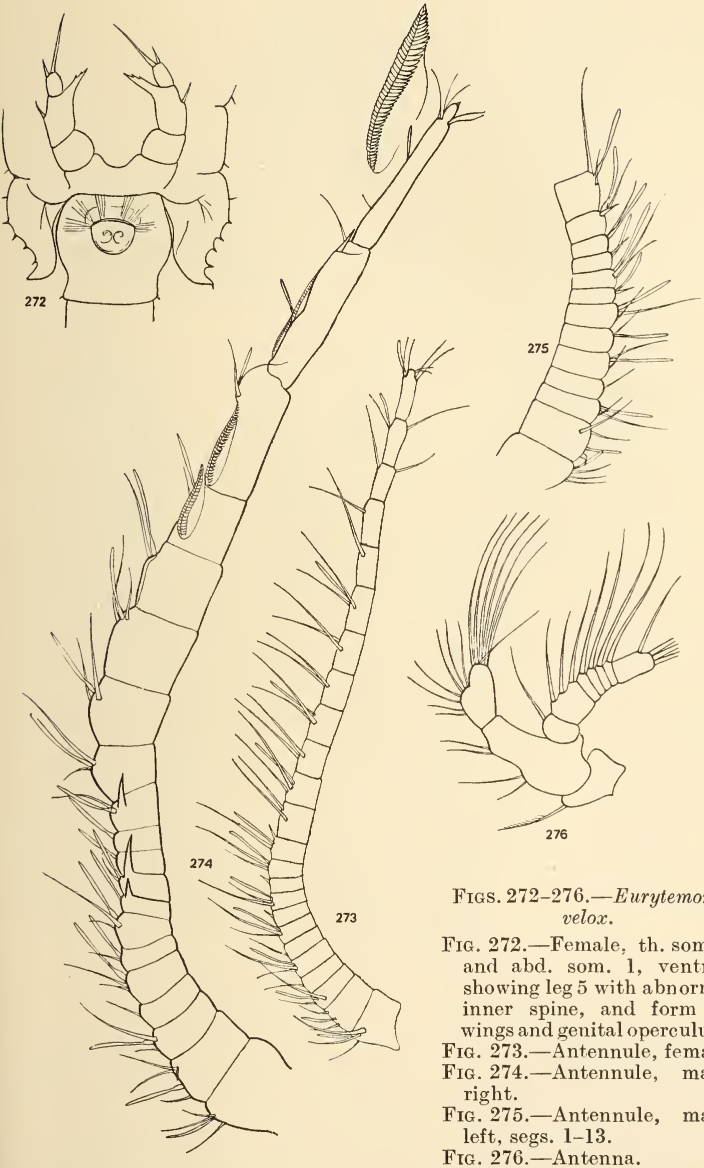
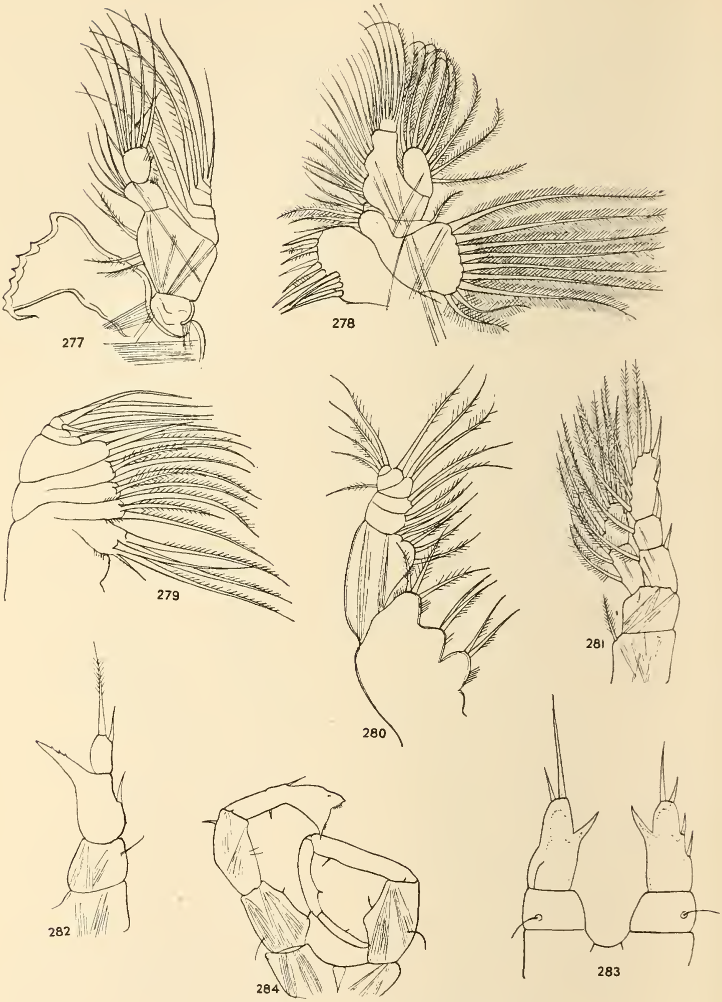
* Brady (1892, p. 42) notes occasional presence of two outer spines.



FIGS. 272–276.—*Eurytemora velox.*

FIG. 272.—Female, th. som. 5 and abd. som. 1, ventral, showing leg 5 with abnormal inner spine, and form of wings and genital operculum.
FIG. 273.—Antennule, female.
FIG. 274.—Antennule, male, right.
FIG. 275.—Antennule, male, left, segs. 1–13.
FIG. 276.—Antenna.



FIGS. 277–284.—*Eurytemora velox.*

FIG. 277.—Mandible.
FIG. 278.—Maxillule.
FIG. 279.—Maxilla.
FIG. 280.—Maxillipede.
FIG. 281.—Leg 2, female.
FIG. 282.—Leg 5, female.
FIG. 283.—Leg 5, female, copepodid V, showing two spines on exop. 1.
FIG. 284.—Leg 5, male.

Furcal rami longer than in female, 6 or more times as long as wide, and generally less hairy; sometimes quite smooth on dorsal surface. Setæ much longer and more slender than in female, about $1\frac{3}{4}$ times as long as ramus. Left antennule as in female, but somewhat stronger, and with 20 æsthetes instead of 13 (see table). Right antennule with segs. 13–16 widened. Schmeil gives as characteristic of the species that segs. 14–16 are unusually widened distally, giving a markedly indented appearance; but this is not always the case. Seg. 11 has usually one seta only, but there may occasionally be 2. The scale-like modified setæ of segs. 17–19 have, on their edge, a double row of spinules arranged like a saw (Fig. 274). Labbé (1924B) has re-discovered and described these peculiar structures, which are correctly described by Schmeil. Leg 5, right: basis dilated in middle, but without a spine on the inner prominence; inner margin with one hair distally. Exopod 1 long and slender, length nearly 6 times the width, with one inner hair. Exopod 2 and 3 distinctly divided, their relative length being about 30 : 23. Exopod 2 bears one inner and one outer spinule, and is not at all dilated at its base. Left leg: basis slightly dilated, with a small hair on inner margin distally. Exopod 1 broad, breadth about $\frac{1}{2}$ length, with strong outer terminal spine and 2 small inner hairs. Exopods 2 and 3 fused into a long segment nearly $1\frac{1}{2}$ times as long as seg. 1, with one inner and one outer marginal spinule. Apex of segment spatulate, with small hairs on the two terminal angles.

Distribution in Britain.

Scotland: North Uist—Loch Oban Nam Fiadh. Jura—Brackish pools by Tarbert Lodge. Mainland—In fresh water; Possil Marsh near Glasgow; old brickfield pond, Dunbar; Castlemilk, Rutherglen pond; in brackish water, Cumbrae; Langbank (Clyde); Seafield near Leith; Aberlady (Forth).

Ireland: Lough Derg and Shannon (*Southern & Gardiner*); Clare Island (*Scourfield*); Malahide; brackish pools (*R. G.*); Lough Erne (*R. G.*).

England: Norfolk—Throughout the Broads district, in all the Broads and rivers, and in many ditches in water both fresh and slightly brackish. Also in salt-marsh pools at Blakeney and Wells in water of very high salinity, in company with *Palæmonetes*. Essex—Epping, Richmond and Higham Park, in fresh water (Scourfield). Somerset—Chard reservoir (R. A. Todd). Surrey—Richmond. Oxfordshire—Oxford reservoir (Lowndes). Hertfordshire—Marsworth reservoir (Popple).

Wales: Pensarn, Merionethshire (Brady).

Distribution Abroad.

The distribution of *E. velox* has been fully treated not only by Tollinger (1911), but also by Siewerth (1926) and Spandl (1926), so that it is not necessary to enter into details. It is a euryhaline species widely distributed within the coastal region of the Baltic, N.W. Germany, Holland and N.W. France, but extending inland and found in perfectly fresh water, though usually in such as communicates with rivers. It is not known from S. France, Spain or the Mediterranean region. On the other hand, it occurs in the north Caspian Sea, in the sea of Azov, in the Volga basin northwards to Kazan, in the Danube delta, and by the eastern coast of the Black Sea. It is therefore a northern form which has reached the Caspian region either by transport down the Volga, or by the northern connection in pre-glacial times to which the Caspian owes other semi-arctic forms, such as *Limnocalanus grimaldii*. Its occurrence in Azov and the Danube delta is no doubt due to the former wide extension of the Ponto-Aralo-Caspian Sea. In Sweden Ekman (1907) regards it as a relict of the Littorina sea. All the thirteen Swedish lakes in which it occurs are within the limits of this sea, and it is absent from all that are not, showing no capacity for passive dispersal.

BIONOMICS.

As the list of records given above shows, *E. velox* tolerates a remarkably wide range of salinity and profound differences in environment, with practically no structural variation. In Norfolk it is the characteristic species of the plankton of the Broads, and yet is found, in enormous number, in small pools on salt marshes. Mr. Lowndes has taken it in pools on rocks jutting out to sea at Millport. The Norfolk Broads are subject to tidal influence and there is generally direct connection with a river, but the species is also found in reservoirs of perfectly fresh water without even indirect connection with the sea.

