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THE FAMILY ASCIDICOLIDAE AND ITS SUBFAMILIES (COPEPODA, CYCLOPOIDA), WITH DESCRIPTIONS OF NEW SPECIES

by

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SUMMARY

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ABSTRACT

A review of the family Ascidicolidae Thorell is presented, with reviews of the included subfamilies Ascidicolinae, Buprorinae, Enterocolinae, Enteropsinae and the new subfamily Enterognathinae. A synoptic presentation is offered of the subfamilies Botryllophilinae and Haplostominae. New species are described in the genera *Styelicola* Lützen, *Buprorus* Thorell, *Enterocola* van Beneden, *Lequerrea* Chatton & Harant and *Enteropsis* Aurivillius. Anatomical details of developmental stages in selected species in *Ascidicola*, *Enterocola* and *Enteropsis* are figured and described in support of our morphological interpretations.

RÉSUMÉ

Une révision de la famille des Ascidicolidae est présentée ici avec une revue des sous-familles qui en font partie : Ascidicolinae, Buprorinae, Enterocolinae, Enteropsinae et la nouvelle sous-famille des Enterognathinae. Les familles des Botryllophilinae et Haplostominae sont présentées de façon synoptique. De nouvelles espèces sont décrites dans les genres *Styelicola* Lützen, *Buprorus* Thorell, *Enterocola* Van Beneden et *Enteropsis* Aurivillius. Des détails anatomiques de différents stades de développement chez certaines espèces de *Ascidicola*, *Enterocola* et *Enteropsis* sont décrits et figurés et viennent renforcer nos interprétations morphologiques.

I. — INTRODUCTION

For many years we have pursued a joint study of copepods living in association with ascidians. The interest goes back to an early phase of study of copepods from the West Coast of North America by the senior author. Early in the research it was found necessary to restudy some of the forms described in the classic literature and a great quantity of material became available to us through a period of time spent by the junior author in laboratories on the Mediterranean, particularly at the Laboratoire Arago, Banyuls-sur-Mer. In addition, the unusual opportunities afforded to us at the Friday Harbor Laboratories have made it possible for us to develop an acquaintance with hosts and their associates in the living state to a degree which has not ordinarily been the lot of previous students of the group.

It is noteworthy that a great variety of organisms live internally with ascidians in varying degrees of relationship. Of the copepods there are members of several distinct lineages that furnish examples. A few members of the Harpacticoida live in definite association with certain ascidians. Most of the associated copepods are assigned to the broad group formerly referred to the Cyclopoida. Of these a few species, and these very probably not in a definite and obligate association, are referrable to the cyclopoid siphonostomes. A few more species, now distributed in a few genera, are members of the poecilostomes. There are particularly numerous and long-standing references to members of the genus *Lichomolgus*. The greatest number of species, and these in a series of genera showing a very wide range of adaptational divergences, are assigned to the Cyclopoida Gnathostoma. These include the many species of the family Notodelphyidae, in the sense of Illg, 1958 ; all but one of the few species so far known in the family Archinotodelphyidae ; and the species of the assemblage to be discussed below, the Ascidicolidae of the present treatment. All the copepods occurring in association with ascidians, and indeed any organism so existing, may properly be termed ascidicoles. The term ascidicolids has historically received a very wide application, as we demonstrate below, and in the treatment of several authors has included the Notodelphyidae as well as the diverse assemblage to which we now propose to restrict the concept. These gnathostome ascidicoles, including the three families mentioned above emphatically demonstrate a very important biological consideration. In every representative for which we have been able to find information the development is based on a lecithotrophic pattern. Although there are free-living developmental stages they are non-feeding and so there is throughout a trophic dependence, in every known species, on the symbiotic existence with an ascidian host. There is a graduation in the pattern expressed in this trophic dependence although exact information on feeding mechanisms and the precise formulation of the dietary components are very difficult to ascertain and rarely recorded. In the many species, probably the majority, living at the level of a rather simple commensalism, the problem is perhaps most difficult. In the cases of some of the actual parasites, which seem to be of rare occurrence, there are available some detailed findings (Dudley, 1968, for the remarkable notodelphyid species *Scolecodes huntsmani*, for example).

The great number of ascidicoles belonging to genera referrable to the family Notodelphyidae probably influenced Sars (1901-1903 ; 1921) when he proposed an ordinal classification for the copepods, to erect a suborder Notodelphyoida, including essentially all the known gnathostome ascidicole genera of that time. Wilson (1932) adopted Sars' taxon and expanded it by including a series of strongly anatomically modified symbionts of various invertebrates. Most of these genera have since been allocated to families substantially removed from the ascidicole complex, falling for the most part among the poecilostomes. Lang (1948) arrived at the important conclusion that the order Notodelphyoida had become obsolete. We concur and do not recognize the order as valid in the overall classification of the copepods. Lang's further suggestion that a considerable series of ascidicole forms, the " Enterocolidae and its relatives " are directly derivative from the poecilostomes as well, furnished in part the motivation leading us to study this group extensively, and particularly through the compilation of representative life histories. The information we have developed leads us to conclude that the gnathostome ascidicole series is for the most part a natural assemblage deriving from free-living ancestors among the Cyclopoida Gnathostoma. We thus revise Lang's suggested outline (1948, p. 27) which proposed a classification for the Cyclopoida Gnathostoma and Cyclopoida Poecilostoma. We alter the ranks of some of his categories and remove his Enterocolidiformes from the poecilostomes to restore it to the gnathostomes. We arrive then at the families Archinotodelphyidae, Notodelphyidae and Ascidicolidae, the latter subdivided into subfamilies Ascidicolinae, Buprorinae, Enterocolinae, Enteropsinae, Botryllophilinae and Haplostominae, with a new subfamily, Enterognathinae, for related forms which are not ascidicole but show many indications of relationship.

We have given much consideration to the matter of *Buprorus* and to *Enterognathus* and *Zanclopus*. Few specimens have ever been studied of these rare organisms and we have very little material. It seems clearly indicated that the only logical position for them in the overall system of the copepods must be in close relation to our group. It has seemed inconsistent to maintain a monotpyic family for *Buprorus*, although there is a long-standing tradition for such treatment. In the case of *Buprorus* all of the information so far available concerns the anatomy of the adult female, in which the appendages are considerably reduced. Study of the male and of the developmental stages has not yet been possible and remains essential for final resolution of the position of this form. Our conclusions derive very substantially from our familiarity with the remarkable series of modifications within the family Notodelphyidae. With these *Buprorus* shares the incubatory cavity in the adult female. However the most modified members among the notodelphyids have very reduced and altered appendages, these modifications falling into a very extensive series as now known, and there is no situation in which the pattern of modification conforms to the condition in *Buprorus*. The appendages here have struck us as basically ascidicolid, as we will attempt to demonstrate in discussion below. This leads us to deal with the question of the incubatory cavity in *Buprorus*, an extremely important diagnostic feature of all notodelphyids, by postulating a convergence. Since we are convinced that the notodelphyid and ascidicolid stocks are genetically fairly close in the first place, and since much more remotely connected copepods also have incubatory cavities, we adopt the convergence explanation as our working hypothesis.

A feature in certain of the lineages that make up the Ascidicolidae in our concept is great taxonomic refractoriness in certain genera. The genus *Botryllophilus* has been widely recorded as offering peculiarly great difficulty to the systematist and our own direct experience amply confirms this idea. A very similar case is involved when an attempt is made to deal with the taxonomy of the European species of *Enterocola*. The particularly accomplished workers Canu and Chatton and his colleagues have already recorded or intimated their problems with the best-known species *E. fulgens* (and its *forma E. betencourti*). Every collection, or even, every new specimen, has shown a tendency to confuse the concept based on pre-existing studies.