Having such wide toleration of high salinities, it is rather surprising to find that, in an open system of waters, its distribution is definitely limited. Thus, in the Norfolk Broads, it is not found in the rivers below the point at which the influence of salt water makes itself felt—about twelve miles from the sea. From this point it is replaced by *E. affinis*. This fact suggests that, while the species as a whole is euryhaline, it actually comprises physiological races of limited toleration.

Observations on periodicity are few and uncertain; but in Norfolk, at all events, the species survives throughout the year, and I have not noted any marked periods of abundance. In certain salt-marsh pools, however, dense masses, at all stages, were found up to June, but later in the summer they had almost disappeared. As the period of decrease corresponded to the hatching and development of great numbers of the larvæ of *Palæmonetes varians*, it is probable that the whole of the *Eurytemora* were eaten up. Elton (1927, 1929) has suggested that *E. velox*, in comparison with *Diaptomus gracilis*, has great powers of dispersal owing to the production of resting eggs, and is therefore found in artificial reservoirs, etc., which *D. gracilis*, which does not produce resting eggs, is not able to reach ; and that, if the two species come into competition, *E. velox* disappears. These conclusions have been disputed by Lowndes (1929, 1930A). While the two species are quite often found together (*e. g.* Norfolk Broads), and Elton's views as to the competition between the species cannot be unreservedly accepted, it is a remarkable fact that this species is so often found in this country in artificial waters. There is evidence that *D. gracilis* does not produce resting eggs, while Ekman states that *E. velox* in Ekoln lays resting eggs in autumn. Where, as in this country, the species is perennial, the production of resting eggs is not easy to prove.

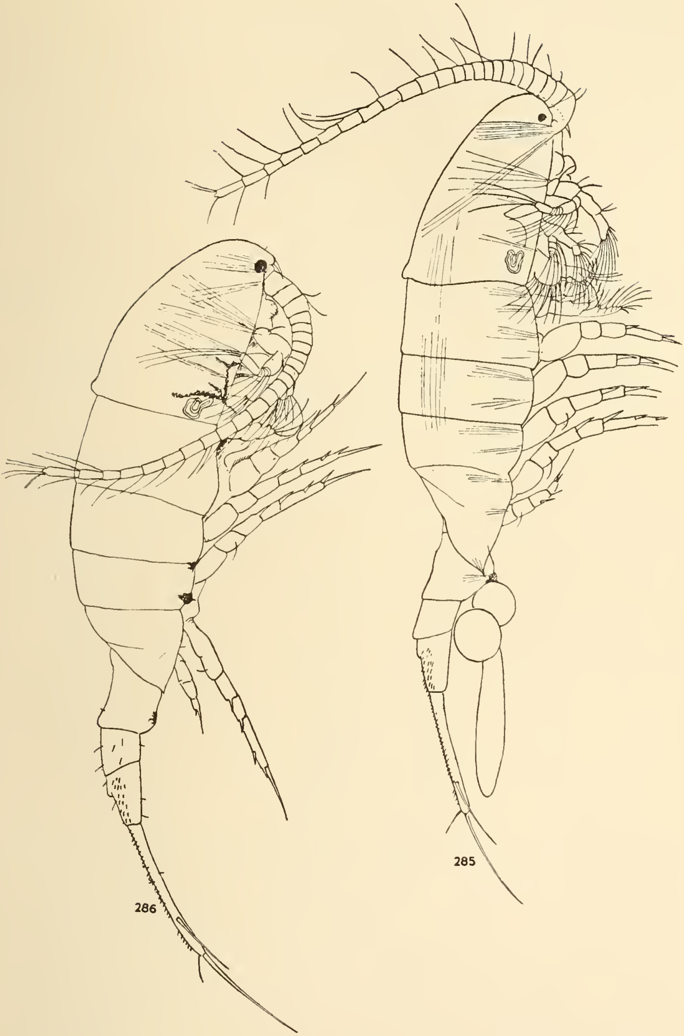
Eurytemora affinis (Poppe).

(Figs. 285–306.)

1853. *Temora velox* (male) Lilljeborg, Crust. Ord. Trib. p. 177, figs.
1880. *T. affinis*, Poppe, Abh. natur. Ver. Bremen, VII, p. 55, figs.
1888. *Temorella affinis*, vars. *hirundoides* and *hispida*, Nordquist, Calaniden Finlands, pp. 48, 53, figs.
? 1881. *E. hirundo*, Giesbrecht, Zool. Anz. IV, p. 258.
1892. *Eurytemora affinis*, Brady, Trans. N.H.S. Northd. XI, p. 107, figs.
1892. *Temorella affinis*, and *T. a.* var. *hispida*, Canu, Ann. Stat. aquic. Boulogne, I, p. 13, figs.
1896. *E. affinis*, Schmeil, Bibl. Zool. XXI, p. 114, figs.
1897. ,, Sars, Ann. Mus. St. Petersb. II, p. 67, figs.
1907. ,, Van Breemen, Tijdschr. Ned. Dierk. Ver. (2), X, p. 314, figs.
1902. *E. hirundoides*, Sars, Crust. Norway, p. 102, figs.
1922. *E. affinis* and *E. hirundoides*, De Lint, Int. Rev. Hydrob. Leipzig, X, p. 81, figs.

Female.—Length about 1·5 mm. In east Norfolk rivers ranging from 1·19 to 1·73 mm.

Body robust ; thorax more or less parallel-sided, the length not much more than twice the width (105 : 48). Cephalothorax usually without median dorsal hump. Th. som. 5 produced on either side into a long pointed wing, sloping outwards, and often reaching back beyond genital somite ; these wings ending in a small spine and with small marginal hairs. Abdomen about two-thirds as long as head and thorax (70 : 105). Genital



FIGS. 285, 286.—*Eurytemora affinis.*

FIG. 285.—Female, side view. Breydon, Norfolk.

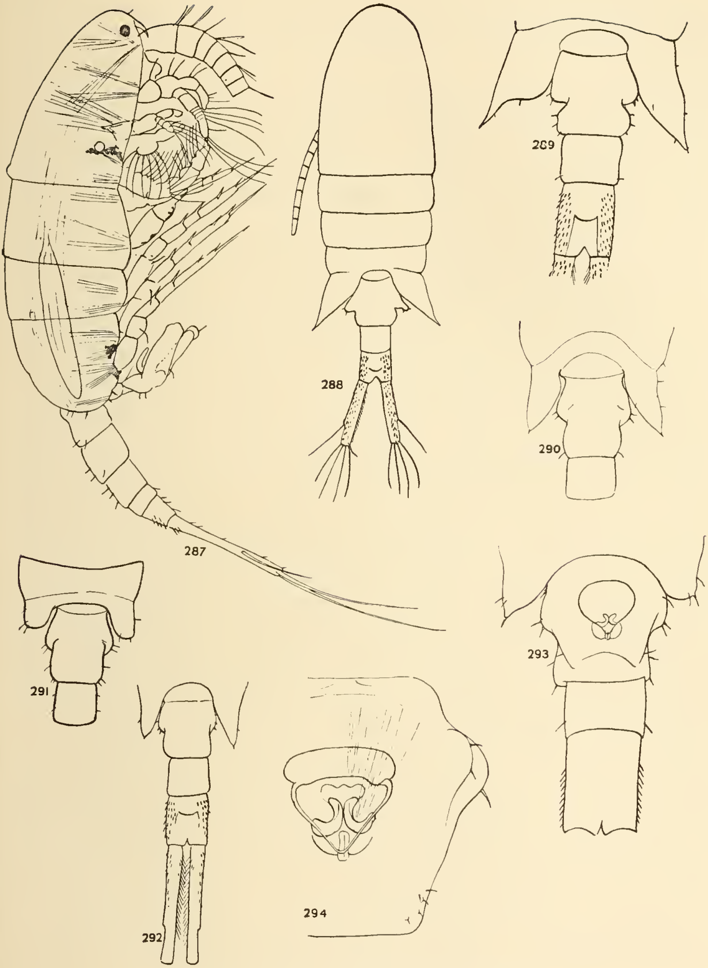
FIG. 286.—Female, side view. R. Tamar.

somite nearly as long as soms. 2 and 3, very broad anteriorly, and sharply narrowing about the middle; shape variable. The anterior part may be produced outwards into a papilliform process (Fig. 288) or simply rounded, and in all cases bears marginal spines. Genital operculum pointed. Som. 3 with dorsal surface thickly covered with spinules. Furcal rami about as long as soms. 1 and 2 together, and 5–8 times as long as wide. Dorsal surface thickly covered with spinules. Inner margin hairy. Outer seta inserted near end (1 : 2). Terminal setæ rather short and stout, shorter than ramus.

Antennule of E. velox *and* E. affinis : *Lengths of Segs.* 14–24.

Segment.	*E. velox.*	*E. affinis.*		
		R. Bure.	Falmouth.	R. Tamar.
14	22	18	12	13
15	22	19	13·5	13
16	25	18	14	14
17	27	22	15	16
18	29	21	15	16
19	28	22	15·5	16
20	29	18	13	14
21	28	20	15	15
22	25	20	13	13
23	30	23	16	19
24	34	36	22	30

Rostral filaments rather long and slender. Upper lip with prominent median lobe fringed with long hairs, and broad lateral lobes. Antennule short, reaching about to end of th. som. 3. Segments shorter than in *E. velox* (see table). Æsthetes very long, without swelling at base. Mandible with all teeth close together. Swimming-legs with small sexual differences. In the female the exopod is somewhat less slender and the outer spines stouter than in the male (Figs. 301, 302). Leg 5 : Basis as broad as long ; exopod 1 with 2 outer spines and straight, smooth, inner spinous process. Seg. 2 small, oval, with 2 terminal spines, of which the outer



Figs. 287–294.—*Eurytemora affinis.*

Fig. 287.—Male. R. Tamar.

Fig. 288.—Female, dorsal view. Chelson Meadow, Plymouth.

Fig. 289.—Female, th. som. 5 and abdomen. R. Tees.

Fig. 290.—Female, th. som. 5 and abdomen. Breydon.

Fig. 291.—Female, th. som. 5 and abdomen. R. Tamar.

Fig. 292.—Female. Norway.

Fig. 293.—Female, ventral. R. Tamar.

Fig. 294.—Female, ventral, genital somite. Falmouth.

is about $\frac{1}{2}$ length of inner. A small spine between the two. Egg sac large, with many eggs.

Male.—Length, 1·36–1·65 mm.

Th. som. 5 rounded. Furcal rami longer than in female; length to width usually about 9 : 1. Generally with spinules on dorsal margin, but fewer and smaller than in female. Apical setæ longer than in female, the longest seta much longer than ramus (87 : 78). Right antennule with spines on segs. 8–12, those of segs. 9 and 12 the longest. Spine of seg. 12 may be longer than seg. 13, slender, and jointed to segment. Seg. 17 with finely serrated marginal scale; seg. 19 with teeth of proximal scale very long and curving distalwards. Æsthete absent from this segment. Leg 5 provided with very numerous small sensory hairs. Right leg: basis with inner projection rather pointed, and with spine at point. Exopod 1 long and slender, about 6 times as long as wide. Exopod 2 rather swollen at base, and sharply curved. Left leg: basis produced inwards into a rounded prominence, much wider than long (40 : 34). Exopod 1 about 3 times as long as wide; exopod 2 longer than exopod 1, widening distally, and deeply hollowed at end when seen from behind. On anterior face is a small median lobe. The spermatophore is often seen attached to this segment, apparently in the hollow enclosed by the median and lateral lobes. Leg 5 in copepodid V differs from that of *E. velox* in having the endopod still further reduced (Fig. 306.)

Colour.—Generally almost colourless, except for patches of blue or violet, as shown in figures.

VARIATION.

The description given above is taken from Norfolk specimens, which agree reasonably well with the description and figures of Schmeil, which may be regarded as fixing the type of the species; but there is great variability, both individual and local, with regard to size, slenderness, and shape of th. som. 5. Nordquist (1888) described two varieties, *hispida* and *hirundoides*, of which the former is admittedly a variety of the type, while the latter has been regarded by Sars and others as an independent species. A third form, *E. hirundo*, Giesb., found in the western Baltic. is distinguished by the rounded lobes of th. som. 5 and a slightly different form of genital somite. The differences, having regard to the variation found in *E. affinis*, are almost inappreciable, and it is difficult to understand how it can be separated from the *hirundoides* form. Writers on the Baltic fauna, however, recognize these three forms as distinct species, and Dutch workers are able to distinguish *E. affinis* and *E. hirundoides* even when occurring together. As the latter has been recorded from British waters it is necessary to determine its systematic position.

So far as concerns British localities, it is true that in estuarine waters of high salinity, as in the Tamar, Thames and Tees, and at Falmouth, there is found a small slender form which has some or all of the characters given for *E. hirundoides*; but it does not seem possible to draw any real distinction between it and the type form. As is commonly the case, if the extreme forms only are known, the distinction is easy, but transitional forms are so common that points of difference disappear. Schmeil (1896, p. 116) has given, from examination of specimens supplied by Nordquist, the characters of *E. hirundoides*.

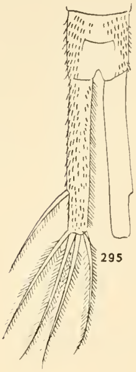
1. Body smaller and more slender. Length about ·9 mm. Furcal rami length to width: female, 8–12 : 1; male, 11–13 : 1.
2. Cephalothorax with median dorsal hump.
3. Th. som. 5 processes pointed or rounded.
4. Spinules on abdomen and rami fewer and smaller. None on dorsal side of rami in male.
5. Furcal setæ without sexual differences.
6. Antennule as long as thorax. Segments more slender.

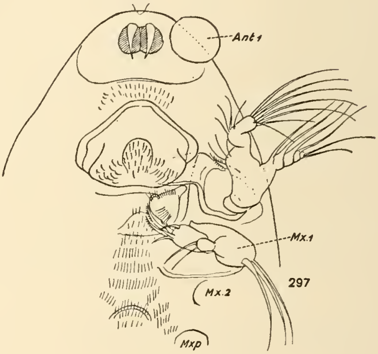
7. Swimming-legs more slender.

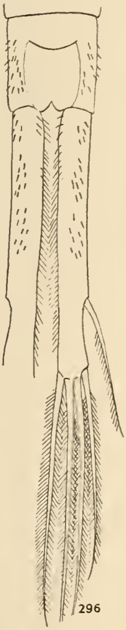
8. Egg-sac with few eggs.

De Lint (1922B, p. 82) adds, as the most important distinction :

9. Greatest width in head region, instead of middle of thorax as in *E. affinis*.







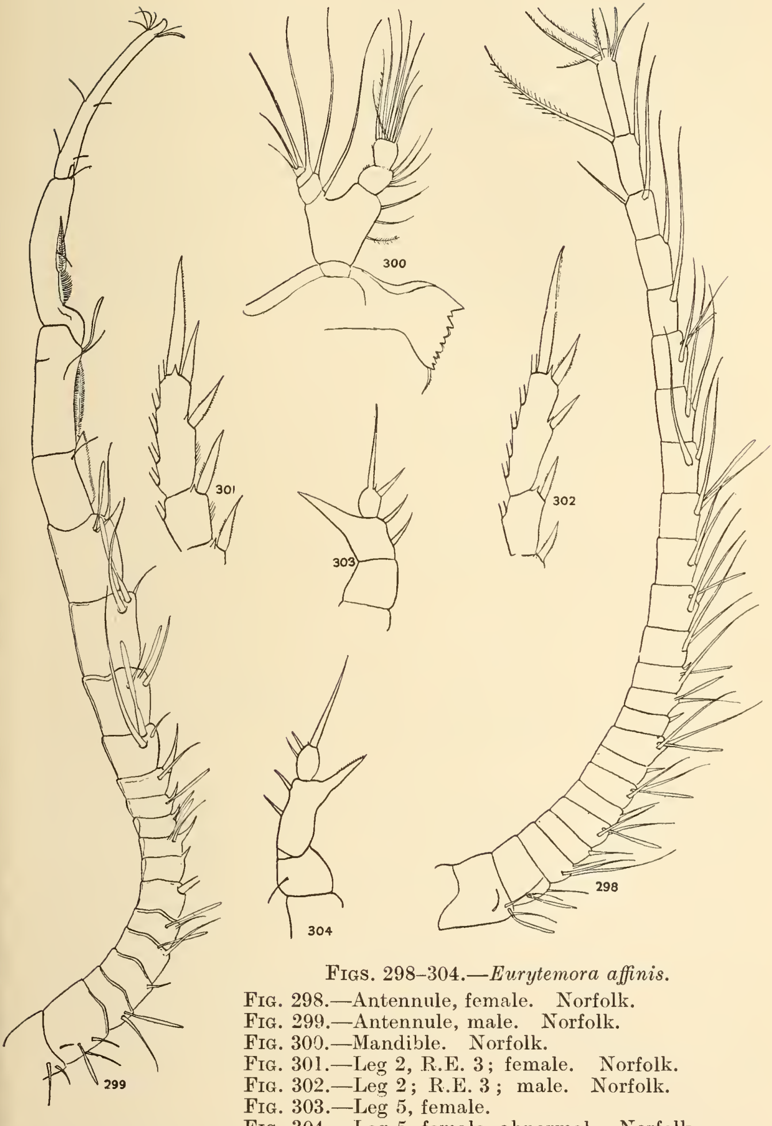
FIGS. 295–297.—*Eurytemora affinis.*

FIG. 295.—Furcal rami, female. Norfolk.
FIG. 296.—Furcal rami, male. Norfolk.
FIG. 297.—Head region, ventral. R. Tamar.

Taking these points in order :

1. So far as size is concerned there is every gradation, and in one population the range is great. For example, Falmouth (females) ·94–1·41 mm. ; R. Bure, 1·2–1·7 mm. ; R. Tees, 1·4–1·9 mm. The only British specimens which fall within the limits given for *E. hirundoides* are those from Falmouth and the R. Tamar.

2. While the dorsal hump is generally absent from the larger, heavier form, it is not always so. It is present in all specimens examined from the Tamar, but absent from the Falmouth form.



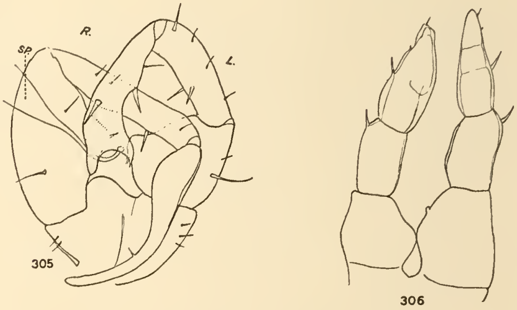
FIGS. 298–304.—*Eurytemora affinis.*

FIG. 298.—Antennule, female. Norfolk.
FIG. 299.—Antennule, male. Norfolk.
FIG. 300.—Mandible. Norfolk.
FIG. 301.—Leg 2, R.E. 3; female. Norfolk.
FIG. 302.—Leg 2; R.E. 3; male. Norfolk.
FIG. 303.—Leg 5, female.
FIG. 304.—Leg 5, female, abnormal. Norfolk.

3. The form of th. som. 5 is the same in all, except in the Falmouth form. Here the lateral wings may be either long and pointed, or rounded as in *E. hirundo*.

4. I have in all cases found some sexual difference in the length of the furcal setæ, but it is less in the pelagic forms, in which the setæ are long and slender in both sexes.

5. The presence or absence of dorsal spines on the rami of the male is not distinctive. They are always fewer in the male, and fewest in the pelagic form. I find the rami smooth in males from Falmouth and Tees.



Figs. 305, 306.—*Eurytemora affinis.*
Fig. 305.—Leg 5, male. Norfolk. *sp.* Spermatophore.
Fig. 306.—Leg 5, male, copepodid V.