As we will discuss below in connection with the Botryllophilinae we are able to present only a sketch of a classification for this subfamily and must leave unresolved matters of synonymy and indeed actual identity of some of the long recorded species.

One of us, with a collaborator (Ooishi & Illg, 1977) have dealt with the basic taxonomy of the subfamily Haplostominae, so only a résumé of our findings is included in the present paper.

The name Ascidicolidae stems from the work of Thorell (1859) ; in his treatment, so remarkable for its day in its anatomical competence, the author restricted the taxon to the genus *Ascidicola*, as the subfamily Ascidicolidae in the family Notodelphyidae. He proposed the monotypic family Buproridae in the same work. The tradition of pioneering anatomical discrimination of the ascidicoles was continued for the Scandinavian and Arctic faunas in the work of Aurivillius and culminated in the monograph of G. O. Sars, (1921). In this approach the descriptionist attitude led to the proposal of many higher level taxa, many of which can be reduced in the general treatment of the present study. Substantial leadership in the modern trend of more synthetic treatment of the ascidicoles has come from the work of Lang (1948, 1949). It is remarkable that throughout the taxonomic history of the ascidicolids there has persisted a great emphasis on the ecological characteristics of association with ascidians. In the periods of synthetic treatment of the group, this criterion has continued to emerge. Even in the strongly comparative morphological and evolutionary outlook of E. Canu (1886, 1892, etc.), there is great persistence of this viewpoint. His family definition was one of the widest in scope of any and was directly influenced by this consideration. In his monograph (1892, p. 107), he states, in discussing Ascidicolidae : « Dans cette famille, j'ai réuni toutes les espèces commensales et parasites des Tuniciers, qui formaient autrefois les diverses familles des Notodelphidés Thorell, des Buproridés Thorell, des Kosmechtridés Della Valle équivalente aux Schizoproctidés Aurivillius, des Enterocolidés Della Valle, des Enteropsidés Aurivillius... Les Ascidicolidés, qui étaient à l'origine de parfaits gnathostomes nageurs, abrités seulement dans la branchie de leur hôte (*Notodelphys*), se sont peu à peu adaptés à l'existence cavicole en modifiant leur mode de locomotion dans différents sens (*Doropygus, Bonnierilla, Guenenotophorus*, d'une part ; *Ascidicola*, d'autre part). Changeant leur genre de vie et devenant de vrais parasites, ils se sont transformés en siphonostomes, par les divers stades : *Agnathaner, Enterocola, Enteropsis, Aplostoma.* »

It is only fair to emphasize that it was actually by comparative anatomical characters that Canu diagnosed the various categories within his group, and further, he was a most successful innovator in the extremely important approach of study of comparative life histories as a taxonomic supplement. In reaching a concept of the family he was much influenced by the strong evolutionary implications and (p. 186) states, in connection with his definitive diagnosis of the family : « ... Mais c'est bien pour les Ascidicolidae que semble écrite la phrase de Lamarck choisie comme épigraphe de ce travail (« Il n'y a que ceux qui se sont longtemps et fortement occupés de la détermination des espèces, et qui ont consulté de riches collections, qui peuvent savoir jusqu'à quel point les *espèces*, parmi les corps vivants, se fondent les unes dans les autres, et qui ont pu se convaincre que dans les parties où nous voyons des espèces isolées, cela n'est ainsi que parce qu'il nous en manque d'autres qui en sont plus voisines et que nous n'avons pas encore recueillies. » Lamarck, *Philosophie zoologique*, Première partie, chapitre III.) ; il n'est point, dans cette famille, d'espèces isolées : toutes s'enchaînent et se relient ; mes prédécesseurs ont pensé différemment parce qu'ils ignoraient encore les espèces établissant les relations les plus importantes, les types de passage sans lesquels ne peut être comprise la biologie de ces êtres.

Malgré la diversité des types qui la composent, je crois inutile de subdiviser actuellement cette faible série de Copépodes, où les délimitations génériques suffisent à tous les besoins de la systématique. »

We acknowledge as Canu's great contribution to the study of these forms his insistence on the evolutionary significance of the many degrees of adaptation to symbiotic existence and on the equal importance of study of development as an approach in analysis of the morphological complexities resulting.

The excellent start produced by Canu in analysis of the strangely modified ascidicolous forms was subsequently continued with great brilliance by Professor Édouard Chatton and two successive associates, M. Ernest Brément and, later, Professor Hervé Harant. It is most unfortunate that this program did not come to a climactic synthetic treatment, because the descriptions of new forms and the beginnings of formulation of concepts as to higher categories are at an absolutely first rank scientific level. The most notable contributions of this group are the extensions of knowledge of the subfamilies Enterocolinae and Haplostominae, both of which were proposed as formal taxa after a long period of usage informally — " enterocoliens " and " aplostomiens, " after terms set forth by Canu (1886a, p. 373-374). The formal diagnoses of Enterocolinae and Haplostominae (Chatton & Harant, 1924 b, p. 360-363 ; 1924e, 416-416) included the explicit statement that latter subfamily was placed in the family Ascidicolidae. Various more recent authors have apparently held a concept that included these taxa within a family Enterocolidae, although it is the usage that has furnished this indication, not explicit statements. The formulations of Chatton & Harant helped to lead us to our conclusion that a reconciliation of the many related but diverse gnathostomes in two major families, Notodelphyidae and Ascidicolidae is possible. It was the inspiration of the work of M. Chatton and his colleagues and the opportunity to study his specimens and to collect more material from his localities which led to the present paper.

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We wish to express our appreciation and hearty thanks to the institutions and persons mentioned in our account of the Material and Methods. Many others have generously contributed information and specimens and shared their time in some manner in connection with our studies. We must acknowledge the continuing support of the Department of Zoology, University of Washington; the number of helpful contributions from our colleagues and friends of the faculty and among the students, past and present, have been too numerous to list individually. The Department of Biology, Barnard College, Columbia University was a similar source of encouragement. We owe thanks in a variety of connections to: Dr. Takasi Tokioka, Seto Marine Biological Laboratory; M^{lle} Françoise Lafargue, Laboratoire Arago; Professor Hervé Harant, Université de Montpellier; Dr. D. L. Abbott, Hopkins Marine Station; Dr. Shigeko Ooishi, University of Mie; Department of Living Invertebrates, American Museum of Natural History; Station Biologique, Roscoff; Dr. J. F. L. Hart (Mrs. G. C. Carl); Mr. David Montgomery.

The base of our long-continuing studies was furnished by the direct collection of specimens and the obtaining of life history material by rearing procedures by Dudley at the Laboratoire Arago. By the courtesy of M. C. Delamare Deboutteville and M^{me} Édouard Chatton there became available to us at the same time the suite of specimens left by Professor Chatton, including many of this type specimens. The study of Dr. Dudley was supported by a grant of the National Science Foundation, GB-6474X2, to the senior author. Subsequent grants provided him the opportunity of several years of collecting, anatomical studies and the drawing and drafting of the preliminary presentation of our findings. Much of this work was done at the Friday Harbor Laboratories, University of Washington, then under the direction of Professor R. L. Fernald.

Some specimens were collected at the Stazione Zoologica, Naples and at the Marine Biological Laboratory, Plymouth by Dr. Dudley. We were able to examine some type specimens and other materials during brief visits at the British Museum (Natural History) and at the National Museum of Natural History (formerly United States National Museum). Many specimens and much advice on the taxonomy of hosts and on symbiotic interactions of copepods and ascidians were furnished by M. C. and M^{me} F. Monniot. Opportunity for the senior author to compile the final draft of this work was made by an invitation from the Muséum National d'Histoire Naturelle, with the sponsorship of Professors C. Lévi and C. Delamare Deboutteville, through the director, M. J. Dorst and his colleagues, as invited Associated Professor in this institution; the sejourn thus made possible was mainly passed in the laboratory of M. C. and M^{me} F. Monniot. We are much indebted to all those mentioned.