Specimens from Norway labelled *E. hirundoides* by Sars (Norman Collection) have dorsal spinules. Dutch authors draw a distinction between *E. affinis*, which is found in fresh water in Holland, and *E. hirundoides*, which replaces it nearer the sea; but specimens from Grouw in Friesland (perfectly fresh, peaty water) have smooth, very slender rami. Great slenderness of the rami is characteristic of all the pelagic forms, but not necessarily associated with other characters of *hirundoides*.

6. The length of the antennule does not seem to be relied upon by De Lint. In one of her figures (1922, fig. 2) it is shown as short in *hirundoides* as in *affinis*. I

find it a little longer in the pelagic forms, but only markedly so in those from Falmouth, where it reaches beyond the thorax.

7. The slenderness of the legs characterizes all the pelagic races, irrespective of other characters.

8. Number of eggs is certainly of no importance. The Norwegian *E. hirundoides* has very numerous eggs, whereas typical *E. affinis* from Norfolk may have very few.

9. Although De Lint's figures seem to make a valid distinction in the shape of the thorax, I find nothing of the kind myself. Specimens from Friesland (which should be *E. affinis* !) are parallel-sided or very slightly wider in the head region. In the British race which most nearly agrees with *E. hirundoides* the greatest width is about the middle.

Measurements of Eurytemora affinis.

		Length.	Furcal rami.		Leg 5, male (left).	
			Width : length.	Dorsal spines.	Exopod 1.	Ex. 1:Ex. 2.
Plymouth . .	♀	1·37	1 : 6	..	..	..
R. Bure . .	♀	1·6–1·73	1 : 6·9	..	..	..
	♂	1·47–1·65	1 : 10·3	Present	2·8 : 1	1 : 1·12
R. Tees . .	♀	1·4–1·9	1 : 6–9·6	..	..	..
	♂	1·4–1·46	1 : 10	None	2·8 : 1	1 : 1·09
R. Alde . .	♀	1·37	1 : 10	..	..	..
	♂	1·27	1 : 10	Present	3 : 1	1 : 1·26
Firth of Forth .	♀	1·25	1 : 6·4	..	..	..
	♂	1·15	1 : 10·7	Present	3 : 1	1 : 1
Falmouth . .	♀	·94–1·4	1 : 8	..	..	..
	♂	·9	1 : 11	None	3 : 1	1 : 1·03
Tamar . .	♀	1·09	1 : 10	..	..	..
	♂	1·00	1 : 10·5	None	2·8 : 1	1 : 1
Friesland . .	♀	1·1	1 : 8	..	..	..
	♂	1·1	1 : 11	None	3·5 : 1	1 : 1·08
Norway . .	♀	1·2	1 : 8	..	..	..
	♂	1·15	1 : 11	Present	2·7 : 1	1 : 1

There is marked variation in the form of exopod 1 of male left leg. In Schmeil's figure it is short and broad (1 : 2·5), whereas in certain races it is nearly or quite

3 times as long as broad. The difference does not, however, distinguish the *hirundoides* form, since the narrow segment is found in all the pelagic races I have seen, including that from Friesland, but not in specimens from Norway, in which the proportion is 1 : 2·5.

There appears, therefore, to be no justification whatever for regarding *E. hirundoides* as a distinct species, and it is not even practicable to distinguish it as a subspecies or variety. It seems clear that, as is commonly the case, the pelagic races are smaller and more slender —no more. There may be here, as in *E. velox*, physiologically distinct races, but in this case there is to some extent an accompanying structural modification.

Distribution in Britain.

In Scotland recorded from the Forth, but the only record north of this is from the Bay of Nigg, Aberdeen (Scott). It appears to be absent from the north of Scotland, since it is not to be found in any of the Scottish Survey collections from North Uist, Orkneys or Shetlands, where it might be expected to occur in brackish water. Brady (1892) gives several localities, in brackish water: Hartlepool Slake, Durham; Burgh Marsh, Carlisle; R. Mersey; Beaulieu Lake, Hants; Swan Pool, Falmouth. He states (Norman and Brady, 1909, p. 114) that he has taken it in Talkin Tarn, a fresh-water lake in Cumberland, 12 miles from the sea. I am much indebted to Prof. Meek for a series of five rich samples of plankton from this lake. No *Eurytemora* were present. Brady has also recorded (1910) *E. lacustris* from Lea Mills pond near Sheffield. Prof. Cannon has kindly obtained samples from this pond, which now contains no *Eurytemora*.

In Norfolk it is abundant in the tidal regions of the rivers from the limit of pure sea-water up to beyond the range of its influence. It has been found established in Hickling and South Walsham Broads, and occasionally reaches Barton and Sutton Broads. Its distribution here overlaps that of *E. velox*. In the eastern estuaries from Thames to Alde I have not found it myself, but have received specimens from the Alde at Orford from Mr. R. E. Savage, while Hardy (1924) found it to be the most important item in the food of young herring in the Thames estuary at Leigh-on-Sea and Southend. I have taken it in the Glaven estuary at Blakeney in pure sea-water. It is abundant in the estuaries of the Tyne and the Tees. I am indebted to Mrs. Bartlett for a rich collection from the latter. In the sample *E. affinis* was dominant, but accompanied by *Acartia longiremis* and *Centropages hamatus*, so presumably they were taken in pure sea-water. In the Tamar, Percival (1929, p. 90) found its range to be between the salinities of $33^{\circ}/_{\circ\circ}$ and $\cdot 1^{\circ}/_{\circ\circ}$. It was dominant at Calstock, where salinity ranged from $7{\cdot}8^{\circ}/_{\circ\circ}$ at high-water to $\cdot 3^{\circ}/_{\circ\circ}$ at low-water.

Bull (1931) finds "*E. hirundoides*" extremely tolerant of oxygen deficiency in the polluted region of the Tyne. Its region of maximum abundance lies between 9 and 13 miles from the river mouth in the area of heaviest pollution, where dissolved oxygen may be *nil*.

Thompson records it in masses in filter-beds at Bootle, and also in the sea between Formby and Southport.

The Norman collection contains specimens from Plymouth, Salcombe and Lytham. I have had specimens from salt-marsh pools at Chelson meadow near Plymouth (R. A. Todd.)

DISTRIBUTION ABROAD.

(See Tollinger, 1911, p. 200.)

The species is abundant on the coasts of the Baltic and North Sea, ranging up rivers from salt, almost to fresh water. In the Elbe it is the commonest species of the plankton from Cuxhaven to Hamburg. In Dutch waters a distinction is drawn between the *hirundoides* form which inhabits the Zuider Zee and other salt waters, and the *affinis* form which lives in fresh water. De Lint (1922B) describes how, in Alkmaarder Meer, the latter alone is found in spring when the water is fresh, but is replaced by the *hirundoides* form in summer when the water level falls and salt water is drawn in from Zuider Zee. Levander draws much the same distributional distinction between the two forms, regarding *E. affinis* as characteristic of the "Bucht-plankton" and *hirundoides* of the "Kustenplankton" of the coasts of Finland. South-westwards it does not appear to extend beyond the coasts of the Channel (Seine and Croisic).

As Tollinger points out, there are two European centres of distribution, the one in the Baltic and North Sea, and the other in the region of the Caspian Sea. It is not found in the Black Sea and Danube delta, but occurs in the Caspian and in the Volga. Sars records it from fresh-water lakes in Central Asia in the territories of Akmolinsk and Atbassar.

In America it is recorded from both fresh and brackish water in the Gulf of Mexico. Marsh gives one locality, Black Bayou, which is 200 miles from the sea and 144 ft. above it. Foster found a small form (♀ ·69 mm., ♂ ·54 mm.) in fresh-water ponds at New Orleans. Northward it is found in the St. Lawrence and in Lake St. John, about 100 miles from the sea and 300 ft. above it (Willey, 1923A). Willey states that it is here a survival of the ancient fauna of the Champlain Sea. It is accompanied in this lake by another European species —*Laophonte mohammed.*

ACARTIIDÆ, Sars.

Body generally slender, the abdomen conspicuously short; th. som. 1 marked off from head; th. soms. 4 and 5 fused. Abdomen of female of 3 somites. Rostral filaments either absent or very delicate. Upper lip large, prominent, trilobed. Antennules long and slender, the segments ill-defined and reduced in number. Setæ generally feathered, some very long, and springing from swellings of the segments. Right antennule of male prehensile, but slightly modified. Antenna with endopod much longer than exopod, very slender, and with numerous setæ on basis. Maxillipede greatly reduced, much smaller than maxilla, and of peculiar form. Swimming-legs slender; endopods 2-segmented, spines of exopod reduced. Leg 5, female, very small, uniramous, 2- or 3-segmented. In male, prehensile, uniramous, of 4 segments in right leg and 3 in left.

Eggs not carried in egg-sacs.

The family was established by Sars for the genus *Acartia*, which had previously been classed by Giesbrecht and others with *Parapontella* and *Tortanus* in a subfamily of the Pontellidæ.

The relation between *Acartia* and *Parapontella* seems to be a very distant one. They have in common the very peculiar form of maxillipede, and, to some extent, of the maxillules, but in other respects they differ profoundly—particularly with regard to the antenna, mandible and swimming-legs. On the other hand, the genus *Acartiella*, with its short endopod on the antenna, endopod on leg 5, and swollen prehensile antennule, differs greatly from *Acartia*, and approaches very closely to *Tortanus*. All these genera are littoral, and primarily, according to Steuer, of tropical origin, and it may be that some of the resemblances are due to convergence; but this can hardly be the case with the strikingly similar leg 5, male, of *Acartiella* and *Tortanus*, and it cannot be doubted that there is some genetic relation between the two. Steuer postulates the origin of *Parapontella* and *Tortanus* from the same stem as *Acartiella*. No system of classification can fully express such relationships, and family divisions must generally be but a matter of convenience. There seem to be two alternatives: either to revert to Giesbrecht's superfamily Pontellidæ, with a subfamily Pontellinæ to include these four peculiar genera; or, if we are to follow Sars and to divide them among Parapontellidæ, Acartiidæ and Tortanidæ, then it seems necessary that *Acartiella* should be separated from *Acartia* and included in the Tortanidæ. It seems to me that the former procedure would be the most natural; but, dealing as we are here only with the genus *Acartia*, it will be easier to follow Sars and adopt the family Acartiidæ, with a definition which excludes *Acartiella*.

ACARTIA, Dana.

1846. *Acartia*, Dana, Ann. Mag. Nat. Hist. XVIII, p. 183.
1853. *Dias*, Lilljeborg, Crust. Ord. Trib. p. 181.
1892. *Acartia*, Giesbrecht, F. Fl. Neapel. XIX, p. 75.
1915. *Acartia* (with subgenera), Steuer, Zool. Anz. XLV, p. 392.

Thorax slender, greatest width usually behind middle; $2\frac{1}{2}$ to 4 times as long as abdomen. Th. som. 5 generally rounded, occasionally pointed or bearing spinules. Genital somite not laterally expanded. Abdominal som. 4 of male very small, sometimes partly fused with 5. Antennule, female, of 17 or 18 rather ill-defined segments. Right antennule of male geniculate, but with segments not expanded, without scale-like spines. Antenna with basis fused with endopod 1; this segment long and slender, with 9 setæ. Exopod shorter than seg. 1 of endopod. Mouth-parts of male and female alike. Mandible with large gap between two anterior teeth; exopod much shorter than endopod. Maxillule with endopod apparently absent. Maxilla with 12 very long curved spines reaching forward to mouth. Maxillipede with coxa apparently absent; basis broad; endopod much reduced. Exopod of leg 1 with long slender outer spine on each seg.; legs 2-4 with outer spines reduced to immovable teeth. Coxa without inner seta; basis generally without outer seta except on leg 4. Leg 5, female, of 3 segments, seg. 3 modified into a long spine. Leg 5, male, right leg the larger, exopod 2 with large inner lobe, and seg. 3 in form of curved clasper.

Type, *A. negligens*, Dana, Giesbrecht.

So far as I am aware no type of this genus has been expressely designated, and, in view of the fact that it will probably be split up eventually, it is important that a type should be fixed. Giesbrecht and Schmeil (1898), by mentioning *A. clausi*, Giesb., first, apparently regarded it as the type ; but according to art. 30 of the Rules of Nomenclature, a species cannot be selected as type which was not originally included in the genus. The genus was founded in 1846 without mention of species ; but in his Conspectus of 1849, and in the final report of 1852, Dana gave the following list of species : *A. limpida*, *A. negligens*, *A. tonsa* and *A. laxa*. As the first cannot be recognized, while *A. negligens* has been identified and redescribed by Giesbrecht, it seems that the latter should be regarded as the type of the genus.

Steuer (1915 and 1923) divides the genus into two series, *Acartiæ arostratæ* and *Acartiæ rostratæ*, and includes within it both *Acartiella*, Sewell, and *Paracartia*, Scott. The former differs so fundamentally from the rest that it should probably be included in the Tortanidæ, while the latter should be regarded as a distinct genus. The remaining Acartias are divided by Steuer into 6 subgenera, as follows :

Acartiæ arostratæ.
  Subg. *Acartiura*, Steuer. Type, *A. clausi*, Giesb.
Acartiæ rostratæ.
  Subg. *Euacartia*, Steuer. Type, *A. Southwelli*, Sewell.
  Subg. *Hypoacartia*, Steuer. Type, *A. macropus*, Cleve.
  Subg. *Acanthacartia*, Steuer. Type, *A. pietschmanni*, Pesta.
  Subg. *Odontacartia*, Steuer. Type, *A. lilljeborgii*, Giesb.
  Subg. *Planktacartia*, Steuer. Type, A. *negligens*, Dana.

While the species generally have the characters associated with life in the plankton of open sea, some of them have a preference for inshore waters and some are found in brackish water. On the British coasts four species have been recorded, and of these only *A. bifilosa*, Giesb., can properly be included in a brackish-water fauna; but *A. clausi*, Giesb., and *A. discaudata*, Giesb., are commonly found in estuarine waters, and their inclusion here may be convenient.

Key to British Species of Acartia.

1. Rostral filaments present . . . *A. bifilosa*, Giesb.
   Rostral filaments absent . . . . . . 2.
2. Furcal rami, female, as broad as long; setæ swollen at base . . . . . . *A. discaudata*, Giesb.
   Rami longer than broad, setæ not swollen . . . 3.
3. Th. somite 5 smooth, or with a row of small denticles. Leg 5, female, seg. 3 short and stout . *A. clausi*, Giesb.
   Th. som. 5 with slender spine either side. Leg 5, female, seg. 3 long and slender . . . *A. longiremis* (Lillj.). (see Fig. 327).

Development of Acartia.

(*A. clausi.*)

(Figs. 307, 308.)

Oberg (1912) has described the nauplius and 1st copepodid stages of *A. bifilosa* and *A. longiremis*, from which those of *A. clausi* are not distinguishable. There are, as usual, six nauplius stages, and the nauplius is characterized by the short furcal spines, oval body, and particularly by the fusion of the basal segments of the exopod of the antenna. This branch has a form strikingly similar to that of a Decapod zoæa, but without outer setæ. Only 5 segments are separated. In the form of the mandible *Acartia* differs considerably from other Calanoida. The masticatory process develops rather later than usual, the antennule having an unusually strong masticatory spine, and perhaps assuming the function of a mandible, as is usual in Cyclopoida. The endopod of the mandible is a large triangular lobe, unsegmented, with large inner spines. It is rather like that of *Paracalanus*, as figured by Oberg, and, in fact, it is to the nauplius of *Paracalanus* that *Acartia* bears most resemblance.

FIGS. 307–309, 311–313.—*Acartia clausi.*

FIG. 307.—Nauplius V.
FIG. 308.—Copepodid I.
FIG. 309.—Female, side view; estuarine form. Blakeney. ·9 mm.
FIG. 311.—Head of female, ventral view.
FIG. 312.—Head of female, side view.
FIG. 313.—Head of male, side view.

The copepodid stages have been described by Grandori (1912, p. 430) for *A. clausi*. According to him there are the usual five stages, but he found also, in the lagoon at Venice, a stage intermediate between III and IV, which did not occur in the open sea. On the other hand, three specimens of a stage in the male intermediate between V and adult were discovered in the open sea. Finally a moulted skin of an adult female was seen, indicating a second adult stage. There are, then, nine possible stages, though it is probable that development normally follows the usual course. At Plymouth I have found only five copepodid stages, the sexes being recognizable at stage IV by form of abdomen and leg 5. Leg 5 does not at any stage show any trace of an endopod. In stage I th. som. 4 is distinct, but the separation of som. 5 may also be indicated, which is unusual (Fig. 308).

Subgenus **ACARTIURA**, Steuer.

A. clausi, Giesbrecht.

(Figs. 309-322.)

? 1878. *Dias longiremis*, Brady, Mon. Brit. Cop. I, p. 51, figs.
1889. ,, ,, Bourne, J. Mar. Biol. Ass. Plymouth, N.S. I, p. 147, figs.
1889. *Acartia clausi*, Giesbrecht, Atti Acc. Lincei (4), V, p. 25.
1892. ,, ,, Giesbrecht, Faun. Fl. Neapel. XIX, p. 507, figs.
1899. *A. ensifera*, Brady, Trans. Zool. Soc. London, XV, p. 33, figs.
1903. *Acartia clausi*, Sars, Crust. Norway, IV, p. 150, figs.
1923. *A.* (*Acartiura*) *clausi*, Steuer, Arb. Z. Inst. Innsb. I, p. 93, figs.

Female.—Length, brackish-water form, ·70–·82 mm.; North Sea form, 1·47 mm.

Th. som. 5 rounded, typically with a row of small spines on either side, variable in number (2–4 either side), and with delicate hairs on ventral margin. In the brackish-water form these spines are absent, or represented by small hairs, and ventral hairs absent. Abdomen less than $\frac{1}{3}$ length of thorax; soms. 1 and 2 with posterior dorsal row of small spines, variable in number. Genital somite not laterally dilated, slightly protuberant ventrally, the protuberance in front of middle and sloping