MATERIAL AND METHODS

Details have been provided in previous publications (Illg, 1958; Dudley, 1966; Ooishi & Illg, 1977) on the collection and processing of materials. Most anatomical studies were pursued on the basis of observations and dissections made by use of the lactic acid method described in the above references. A serious objection to this procedure has been the difficulty of preparation of permanent slide mounts of the dissections. A variety of media have been tried, but none has proven entirely satisfactory. Methods by which the dissected appendages arrive in a mounting medium by washing and transfer procedures are likely to result in the loss of some of the minute structures, such as the reduced mouth appendages of many of the species treated here. Mainly for this reason we have tried always to provide an entire animal as the holotype, preserved in alcohol, and we consider the preparations from which most of the anatomical drawings have been made as paratypic material. Types, as will be designated below, are installed in the National Museum of Natural History, Washington (numbers are designated by the traditional USNM rubric), in the Muséum National d'Histoire Naturelle, Paris, and in the personal collection of the senior author.

Drawings were almost entirely made by camera lucida. We take the opportunity to present a few illustrations prepared from the records of Professor CHATTON. Inking of the drawings, a number of the camera lucida renderings and most of the laborious task of composition of the plates have been the work of Ruth ILLG.

II. — FAMILY ASCIDICOLIDAE THORELL, 1859

Notodelphyidae, Thorell, 1859, p. 344-3589 (part) ; 1860, p. 117, 124-140 (part) ; 1862, p. 7-9, 14, 15-26 (part). — Claus, 1862, p. 102 (part). — Gerstaecker, 1863, p. 404 (part). — Claus, 1864, p. 379-380 (part). — Buchholz, 1869, p. 100-101 (part). — Brady, 1878 (vol. 1), p. 18, 30, 122-124 (part). — Claus, 1880, p. 553 (part). — Carus, 1885, p. 341 (part). — Thompson, 1893, p. 189-190 (part). — Graeffe, 1902, p. 39-40 (part). — Norman & Scott, 1906, p. 201-203 (part). — Norman & Brady, 1909, p. 400, 402 (part). — Schellenberg, 1922, p. 219-220 (part). — Brehm, 1927, p. 490 (part). — Sewell, 1949, p. 174 (part). — Barnard, 1955, p. 237 (part).

Notodelphidae Gerstaecker, 1863, p. 4021 (part).

Notodelphyiden Claus, 1875, p. 350 (part). — Timm, 1894b, p. 396 (part).

Ascidicolidae Thorell, 1859, p. 338, 340, 344-358, subfamily of Notodelphyidae (+ Buproridae, p. 340, 358-359) ; 1860, p. 119 (+ Buproridae, p. 119, 139-141) ; 1862, p. 14, 18, 56-57(+ Buproridae, p. 7, 14, 17, 61). — Gerstaecker, 1870-71, p. 719 (part). — Kossmann, 1874, p. 288-289. — Aurivillius, 1882b, p. 96-97, 108, 109 (part) ; 1883, p. 92-93, 104 (part). — Giard, 1888, p. 505 (part). — Canu, 1891a, p. 472, 475 (part) ; 1892, p. 25-30, 46, 54, 64-95, 107-108, 116-119, 127-133, 186-224 (part). — Giesbrecht, 1901, p. 76-77 (part) ; 1902, p. 455 (part). — Thompson and A. Scott, 1903, p. 273, 255 (part). — T. Scott, 1906, p. 363. — Calman, 1908, p. 177, 182 (part) ; 1909, p. 103 (part). — Chatton, 1909, p. 14 (part). — Chatton & Brément, 1909a, p. 12 (part) ; 1909b, p. 196 (part). — Smith, 1909, p. 66 (part). — Stebbing, 1910, p. 550 (part). — Gravier, 1912a, p. 70 (part) ; 1913, p. 66 (part). — Chatton & Brément, 1915, p. 143-144 (part). — Chatton & Harant, 1924b, p. 361 (part) ; 1924e, p. 416 (part). — Pesta, 1934, p. 8, 9, 11 (+ Buproridae, p. 8). — Lang, 1948, p. 25-27 (+ Buproridae, p. 6, 25, 26, 27 ; + Botrylliphilidae, p. 23, 25) ; 1949, p. 6. — Sewell, 1949, p. 153 (part). — Changeux & Delamare Deboutteville, 1956, p. 155 (part). — Gotto, 1957, p. 282. — Stock, 1959, p. 74 (part). — Bresciani & Lützen, 1962, p. 373. — Bocquet & Stock, 1962, p. 293. — Monniot, 1965, p. 158. — Stock, 1966, p. 211, 215. — Lützen, 1968, p. 96-97. — Gotto, *in* Anderson & Rossiter, 1969, p. 464. — Ooishi & Illg, 1977, p. 147.

Ascidicolidés, Gravier, 1913, p. 28. — Chatton & Harant, 1922c, p. 251.

In many regards the characters of the family still can be particularized in terms of the excellent discussion by SCHELLENBERG (1922, p. 277-281), although he refers to the assemblage as the subfamily Ascidicolinae and there are certain corrections to be applied to his terminology of the mouthparts. He does not include *Buprorus*, but the range of his discussion accounts for the genera *Ascidicola*, *Botryllophilus*, *Enterocola*, *Enteropsis*, " *Aplostoma* " and *Mychophilus*.

His approach was to construct a range of variation for each appendage and to show for this range two important considerations : 1) that the characters as they appear through the various genera, form the graduation ; and 2) that it is the graduation in variation that is the essential character for the familial definition. To a considerable degree he presses the points that the graduations consist of reductions and that these represent adaptations to progressive degrees of parasitic (or otherwise symbiotic) existence

Schellenberg demonstrated his conviction as to the close affinity of the ascidicolids and notodelphyids by including them in a single family. This view, it would appear, also led him to develop an impression of great significance of prehensile adaptations in the head appendages of the whole assemblage. A major defining feature of the Notodelphyidae then emerged in the very persistent presence of the prehensile antenna. By adding the incubatory cavity of the female, a diagnostic morphological criterion for this family, has been formulated which has very successfully confronted the addition of a great number of newly described forms (Illg, 1958; Illg & Dudley, 1961; 1965, Stock, 1967), and has also held good in a scrutiny of developmental evidence (Dudley, 1966).

Unfortunately to extend this first phase of the approach to the formulation of a definition of the Ascidicolidae involves the intellectually very unsatisfactory procedure of invoking negative criterian — the absence of prehensile modification of the antenna, and the absence of the incubatory cavity in the female. Indeed, even the negative criterian are not thoroughly applicable since the species of *Styelicola* and copepodids and males of *Enterocola* species have antennae with somewhat the aspect of prehensile modification, and females of *Buprorus* have the incubatory cavity (Schellenberg, in fact, was apparently puzzled by the indicated affinities of *Buprorus*, since he indicated in his treatment that he considered the relationship of the genus as unknown).

In developing his thesis on modification of appendages in ascidicolids, Schellenberg pointed out that his base forms — *Ascidicola* and *Botryllophilus* — show a very fair conformity in the head appendages to the notodelphyids, except for the antennae and the maxillipeds. The latter appendage shows a very strong modification for prehension in *Botryllophilus* (indeed, in all botryllophilins and haplostomins) in very distinct contrast to all notodelphyids. The conformity to this prehensile pattern in the maxilliped, or some degree of degeneration from it, formed a concept of emphatic significance in Schellenberg's definition of the Ascidicolinae. To some degree he was led into error by considering the maxillae of enteropsins and enterocolins to be maxillipeds and thus to conform to his series. In fact the latter two subfamilies lack maxillipeds entirely. But, this situation might in a way be considered to conform to a concept of modification of mouthparts as the essential prehensile device, with the transfer from one appendage to the next anterior of this powerfully expressive adaptive function forming part of a single evolutionary trend.

A character which Schellenberg also stressed as one unifying the ascidicolin (his term) lineage is the structure of the fifth legs. This can also be very reasonably endorsed in light of modern information. The pattern here is very emphatically a complex one, involving on the one hand trends to formation of very complicated structures including body elements beyond the mere appendages, and on the other hand proceeding in reduction to the point of complete disappearance.

Schellenberg discussed all the appendages in his diagnostic treatment. The range of material available to him from literature and from collections was distinctly limited, so that his presentation amounts essentially to a sketch. In adopting his basic viewpoint on the composition of the group and his approach in defining it, we propose to develop the treatment of the appendages, after his method, to the extent we can do so with our information.

The pronounced sexual dimorphism of the ascidicolids and the variety of habituses assumed by the females in relation to the various modes of symbiotic existence are reflected in great superficial anatomical diversity. This is dealt with below by describing the range of variations for each of the features of the body and the divergences found in the two sexes, as far as we can judge.

Body form is so variable in the Ascidicolidae as to defy formulation of an unequivocal statement in positive terms. Segmentation varies from clear-cut with well-demarcated units making up the greater part of the body to a condition of grub-like obsolescence of segmental boundaries and cuticular demarcations. The appendages demonstrate that there are as usual an apical piece bearing antennules and eyes and typically this is incorporated into a cephalosome including as well the antennae, the gnathal appendages, and the segment of the maxillipeds. The latter appendages are lacking in several instances but there are some developmental grounds for assuming the persistence of the segment itself. The first to fourth legs may originate on clear-cut segments, with good articulation of the protopodite on the body; alternatively there is a degree of graduation to a metasomal section without segmental demarcations. The substance proper of the fifth legs seems to participate in the formation of pediform projections, including these legs themselves as well, often serving to envelop the anterior portions of the egg sacs. There is often no clear demarcation between the metasome, the element of the pediform processes and the segment bearing the genital apertures ; as a result a complex not often found in other copepods makes its appearance here and suppresses the usual copepod major body articulation.

The urosome typically includes true abdominal segments, up to three, and the anal somite. There are two lines of modification. In many forms abdominal segmentation is reduced or obsolescent. In the botryllophilins a phenomenon of something like cuticular annulation either gives rise to supernumerary segments or results in the appearance of doing so ; exact morphological information for precise opinion in the matter is so far lacking.

Great inflation of the body and development to gigantic size, 8 mm body length in species of *Enteropsis*, are frequent among the trends in body modification. The cephalothorax tends somewhat less to modification and reduction than does the urosome. There are typically paired external ovisacs ; these may be fused, as in species of *Botryllophilus* ; in *Buprorus* there is an internal incubatory cavity and it is not known whether the egg mass is subdivided. The appendages are all modified ; in the females none retains the basic cyclopoid habitus, and a variety of modifications at the generic level is found. The basic form of the males is certainly of generalized cyclopoid habitus, but there are modifications of appendages. In most of the genera for which they are known, the males are actively swimming forms, and indeed this propensity may be the reason for the rarity of discovery of males in the hosts of the females.

There seems to be a rostrum basically, but it is reduced to absent in many representatives.

The antennule throughout conveys the impression of reduction and specialization. Among the females, of the long known species that of *Ascidicola* has the most developed segmentation, with five segments. There is a great number of setae borne on these segments, possibly indicative of a suppression of segmentation. Heavy sclerotization also suggests a considerable degree of specialization. In *Styelicola* there are seven or eight antennular segments. It would be easy to visualize a more numerously segmented antennule of quite reasonable correspondence to the cyclopinid type as the forerunner of this appendage in either case. One of the least well-known of the species we include is *Buprorus nordgaardi* Sars 1921. In the few figures he gives for the features of this animal, Sars depicts (pl. 37, fig. 1a 1), and corroborates by statement in the text, an antennule of seven segments. The appendage has a distinctive flattening and some slight suggestion of sclerotization. The general pattern of the segmentation and the setation suggest great correspondence with the antennules of the other species of *Buprorus*, which, however, have reduced segmentation (3 segments). A similar correspondence of the basic elements of the profusely setiferous 4-segmented antennules of some *Botryllophilus* females could also be surmised without too great exaggeration. In the other subfamilies of the present treatment the pattern of reduction of the antennule reaches such a degree that morphological continuities cannot be reasonably traced out. The antennule, or possibly the antenna, disappears in *Lequerrea*.

Although the most developed segmentation of the antennule is in the males and evidently the dimorphism is considerable, no male has been found with prehensile antennules. Unfortunately, the male of *Styelicola* is still unknown. The greatest number of antennular articles found is in the male of *Enterocola*, with seven or eight articles. These actually have fewer setae than the five-segmented antennule of male *Ascidicola*. The indications are that the males of enteropsins have nearly as full antennular segmentation and setation as in *Enterocola*. In males of *Botryllophilus*, as in the females, there are only four antennular articles, and a reduced setation, but on the basal article there is developed an enormous number of aesthetes. The male of the genus *Haplostoma* shows the same feature (Ooishi & Illg, 1977). The male is not known at all for buprorins.

The antenna strongly suggests affinity with notodelphyids in basic construction but differs in adult females of all genera but *Styelicola* by absence of a terminal, articulated, prehensile hook. The trends in reduction and specialization are distinctly different from any such in the notodelphyids. Our studies of development show that the basic antenna consists of a single protopod segment and a two-segmented endopod.

In the unfortunately little known genus *Buprorus* there is an antenna of such generalized cyclopoid aspect, with three segments, the terminal one bearing numerous setae, that it could be encountered on a species of cyclopinid. In several lineages — the botryllophilins, the haplostomins, enterocolins and enteropsins, although the modifications of the antenna are various, there is a strong trend to flattening of the whole appendage and to reduction in segmentation. In most of the subfamilies the antenna of the male is similar to that of the female. A most interesting exception is in *Enterocola*, where the antenna in the male bears a prehensile seta and is of a very different general aspect from that of the female. This is interesting also in reference to the presence on the early copepodids of *E. fulgens*, as depicted by Canu (pl. XIX), of somewhat similar antennae, extremely reminiscent of the appendage as it occurs in copepodids throughout the Notodelphyidae. In *Haplostomella* the males and females bear comparable highly distinctive antennae, with a distal curvature and stout terminal seta, suggestive of a possible prehensile adaptation.

There is typically a prominent labrum, and in many forms it exhibits distinctive ornamentation, but there does not seem to be an available generalization in this regard, serving as a family characteristic. Paragnaths and labium have not heretofore been found in any representative, this in contradistinction to the persistent occurence throughout the notodelphyids. However, in some ascidicolids there is a somewhat sclerotized, or even spinulose, postoral area on the integument, and for *Enterocola petiti* Guille, there is depicted (1964, fig. 1, d) a postoral area with seta-like structures inserted bilaterally. We present below a figure (fig. 1, g) of the paragnath of *Ascidicola* ; it is notahly like those of a number of notodelphyids. *Enterognathus* has been known since the original description to possess well-developed paragnaths.