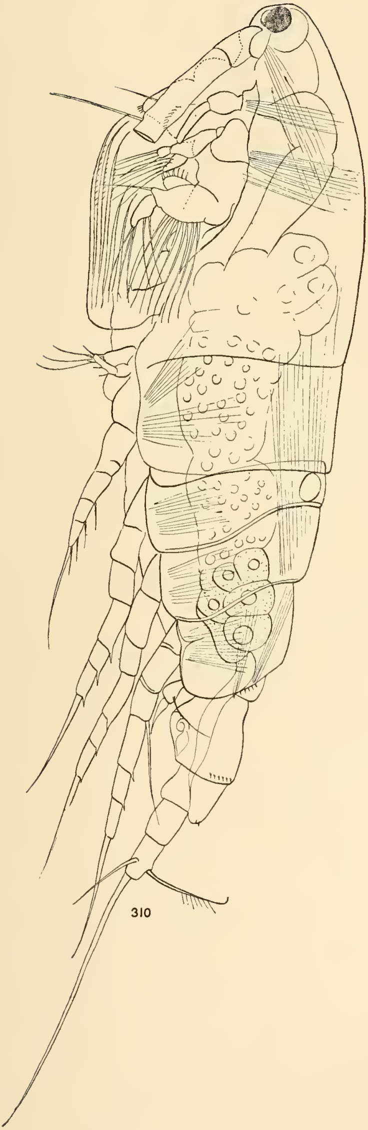
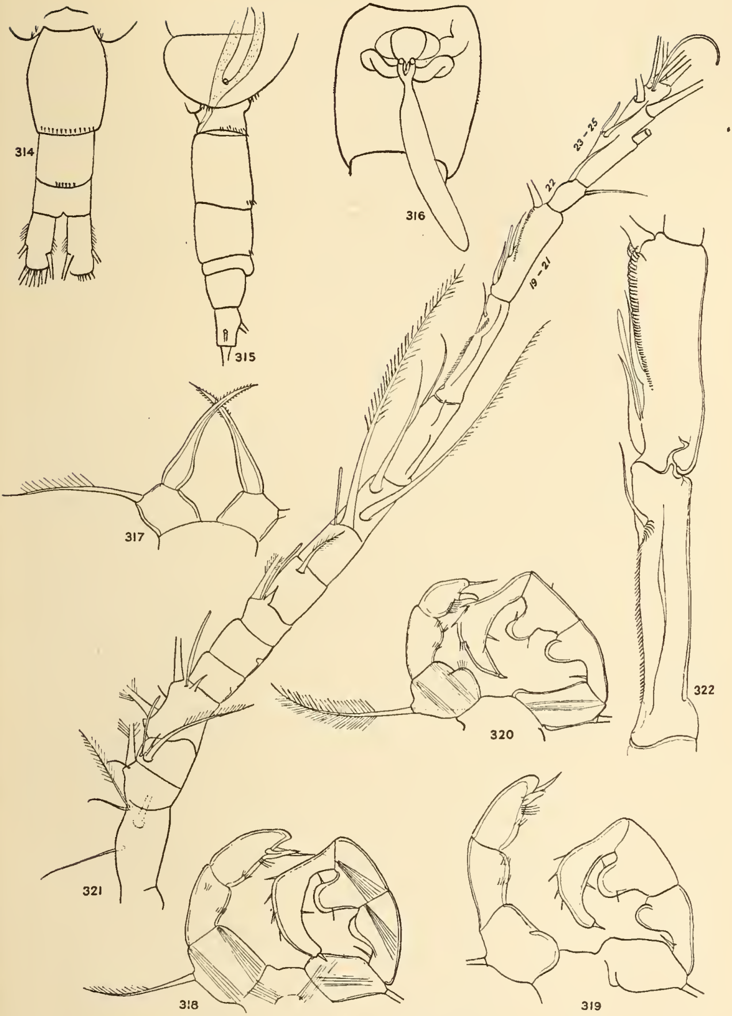


Fig. 310.—*Acartia clausi*, female. Plymouth.

backwards without indentation. Genital openings covered by an operculum. Receptaculum in the form of two coiled tubes meeting in middle line, where each has a small pore, and communicating on either side with oviducts. Furcal rami twice, or more than twice, as long as wide, the margins hairy in marine forms, but usually smooth in those from brackish water. Furcal setæ longer than abdomen. Rostral filaments absent. Upper lip large and prominent, fringed with short spines and with small spinules on surface; lateral lobes well defined. A large rounded protuberance in front of upper lip, with spinules on surface. Antennule reaching beyond end of thorax. Leg 5 with basis wider than long, outer seta very long. Exopod unsegmented, in form of a stout spine, slightly curved, and about three times as long as basis; armed towards end with stout spinules on either side.

Male.—Length, brackish-water form, ·71 mm.; North Sea form, 1·31 mm.

Abdomen relatively longer than in female; som. 4 well defined, but small. Furcal rami shorter than in female. Head, seen from side, with ventral outline different from female. In place of the large prominence at base of upper lip there is a small ridge, and another small prominence between it and the eye (Fig. 313). This sexual difference does not appear in the copepodid stages. Antennule shorter than thorax. Part distal to hinge consisting of 2 long segments, but a small segment corresponding to seg. 22 may sometimes be indistinctly marked off. Segs. 19–21 fused, but distinguishable by their setæ. Seg. 19 with spine-like seta and æsthete; seg. 20 with spine-like seta; seg. 21 with very long seta and anterior comb of stiff curved hairs. Seg. 18 has also an anterior comb of stiff hairs. (North Sea form, not in that of brackish water.) Leg 5 (brackish-water form), right side: basis longer than wide (25 : 19). Lengths of basis and exopod 1 and 2, 25 : 32 : 29. Inner lobe of exopod 2 very prominent,



FIGS. 314–322.—*Acartia clausi.*

FIG. 314.—Abdomen, female, dorsal view. Plymouth.
FIG. 315.—Abdomen, male, side view. Plymouth.
FIG. 316.—Genital somite, female, ventral view, showing spermatophore. Plymouth.
FIG. 317.—Leg 5, female. North Uist (brackish water).
FIG. 318.—Leg 5, male. North Uist.
FIG. 319.—Leg 5, male. Tunisia.
FIG. 320.—Leg 5, male. North Sea.
FIG. 321.—Antennule, right, male. North Sea.
FIG. 322.—Antennule, right; segs. 18 and 19 same antennule.

about as long as wide. Exopod 3 very narrow at base, curved, with 4 spines on outer edge and 1 on inner. Left leg: Lengths of segments, 29 : 27 : 34. Exopod 2 elongated, more than twice as long as wide, bearing distally a long spine on posterior face and a curved process with a brush-like truncated end. Spermatophore forked at point of attachment, each branch apparently a canal delivering spermatozoa to one receptaculum (see Steuer, 1923, p. 44).

VARIATION.

Steuer (1929) finds great differences in size between various races of *A. clausi*, and concludes that they are not geographical races, but that the smallest are found where salinity is lowest. Also that the number of spines on th. som. 5 varies inversely with the size. My own material confirms this conclusion, and it appears that the estuarine or brackish-water form is distinct from that of the high seas. I have had for comparison specimens from the North Sea, the Channel and from Garaa Achkel, a lake in Tunisia with a periodic connection with the sea at Bizerta. Here the water is of very low salinity in spring, and *A. clausi* is associated with *Paracartia latisetosa* and *Poppella guernei*. The following table of measurements shows how wide a range of variation is found. The estuarine form of Britain agrees with the Tunisian race in size and other details, and both are strikingly smaller than any high sea form. The specimens from the North Sea are larger than any mentioned by Steuer. A comparison of these giant individuals with the estuarine form shows certain small structural differences. In the Tunisian form there are a few minute teeth on th. som. 5, but none as a rule in British estuarine specimens. Also, in these brackish specimens there are no spines on the abdominal somites, and the rami are without hairs. The antennule is generally a little longer in the estuarine form. In leg 5 of male exopod 2 of left leg is markedly

Acartia clausi: *Table of Measurements.*

	North Uist, Loch Obisary.		Tunisia, Garaa Achkel.		Port Said Harbour.	North Sea.		Norway (G.O. Sars.)	
	♀	♂	♀	♂	♀	♀	♂	♀	♂
Length	·77–·82	·71	·83	·76–·82	1·13	1·36–1·47	1·28–1·31	1·15	1·00
Thorax to abdomen	3·6	2·6	2·86	2·7	2·57	3·3	3·7	2·9	..
Abdomen to rami	3·5	4·4	2·88	4·5	..	3·8	5·1	3·8	..
Rami—length : width	2·0	1·5	2·7	2·2	1·8	2·16	1·6	2·0	1·6
Denticles on th. som. 5	Absent		Small		Large	Large		Large	
Male leg 5: Length of basis and exopod 1, 2—									
Right	25 : 32 : 29		28 : 31 : 31		..	26 : 30 : 25		20 : 26 : 22	
Left	29 : 27 : 34		32 : 29 : 34		..	23 : 25 : 22		17 : 20 : 16	

longer than in the North Sea form, while the right leg of the latter has basis and exopod 1 distinctly more slender.

These differences are small, but quite definite, and it seems clear that there is an estuarine race physiologically and structurally distinct. It is probably this form which is mentioned by Farran (1913, p. 5) as found in Blacksod Bay, Clare Island. He states that a small form (♀, ·7 mm.) was found plentifully, together with others of normal size (♀, 1·15 mm.). On the other hand, De Guerne and Richard (1892, p. 12) record the finding of a relatively large form (1·15 mm.) in fresh water in the river M'bao, between Dakar and Rufisque, 3 km. from the sea.

The only marked variety of the species described is var. *gaboonensis*, Scott (Steuer, 1923, p. 7).

DISTRIBUTION.

This is a common species in marine plankton all round our coasts. Off the west of Ireland Farran states that it is always present at all depths from surface to 1000 fathoms; but that it also occurs in bays and harbours with low salinity together with *A. discaudata*. The small, brackish-water form has been seen in North Uist (L. Obisary) and in the River Orwell at Pinmills, near Ipswich. The typical form is distributed over the whole of the North Atlantic as far as the Faroes and Iceland, and in the Mediterranean eastwards to the Black Sea. It penetrates into the Suez Canal as far as Ballah. Westwards the typical form does not seem to extend beyond the 40th parallel, but it is represented on the American coast (Gulf of St. Laurence) by *A. clausi hudsonica*, Pinhey. Willey records the species from the Alaskan coast, but it is possible this was actually Pinhey's subspecies.

In the "Terra Nova" collections Farran (1929) found *A. clausi* common off New Zealand, and reaching as far south as 54° S. Brady's *A. ensifera* from New Zealand is a synonym of *A. clausi*.

Kuhlgatz (1898) has some interesting observations on the occurrence of *Acartia* in the Schwentine estuary near Kiel, but he did not discriminate between *A. longiremis* and *A. clausi*, so that some of the value of his facts is lost. Taking the two species together he found that the proportion of young to adults decreased from the sea river-wards, and there was also a decrease in total numbers, indicating that the species were not established in the estuary, but were recruited from the sea. On the other hand, some figures he gives (p. 14) make it probable that he had before him the two races of *A. clausi*, the one native to the sea and the other to the estuary. At the five stations, proceeding from B1 in open sea to M in nearly fresh water, the numbers were :

	B1.	B2.	D.	H.	M.
A. clausi *A. longiremis*	19	14	22	85	161
A. discaudata	12	3	4	25	38
A. bifilosa	1	1	1	1	1

These numbers are calculated against *A. bifilosa* = 1, but the absolute numbers show a great decline except at H, where I should postulate the stronghold of the estuarine form. The mean surface salinity per mille was :

B1.	B2.	D.	H.	M.
11·16	8·33	3·77	3·18	1·88

The figures show further that there is a distinct increase in *A. discaudata* at station H, which seems to suggest that there may be an estuarine race of this species too.