The mandible tends to show clearly the basic gnathostome derivation of the whole stock. The masticatory base in *Ascidicola*, *Buprorus*, and *Botryllophilus* is typical. The reductions in mandibles in a somewhat graded series of examples we can also find paralleled in sequences of forms of notodelphyids. However, the mandibular palp, in such comparison with notodelphyids, is reduced even in the most generalized of examples, such as *Botryllophilus*. In some ascidicolids (enteropsins, enterocolins) the mandible disappears in the adults ; the comparable cases known among notodelphyids are in extremely modified forms only. Even in genera in either family lacking the adult mandible the persistence of the appendage in the early copepodids shows the gnathostome affinity, as constrasted with poecilostome development. Some of the trends in reduction in segmentation and setation seem to parallel somewhat those in cyclopinids. In the genera *Botryllophilus* and *Haplostoma* there is a sexual dimorphism in regard to characters of the mandible and in most cases for which the male is so far known, if the appendage is lacking in the female it does not occur in the male.

The maxillule is typically a modified appendage, and remarkably enough, is very rarely absent. The basal endite is present in botryllophilins, ascidicolins and buprorins, where it is well developed, with numerous setae, and overall strongly resembles that of notodelphyids and thus also cyclopinids and archinotodelphyids. The haplostomins show a graduation in this feature, since some genera lack the maxillule, but *Haplostomides* has a maxillule resembling that in botryllophilins ; the endite is prominent. The palp in these forms shows reduction of the exopodite to obsolescence and a general coalescence of the distal elements of the appendage. In enteropsins and enterocolins there is a distinctive modification. The bilohed appendage appears to preserve some biramous indications, although modified by coalescences. It remains probable also that one of the conspicuous lobes is actually the modified endite. Such a modified appendage suggests an aspect of arrest in a developmental stage.

The maxilla is remarkable in being almost typically cyclopoid in general aspect in botryllophilins and with little more modification in ascidicolins and buprorins. In none of these, however, will there be found the full development of endites or setae of the generalized appendage. The hasic cyclopoid elements are more strongly modified, strongly suggesting prehensile adaptation, in enterocolins and possibly *Enterognathus* and extremely so in enteropsins. In haplostomins the appendage is suppressed to absent and when present is a much rediced setiferous lobe. The appendage in botryllophilins, ascidicolins and buprorins is remarkahly similar to that in some of the modified notodelphyids living in compound tunicates. In enterocolins and enteropsins the maxilla is massive, seems to approach a prehensile condition and is very prominent in the mouthpart series. It resembles strikingly the maxilliped in botryllophilins and haplostomine.

Maxillules and maxillae are the same in the male as in the female of ascidicolins. There is good evidence to suggest sexual dimorphism in the maxillules and maxillae in botryllophilins and haplostomins, and the features involved in turn reinforce the impression of rather close relationship of these two subfamilies. In the male of some species of *Botryllophilus* the maxillules and maxillae are so suppressed in the adult stage that they have been overlooked in some examinations. In the enteropsins, based on what little knowledge we have of males these appendages may be expected to show much less dimorphism, but all indications are of some degree of reduction in males. The males of *Enterocola* show a distinctive trend of modification, with elongation of the appendages and their setae and loss of the gnathal processes.

The maxillipeds exhibit great diversity and the aspect in all cases is of strong modification from the basic cyclopinid appendage. In ascidicolins and buprorins the appendage is a reduced setiferous lobe like that in some modified notodelphyids from solitary tunicates. Enteropsins and enterocolins have lost the appendage. In *Enterognathus* either the maxilla or maxilliped is lost. In the botryllophilins and haplostomins there is an exaggerated modification to render the maxilliped the most salient appendage of the forebody. It becomes massive, conspicuously prehensile, and acts in a variety of functional applications. It remains remarkably consistent in structure throughout both subfamilies.

From indications so far, there is little dimorphism in the maxilliped ; the males of haplostomins and botryllophilins seem to have the appendage as well developed in proportion to the other appendages as do the females. In the family in general when the appendage is lacking in females it is also lacking in the males.

The four pairs of appendages of the second to fifth thoracic segments, usually referred to in copepods as the swimming legs, always show distinct modifications toward other functional applications in the females throughout the ascidicolids. The patterns are essentially generic and details will be provided below in the subfamilial or generic diagnoses. The sexual dimorphism of these appendages is pronounced and males tend to have the aspect of cyclopinids, with legs of actual swimming function, except perhaps the first leg of the male of *Botryllophilus*, and some species of *Haplostoma*, in which the endopodite is modified into a clasper-like structure.

The fifth legs in female ascidicolids show extremes of modification and, alternatively, reductions to disappearance. There are strong indications that protrusions of the actual body participate in the structure, particularly in the notably expanded legs. In the literature the various protrusions of the corresponding somite might be found referred to as pterostegites, oostegites, or fifth legs. In particular the school of Chatton tends to term the protrusions oostegites, doubtless because of the usual close association with the ovisacs. An early viewpoint suggested there was direct homology of the lamellar fifth legs of ascidicolids with the dorsal excrescences of various notodelphyids, such as *Notopterophorus*, and with the incubatorium of notodelphyids. This latter idea, particularly, has been refuted by Chatton and his associates. We are much inclined to agree in large part, except for designating the structures as oostegites, with the position of Chatton's group as stated in Chatton & Harant, 1924c, p. 405-406 : " Thus the oostegites of the Ascidicoles must be considered, not as being themselves the hypertrophied pereiopods of the fifth pair, but as dorso-lateral duplicatures homologous to those observed in *Notopterophorus*, some *Enterocola* species and in *Haplostomella tuberculata*, and carrying the pereiopods of the fifth pair, or their vestiges, on the free margin. They thus are not to be considered as simple appendages but as complexes formed of an appendage of ventral origin and of an integumental duplicature of dorsal origin. " We cannot go entirely as far as this statement. There are quite possible cases where the fifth legs have not appeared at all, in which case the protrusion on the sixth thoracic somite would be only a pterostegite. The homologies involved cannot be thoroughly traced until full anatomical information and the developmental sequences in the late copepodid stages have been worked out. It is pertinent to note that there are very few descriptions available of male ascidicolids, but those known are comparable in urosomal segmentation and in development of ventrally placed fifth and so-called sixth legs with those known from the notodelphyids.

We feel the term oostegite should not be used in application to any protrusion of the thorax, because of confusion with the term as otherwise applied in the higher Crustacea. There are undoubted cases of occurrence of pterostegites (i.e., *Enterocola pterophora*). There are perhaps instances of plate-like fifth legs (*Buprorus* spp.). But in light of present knowledge we prefer to use throughout the ascidicolids, for the females, the term pediform projection wherever the structure seems to support setae referrable to the cyclopoid fifth leg, and where the amount of involvement of additional structure is uncertain. In many cases in the ascidicolids these pediform projections are lamellate and, although they derive structurally from the somite of the fifth legs they associate very consistently with the oviducal apertures and with the ovisacs. The position may be ventral, lateral, or considerably dorsal, but they essentially take origin on the metasome. The pediform projections in botryllophilins, which are supportive of the dorsal ovisacs, fused into a single globular mass in most cases, are seen to originate more anteriorly from the metasome and thus apparently protrude from the segment of the fourth legs, because the somites are fused. In *Ascidicola* and *Styelicola* the body articulation is complicated by the great extension of the sixth and seventh thoracic somites and the accompanying enlargement of the pediform projections. A parallel situation appears in the Botryllophilinae; where in *Schizoproctus inflatus* and its near allies the pediform projections enclose the ovisacs and the body articulation is obscured by the related fusions and complexities. The Enteropsinae are distinctive in lacking fifth legs or pediform projections.

The pediform projections, in relation to the ovisacs, may envelop them completely, as in *Ascidicola* and *Schizoproctus*. They may tend to encircle the egg masses (or mass) extensively, without completely covering them, as in *Botryllophilus*. In many species of haplostomins and enterocolins the pediform projections form caps over the proximal portions of elongate egg strings and may almost encircle the urosome. In *Buprorus*, which has developed an internal incubatory cavity, the pediform projections are ventral and extend prominently, with no relation to egg protection, and they are perhaps no more than truly enlarged fifth legs.

On the seventh thoracic somite of female ascidicolids there may also be found setiferous projections, located at the oviducal apertures (*Ascidicola*, enteropsins, *Schizoproctus*, and others). These were referred to as vulvae in some of the descriptions of CHATTON and associates, but this usage does not seem appropriate. Such structures, when there are prominent setae, have often been referred to as sixth legs in the literature on cyclopoids. There is a possibility that some of the claimed occurrences of fifth legs in ascidicolids may derive from misidentification of these structures (see p. 96 below, in the discussion of Enteropsinae). These setiferous projections vary greatly in aspect through the various species and are undoubtedly complicated in anatomical composition. There is insufficient evidence to attempt further analysis of them at present.

The great complication in formation of the metasomal-urosomal articulation in the female ascidicolids to some degree parallels the phenomenon in notodelphyids, but only in the case of *Buprorus* does the ascidicolid body develop an inclosed incubatory cavity. It is rather more usual for the ascidicolids to form a genital-urosomal complex, but the diversity of arrangements is so extensive that no further general statement can be made. There is a great tendency for the oviducal apertures, supposedly diagnostic of the seventh thoracic somite, to open near the posterior basal juncture of the pediform projection with the body, just posterior to it, and on the urosome.

The notodelphyid and ascidicolid females evoke an impression of considerable similarity in the structure of the female insemination apparatus, and indeed the characteristic median insemination pore, also widely referred to as the vulva, is considered by CANU to be found throughout gnathostome cyclopoids, and still other major copepod stocks. The median pore of the female, the site of attachment of the spermatophores, is usually conspicuous and may have accessory sclerotizations ; it communicates by diverging branches with paired seminal receptacles lying laterally close to the terminations of the oviducts. Here at the apertures will be found the structural features discussed above as often referred to as sixth legs.

There is a great variety of modifications at the generic level of the caudal rami, particularly in females. Many of the features can be found to resemble most interestingly similar specializations among some of the notodelphyids. Reduction, but with only extremely rares case of complete disappearance perhaps forms one such trend. Sclerotization, as in *Ascidicola*, tends also to progress to conversion of the setae into hook-like elements, as in *Botryllophilus*. In the males, the caudal rami are much more cyclopoid, but too few instances are known to make broad generalization possible at this point.

In summary we can say that no ascidicolid adult female has a generalized cyclopoid habitus, although the appendages are basically cyclopoid, so such females could only be confused with nonovigerous notodelphyids and certain vermicole cyclopoids of more or less uncertain taxonomic position among the poecilostomes. The antennae of female ascidicolids almost always lack the terminal prehensile hook which is present throughout female notodelphyids. We find the configuration, segmentation, and setation of the antennae of ascidicolins, haplostomins, botryllophilins and buprorins to conform so consistently that we consider this a strong indication of the familial relationship, and diagnostic of the family. In the remaining subfamilies the antennae are extremely modified but we conclude they derive from this pattern. In a somewhat similar way the development of extensive expansions involving the fifth legs associates all the subfamilies except the enteropsins and contrasts with all notodelphyids. The enteropsins are so similar to the enterocolins in the remarkable modification of the mouthparts, including loss of the mandibles and maxillipeds, that there is no difficulty in assigning both to the ascidicolids. Although so few examples are known, the males have so far been assignable to their genera by the structure of the mouthparts. In assigning a male to the family, only the mouthparts would be satisfactorily diagnostic, and the whole series of these would have to be considered in combination.

KEY TO THE SUBFAMILIES

Mature females, preferably ovigerous, can be assigned to subfamilies by use of the following key :

1\. Internal dorsal brood-sack .... *Buprorinae*, p. 30

1″. No internal brood-sack 2

2\. No pediform projections or fifth legs .... *Enteropsinae*, p. 94

2″. Pediform projections and/or fifth legs varyingly developed 3

3\. Caudal rami ornamented terminally with clawed prehensile hook-like elements .... *Botryllophilinae*, p. 136

3″. Caudal rami ornamented with spiniform or setiform elements which may be much reduced. 4

4\. Pediform projection-fifth leg lobate, set with few, reduced setae, tend to substantial reduction.. *Haplostominae*, p. 132

4″. Pediform projections substantially expanded, lamelliform or lobate, usually setiferous.... 5

5\. Antennules well developed with 5 to 8 well-articulated setiferous segments .... *Ascidicolinae*, p. 16

5′. Antennules expressive of substantial reduction, few-segmented, weakly setiferous........ 6

6\. Basipodites of legs 1 to 4 with setae reduced to absent.................. *Enterocolinae*, p. 35

6′. Basipodites of legs 1 to 4 with conspicuous long lateral setae...... *Enterognathinae*, p. 151

We have felt it necessary to remove a species of ascidicolid from the genus in which it was described, because the details furnished by the author depart substantially from what are now rather well tested generic concepts. We suspect an actual confusion of parts of specimens was involved in constructing the original description, as discussed below (p. 132). We are at a loss, with the information available as to which subfamily would accept the species as described, so must place as *species incerta sedis* in the family Ascidicolidae *Enteropsis pilosus* Canu, 1886.

SUBFAMILY ASCIDICOLINAE, THORELL, 1859

Notodelphyidae Thorell, 1859, p. 344-358 (part) ; 1860, p. 117, 124-140 (part) ; 1862, p. 7-9, 14, 15-26 (part). — Buchholz, 1869, p. 100-101 (part). — Claus, 1862, p. 102 (part) ; 1872, p. 418-419 ; 1880, p. 553 (part). — Thompson, 1893, p. 189 (part). — Graeffe, 1902, p. 39-40 (part). — Norman & Scott, 1906, p. 201 (part). — Norman & Brady, 1909, p. 400, 402 (part).

Cetochilidae White, 1850, p. 115-116 (part).

Notodelphidae Thorell, Gerstaecker, 1863, p. 404 (part).

Ascidicolidae, Thorell, 1859, p. 338, 344-358, subfamily of Notodelphyidae ; Thorell, 1860, p. 117, 124-140 ; 1862, p. 7, 9, 14, 15-26. — Buchholz, 1869, p. 101. — Gerstaecker, 1870-1871, p. 719 (part). — Claus, 1872, p. 419 (part). — Kossmann, 1874, p. 288-289. — Brady, 1878, vol. 1, p. 30, 144-145. — Della Valle, 1883, p. 252. — Canu, 1891a, p. 20, 472, 475 (part) ; 1892, p. 64-96, 107-108, 116-119, 127-128, 130, 133, 186-224 (part). — Scott, T., 1901b, p. 241-245 (part) ; 1902, p. 455 (part). — Thompson & Scott, 1903, p. 255 (part). — Calman, 1908, p. 177, 182 (part). — Chatton, 1909, p. 14 (part). — Chatton & Brément, 1909b, p. 196 (part). — Smith, 1909, p. 66 (part). — Stebbing, 1910, p. 550 (part). — Gravier, 1912, p. 70 (part). — Chatton & Brément, 1915, p. 143-144 (part). — Sars, 1921, p. 63. — Chatton & Harant, 1924b, p. 361 (part) ; 1924e, p. 416. — Pesta, 1934, p. 8, 9, 11. — Lang, 1948, p. 25, 26, 27 ; 1949, p. 6. — Changeux & Delamare Deboutteville, 1956, p. 155 (part). — Gotto, 1957, p. 282. — Stock, 1959, p. 74 (part). — Bresciani and Lützen, 1962, p. 373. — Stock, 1966, p. 211-215 (part). — Lützen, 1968, p. 96-97.