Acartia discaudata, Giesbrecht.

(Figs. 323–326.)

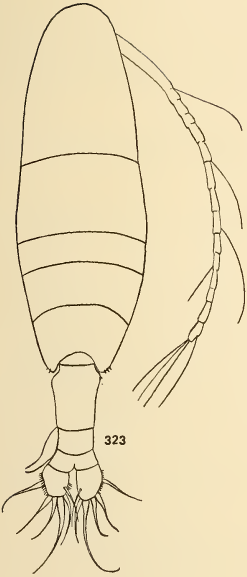
1881. *Dias discaudatus*, Giesbrecht, Zool. Anz. IV, p. 257.
1882. ,, ,, Giesbrecht, Ber. Komm. D. Meere, IV, p. 148, figs.
1892. *Acartia discaudata*, Giesbrecht, Fauna Fl. Neapel. XIX, p. 507, figs.
1903. ,, ,, Sars, Crust. Norway, IV, p. 152, figs.
1923. ,, ,, Steuer, Arb. Z. Inst. Innsbruck, I, p. 99, figs.

Female.—Length, 1·0–1·2 mm.

Body rather more robust than in *A. clausi*; greatest width behind middle of thorax. Th. som. 5 rounded, with a few small, irregularly placed spinules. Abdomen about two-fifths length of thorax, the somites smooth dorsally. Genital somite very protuberant ventrally and conspicuously broadened anteriorly. Som. 3 very much wider than som. 2. Furcal rami as wide as long, the margins fringed with spinules. Furcal setæ rather short, dilated at bases. Rostral filaments absent. Antennule reaching to end of thorax or just beyond it. Leg 5: Basis as wide as long; exopod slender, nearly straight, with or without marginal spinules.

Male.—Length, ·9–1·1 mm.

Upper lip showing the same sexual difference as in *A. clausi.* Abdomen with seg. 4 small, but distinct. Furcal rami longer than wide, with normal setæ. Antennule, right, with inner fringe of delicate spines on segs. 18 and 19 (Fig. 324). Leg 5, left: Basis with inner fringe of hairs; exopod 1 twice as long as wide, longer than exopod 2. Exopod 2, two spines, of which the proximal is the longer. Right leg very long and slender; basis with inner protuberance; exopod 1 more than twice as long as wide, with small basal prominence bearing a seta; exopod 2 with finger-like inner prominence; exopod 3 slender, much curved, with small denticles on outer margin. Spermatophore very large, broad in middle and rather pointed at distal end.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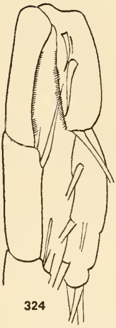
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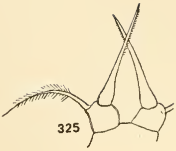
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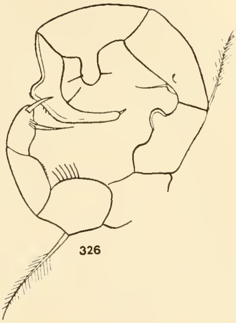
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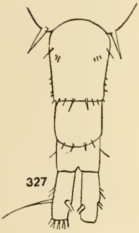
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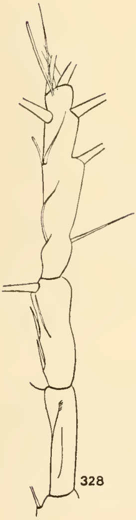
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Figs. 323-328.

(Figs. 323–326, *Acartia discaudata;* Figs. 327, 328. *Acartia longiremis.*)

Fig. 323.—*Acartia discaudata,* female, dorsal view, showing spermatophore.
Fig. 324.—*A. discaudata,* antennule, male, terminal segment.
Fig. 325.—*A. discaudata,* leg 5, female.
Fig. 326.—*A. discaudata,* leg 5, male.
Fig. 327.—*Acartia longiremis,* th. 5 and abdomen, female, dorsal view.
Fig. 328.—*A. longiremis,* antennule of male, part.

DISTRIBUTION.

The typical form is confined to the North Sea, English Channel, and Baltic ; a distinct form var. *mediterranea*, Steuer (1929) inhabits the western Mediterranean. British records :

Ireland : Ballynakill and Killary Harbours, Clare Island (*Farran*).

Scotland : Forth estuary (Scott).

England : Salcombe ; Fowey ; Plymouth (Norman & Scott).

I have found it myself in the Thames estuary at Burnham, and in Norfolk in Breydon Water, and the lowest reaches of the Bure, in almost pure sea-water. At times of exceptionally high tides it has been found at Stokesby, about 10 miles from the sea. A few specimens were found in one of the Scottish Lake Survey collections from Loch Obisary in North Uist, with *A. clausi*.

Kuhlgatz notes that, in the Schwentine mouth, it is most abundant in October and November, and that males greatly exceed females, the disproportion being the greater the less the salinity. According to his figures, it is tolerant of very low salinity.

It appears to be a species characteristic of river mouths and harbours, where the influence of fresh water is scarcely felt.

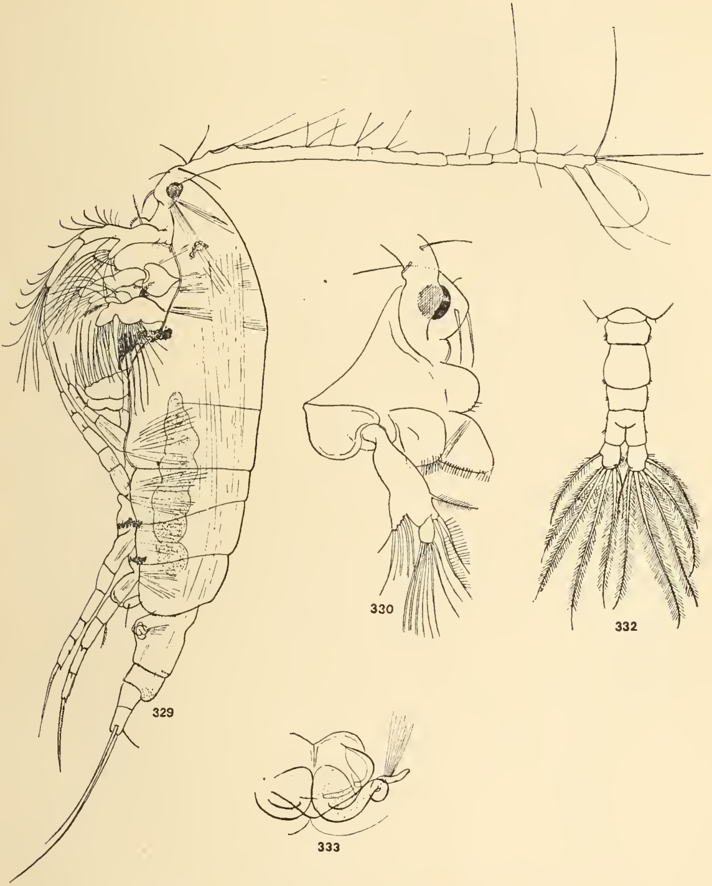
Subgenus **ACANTHACARTIA**, Steuer.

Acartia bifilosa, Giesbrecht.

(Figs. 329–344.)

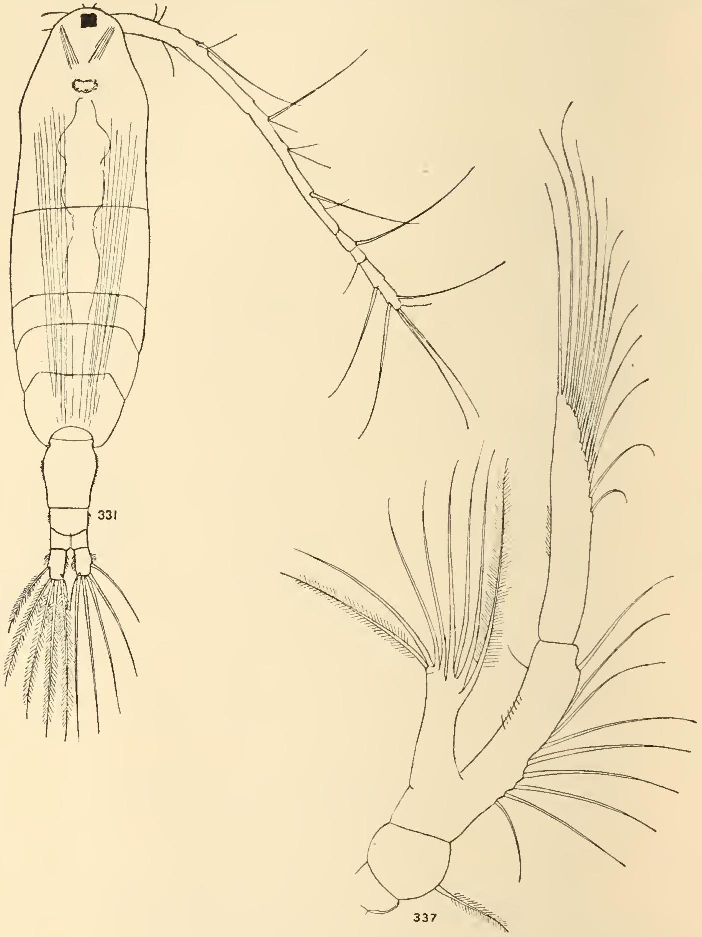
1881. *Dias bifilosa*, Giesbrecht, Zool. Anz. IV, p. 257.
1882. ,, ,, Giesbrecht, Ber. Komm. D. Meeres, IV, p. 147, figs.
1885. ,, *intermedius*, Poppe, Abh. Ver. Bremen, IX, p. 173, figs.
1888. ,, *bifilosus*, Nordquist, Calaniden Finlands, p. 81, fig.
1892. *Acartia bifilosa*, Giesbrecht, Fauna Fl. Neapel. XIX, p. 507, fig.
1923. ,, ,, Steuer, Arb. Z. Inst. Innsb. I, p. 110, figs.