Ascidicolinae Brady, 1878, (vol. 1), p. 144-145. — Carus, 1885, p. 341. — Chatton, 1909, p. 14. — Chatton & Brément, 1915, p. 143-144, 145, 148 (part). — Schellenberg, 1922, p. 277-298 (part). — Brehm, 1927, p. 490 (part). — Barnard, 1955, p. 237 (part). — Bresciani & Lützen, 1962, p. 373. — Gotto, 1966, p. 192.

Ascidicolinen Thorell, Claus, 1875, p. 350.

This taxon has been known for a very long time as monotypic, often under rather confusing alternative designation of Ascidicolidae, family, or Ascidicolinae, subfamily. The discovery by Lützen, 1968, of a second genus, *Styelicola*, represented at that time by a single species of very different habitus from that of *A. rosea*, produced a considerable expansion of the concept of the subfamily. The new species to be described below conforms very well in most features to Lützen's genus, but in general habitus is very similar to *A. rosea*. The male is not known for *Styelicola* so the formulation of a concept of the subfamily depends on the characters of the female.

The form of the body is variable, but in *A. rosea* and the new species of *Styelicola* the aspect is fusiform, with well-marked segmentation, obscured at the mid-body for formation of a complex bearing the expanded lamelliform pediform projections involving the fifth legs. In *Styelicola bahusia* the body might well be said to be enterocoliform, but most of the appendages and in particular the lamellate projections involving the fifth legs are readily diagnostic. The antennules are regularly tapered, of fairly numerous segments and regularly and fairly abundantly setiferous. The antenna is trimerous, the terminal segment with a prominent claw-like apical element in *Styelicola* ; in *Ascidicola* with four setae and a stouter spine-like element with a suggestion of prehensile modification. The mandible has a very strong, markedly toothed masticatory coxal lamella and a fairly prominent palp bearing several elements. The other mouthparts show distinct modifications, but form a part of a graduated series of adaptations found throughout the family. The "swimming" legs one to four show distinctive modifications, these varying most strikingly with the species. The fifth legs are involved in expanded lamelliform projections, each of which shelters a part or the whole of an ovisac. In *Styelicola* the fifth leg is further represented by an articulated endopodite bearing several well-developed setae. In *Ascidicola* the lamella is set with a single seta near its apex ; the configuration is not readily separated in description from the lamellate projections found in species of *Schizoproctus* in the Botryllophilinae. The caudal rami in the ascidicolins are variously modified and bear apical setae. Females of the two genera may be differentiated by means of the following key.

KEY TO THE GENERA

1. Fifth legs conspicuous expanded lamellae ; ornamentation a single seta. *Ascidicola* Thorell, 1859

1′. Fifth legs include a conspicuous expanded lamella, this supporting an articulated endopodite bearing several long setae.................................. *Styelicola* Lützen, 1968

Ascidicola Thorell, 1859

Notodelphys Allman, 1847, p. 2 (type, by monotypy, *N. ascidicola* Allman, 1847 [indeterminable species]) (part). — White, 1850, p. 116 (part). — Leuckart, 1859, p. 247 (part).

Ascidicola Thorell, 1859, p. 337, 340, 356, 347 (type, by monotypy, *A. rosea* Thorell, 1859) ; 1860, p. 116, 119, 127, 128 ; 1862, p. 6, 14, 57-59. — Claus, 1862, p. 102 ; 1864, p. 380. — Hesse, 1866, p. 52. — Buchholz, 1869, p. 149. — Gerstaecker, 1870-1871, p. 719. — Claus, 1872, p. 419. — Kossmann, 1874, p. 288-289. — Claus, 1875, p. 350-351, 360. — Brady, 1878, p. 21, 30, 145. — Kerschner, 1879, p. 20. — Aurivillius, 1882b, p. 95-97, 109, 110 ; 1883, p. 91-93, 105, 106 ; 1886, p. 45-46. — Canu, 1891a, p. 475 ; 1892, p. 29, 108, 204, 208-209, 214. — T. Scott, 1901a, p. 352. — Graeffe, 1902, p. 40. — T. Scott, 1907, p. 367. — Calman, 1909, p. 103. — Norman & Brady, 1909, p. 402. — Smith, 1909, p. 66. — Hartmeyer, 1909-1911, p. 1734, 1735. — Chatton & Brément, 1915, p. 144, 145, 147. — Sars, 1921, p. 64. — Schellenberg, 1922, p. 280, 281. — Brehm, 1927, p. 90. — Harant, 1931, p. 370. — Wilson, 1932, p. 599, 600, 626. — Pesta, 1934, p. 11-12. — Neave, 1939, p. 314. — Lang, 1949, p. 6. — Gotto, 1957, p. 281-289. — Monniot, 1959, p. 158 ; 1965, p. 158-159, fig. 43A-43U. — Gotto, 1966b, p. 162. — Lützen, 1968, p. 97, 101.

Coiliacola Hesse, 1862, p. 343 (type, by monotypy, *C. setigera Hesse*, 1862). — Neave, 1939, p. 794.

Coiliacea Hesse, 1863, p. 110 (misspelling for *Coiliacola* Hesse).

Coeliacola Sars, 1921, p. 64 (in synonymy, misspelling for *Coiliacola* Hesse).

We consider *Ascidicola* to be monotypic, so the characters of the genus are the same as those presented for the single species below. To assure the identity of the example from the Pacific Ocean studied by us with the species as long known from Europe we have had to study the anatomy of European representatives in detail We illustrate below mainly from specimens from France and find that the features correspond in our local specimens. We have collected here only females and cannot give new information about males.

Ascidicola rosea Thorell, 1859

(figures 1, 2, 3)

Notodelphys ascidicola Allman, 1847, p. 2-6, pl. 1, fig. 14, pl. 2, figs. 15-21 (type locality, Ireland, British Isles, in *Ascidia communis*) (part). — White, 1850, p. 116 (part).

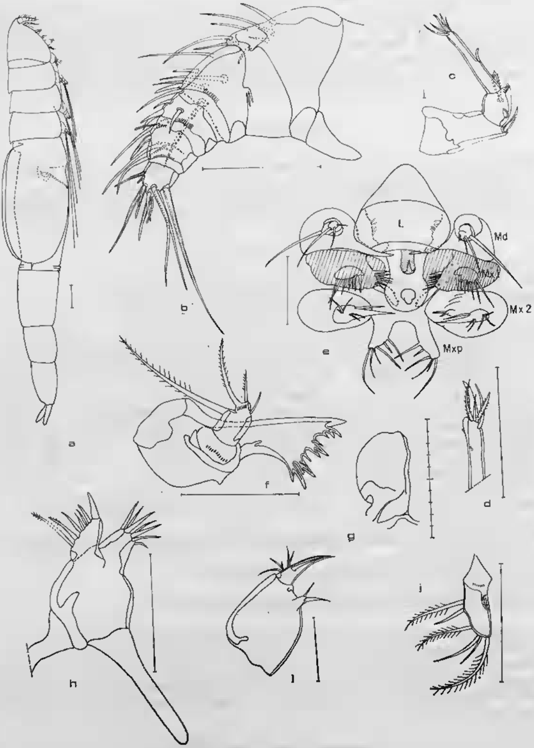

Fig. 1. — *Ascidicola rosea* Thorell, female : a, habitus, lateral view ; b, antennule ; c, antenna ; d, end of distal segment of antenna ; e, *en face* view of some cephalosomic appendages : L = labrum, Md = mandible, Mx1 = maxillule, Mx2 = maxilla, Mxp = maxilliped ; f, mandible ; g, paragnath ; h, maxillule ; i, maxilla ; j, maxilliped. Scale for a = 0.2 mm ; other scales = 0.1 mm.