Female.—Length, ·77–·9 mm. (R. Tamar, Plymouth). Greatest width of thorax in first free somite. Th. som. 5 rounded, without spines, but with a few small hairs. Abdominal somite 3 deeply cleft; som. 2 somewhat projecting dorsally, and overhanging the anus. Soms. 1 and 2 have transverse dorsal rows of minute hairs. Furcal rami nearly twice as long as wide, with hairs on both margins. Dorsal seta scarcely longer than ramus, delicately feathered. Terminal setæ not swollen



FIGS. 329, 330, 332, 333.—*Acartia bifilosa.*
FIG. 329.—Female, lateral, showing patches of blue colour.
FIG. 330.—Female, head, side view.
FIG. 332.—Male, abdomen, dorsal view.
FIG. 333.—Genital somite, female, ventral, showing receptaculum.

and very long. Relative length of thorax, abdomen (with furca) and furcal setæ 172 × 54 : 49 : 48. Rostral filaments present, long and slender. Antennule reaching to or just beyond end of thorax. Leg 5 : Basis about 1½ times as long as wide ; exopod more than twice as long as basis, straight and slender, with fine marginal spinules.

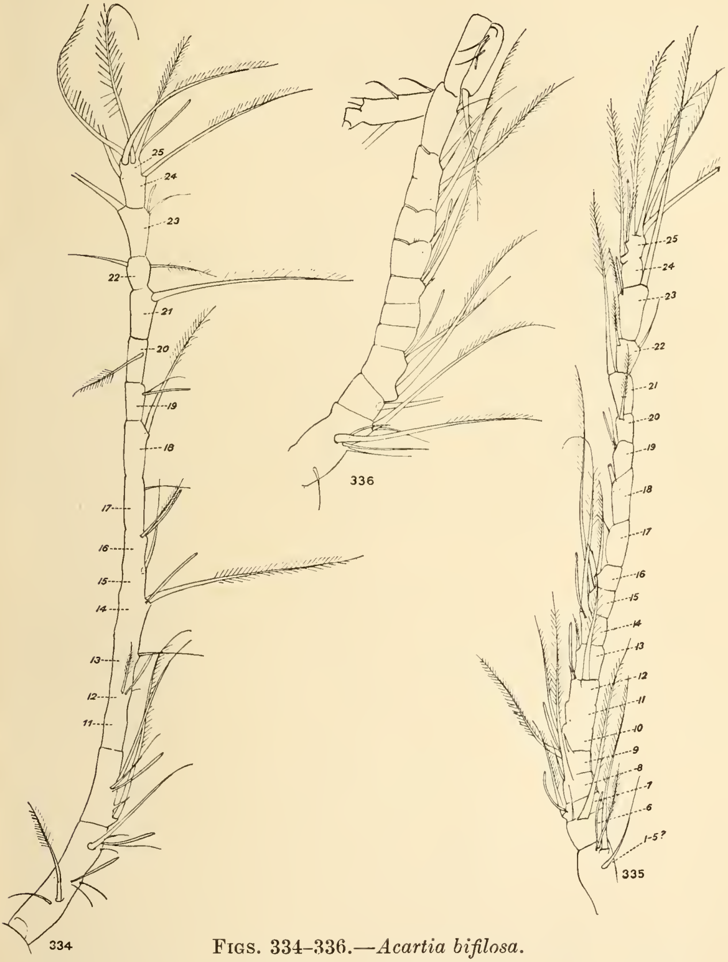


Figs. 331, 337—*Acartia bifilosa.*

Fig. 331.—Female, dorsal view. Fig. 337.—Antenna.

Male.—Length, ·77–·86 mm.

Lengths of thorax, abdomen and setæ 145 : 59 : 55. Furcal setæ 5 times as long as ramus. General form as in female, but eye larger and ventral outline of head differing, as in *A. clausi*. Abdominal somite 2 the longest: som. 4 scarcely defined dorsally. Furcal rami broader



Figs. 334–336.—*Acartia bifilosa.*

Fig. 334.—Antennule, female. Fig. 335.—Antennule, male, left.
Fig. 336.—Antennule, male, right.

than in female. Antennule not reaching end of thorax. Segs. 18 and 19 of prehensile antennule without inner comb of spinules. Leg 5, left: Basis a little longer than wide, with inner lobe; exopod 1 and 2 of equal length, the latter with 2 curved apical spines. Right leg: Inner margin of basis sinuate; exopod 1 with 2 small inner lobes; exopod 2 about as long as exopod 1, with an enormous inner lobe; exopod 3 rather slender, with outer marginal spinules, not greatly curved.

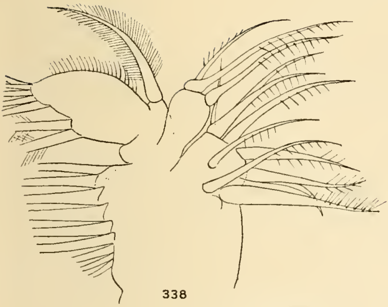
Variation.

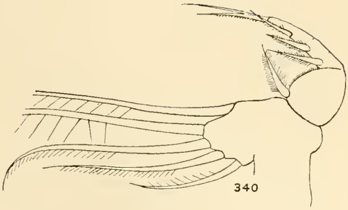
The form from the Jade estuary described by Poppe as *A. intermedia* is regarded by Van Breemen and by Steuer as a synonym of *A. bifilosa*. On the other hand, Timm (1896) states that it is distinguishable from the typical form and that it is characteristic of the coastal region from the Ems to the Elbe. Possibly this is a brackish-water form comparable to the small form of *A. clausi*; but I can offer no opinion on the subject, having had no material for comparison.

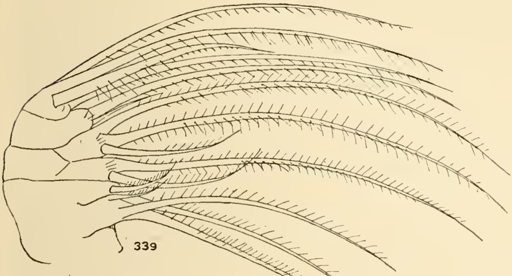
Distribution.

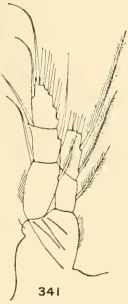
The distribution of the European *Acartias* is not very satisfactorily known, since, in the older literature, both *A. clausi* and *A. bifilosa* were confused with *A. longiremis*, which is, in fact, a northern and arctic species not found on our southern coasts.

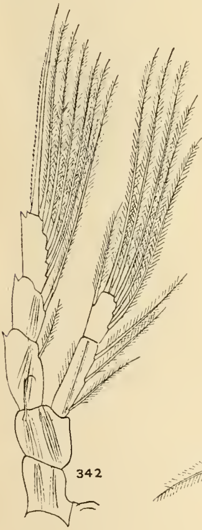
A. bifilosa is a species of limited distribution found throughout the Baltic, in the English Channel, the North Sea between Scotland and Norway, and on the Dutch coasts. It is not included by Sars in the fauna of Norway. Though recorded for the open sea, it is a characteristically brackish water and estuarine species. In the Baltic, for example, it occurs in the bays of Finland with low salinity (*e. g.* $2{\cdot}89\,^{\circ}/_{\circ\circ}$ Cl.) in company with *Eurytemora* and fresh-water fish, such as *Abramis brama* (Levander, 1901). In the Zuider Zee it forms 90% of the plankton, and the main food of Clupeids. In a salinity of $2{\cdot}8\,^{\circ}/_{\circ\circ}$

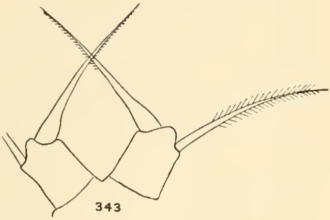


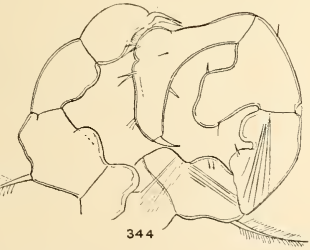












FIGS. 338–344.—*Acartia bifilosa.*

FIG. 338.—Maxillule.
FIG. 339.—Maxilla.
FIG. 340.—Maxillipede.
FIG. 341.—Leg 1.
FIG. 342.—Leg 4.
FIG. 343.—Leg 5, female.
FIG. 344.—Leg 5, male.

De Lint found 125 *A. bifilosa* to 1 *Eurytemora hirundoides* (1922, p. 295). Cleve (1900) records *A. bifilosa* from the mouth of the Congo, and gives its range as between 6° S. and 63° N. latitude.

British records are few. The Norman collection contains specimens from the Faroe Channel and N.E. Scotland, but it is not mentioned in any of T. Scott's numerous papers on British Copepoda, nor is it recorded by Norman and Brady from Northumberland and Durham, or by Norman and Scott from Devonshire.

In Norfolk it is common in the plankton of Breydon Water, and in the estuarine region of the rivers which discharge into Breydon, but it is only found in waters which are rather salt than brackish, and gives place to *Eurytemora affinis* as the salinity falls.

I have received abundant material from Prof. Percival taken in the Tamar estuary. Here there is a definite succession—*A. clausi. A. bifilosa, E. affinis.* As is the case in Norfolk, *E. bifilosa* is replaced by *E. affinis* as the salinity falls, its own range of tolerance being about $32°/_{oo}$ to $\cdot 3°/_{oo}$. As Percival's diagram (1929, p. 84) shows, the species dies out about at the point where there is a sudden drop in the salinity from $20°/_{oo}$ to $7°/_{oo}$. The only other locality in which I have met with it is Loch Obisary in North Uist (Scottish Lake Survey collections). The loch is the largest in the island, and consists of a number of deep basins connected by narrow channels. There is a small opening to the sea, and it is said to be tidal and to contain marine animals, such as mussels, but the weeds are those of fresh water.

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