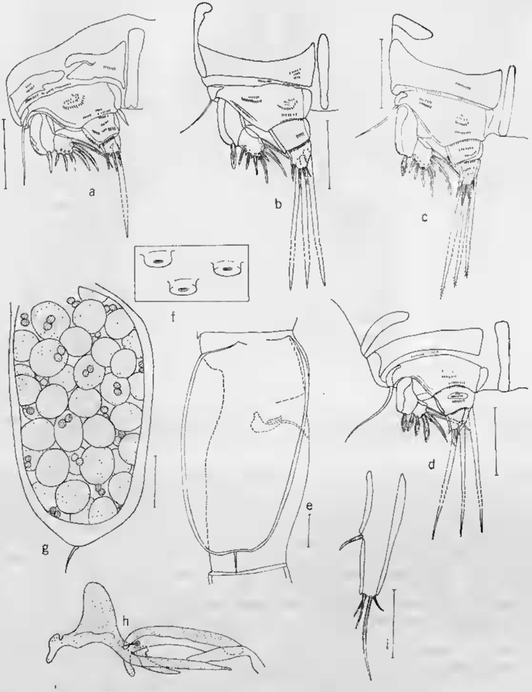

FIG. 2. — *Ascidicola rosea* Thorell, female : a, first leg ; b, second leg ; c, third leg ; d, fourth leg ; e, pediform projection-fifth leg, lateral view ; f, surface ornamentation of " fifth leg " ; g, internal surface of fifth leg enclosing sac of ova ; h, genital aperture ; i, caudal ramus. Scales for e and g = 0.2 mm ; other scales = 0.1 mm.

Source : MNHN, Paris

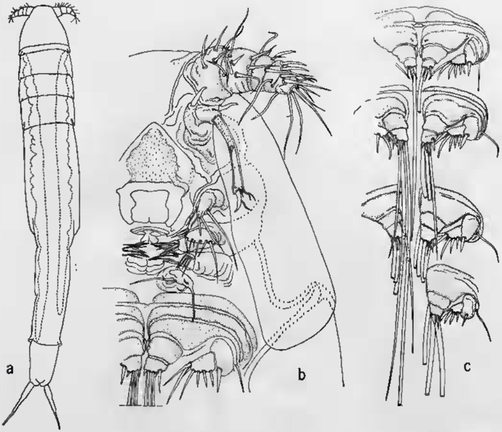

FIG. 3. — *Ascidicola rosea* Thorell, female, original figure by M. E. Chatton : a, habitus, dorsal view ; b, cephalosome and first legs, ventral view ; see figure 1 for labels ; c, legs 1 to 4, in place, ventral view.

Ascidicola rosea Thorell, 1859, p. 335, 337, 340, 343 (type locality, Skagerrak, Sweden, in *Ascidia intestinalis*, *A. parallelogramma*, *A. canina*, *A. aspersa*) ; 1860, p. 114, 115, 119, 123, 138 ; 1862, p. 5, 6, 7, 59-61, pl. 9, 10, fig. 13. — Buchholz, 1869, p. 101, 149-150. — Gerstaecker, 1870-1871, p. 775, 776, 777, 801. — Claus, 1872, p. 419. — Brady, 1878, p. 145-146, pl. 30, fig. 1-10. — Aurivillius, 1882a, p. 46 ; 1882b, p. 87-95, 111, 113, pl. xvi, fig. 13-22 ; 1883, p. 83-91, 106, 109, pl. 7, fig. 13-22 ; 1886, p. 45, 46. — Herdman, 1891, p. 210. — Canu, 1892, p. 67, 209. — Timm, 1894a, p. 159 ; 1894b, p. 396. — T. Scott, 1901a, p. 352. — Graeffe, 1902, p. 40. — Norman & Scott, 1906, p. 202. — T. Scott, 1906, p. 363 ; 1907, p. 367. — Norman & Brady, 1909, p. 402. — Riddell, 1909, p. 140. — Smith, 1909, p. 66. — Hartmeyer, 1909-1911, p. 1734, 1735. — Chatton & Brément, 1915, p. 145. — Sars, 1921, p. 64-66, pl. 31. — Schellenberg, 1922, p. 293. — Harant, 1931, p. 370. — Pesta, 1934, p. 12, fig. 8. — Leigh-Sharpe, 1935, p. 48. — Oorde-de-Lint & Schuurmans Stekhoven, 1936, p. 121, fig. 78. — Lang, 1948, p. 3, 19, 20-21, fig. 17 ; 1949, p. 6. — Sewell, 1949, p. 182, 184, 188, 190. — Millar, 1953, p. 78. — Gotto, 1957, p. 281-290 ; 1960, p. 216, 221. — Monniot, C., 1961, p. 98-99, fig. 1. — Bresciani & Lützen, 1962, p. 373. — Monniot, C., 1965, p. 158-159, 160, 161, fig. 43, A-U. — Gage, 1966, p. 229. — Gotto, 1966b, p. 162. — Lützen, 1968, p. 97, 101. — Hamond, 1973, p. 350.

Coiliacola setigera Hesse, 1862, p. 343-349, pl. 18, figs 1-15 (type locality, Finistère coast, in *Phallusia canina* and *P. intestinalis*).

Asidicola aculeoretusa Lang, 1949, p. 6, fig. 14-16 (type locality ,South Georgia, in *Pyura georgiana* Michaelsen). — Gotto, 1957, p. 283. — Lützen, 1968, p. 97, 101.

Distribution : Mediterranean to Norway and Sweden, British Isles, South Georgia.

Hosts : „ *Ascidia communis* ", *Ascidia aspersa, A. canina, A. intestinalis, A. mentula, A. parallelogramma, A. sordida, A. virginea.*
Ciona intestinalis, C. canina.
Corella parallelogramma.
Cynthia papillata.
Halocynthia papillosa.
Microcosmus, M. claudicans, M. nudistigma, M. polymorphus, M. sabatieri, M. vulgaris.
Phallusia canina, P. intestinalis, P. mentula, P. obliqua, P. virginea.
Pyura georgiana, P. micrososmus, P. papillosa, P. squamulosa.

We have listed the names of hosts above as we encountered them in the records of the various authors, leaving the task of compiling the proper synonymies to the authorities on ascidians. Our new records add some interesting host associations.

Specimens examined :

From *Microcosmus sulcatus* (Coquebert), *s. lat.* :
From Gaiola, Bay of Naples, Italy, 30-40 m, October 7, 1957, 2 females. Near Port Vendres, near Banyuls-sur-Mer, France, 50-25 m, May 13, 1958, 1 female.

From *Halocynthia papillosa* (Linnaeus) :
Gaiola, Italy, 30-40 m, October 8, 1957, 1 female.
Gaiola, Italy, 40 m, November 29, 1957, 1 female.
Cap l'abeille, near Banyuls, France, 25 m, May 7, 1958, 1 female.

From *Ascidiella aspersa*
Pozzuoli, Bay of Naples, Italy, 35 m, January 25, 1958, 1 female.

From *Rhopalaea neapolitana*
Gaiola, Italy, 30-40 m, October 7, 1957, 1 female.

From *Phallusia mammillata*
Stazione zoologica, Naples, Italy, physiological laboratory, January-February, 1958, 3 females.
Near Port Vendres, France, 70 m, 60-30 m, mixed trawl, May 6, 1958, 1 female ; 50-25 m, May 13, 1958, 1 female.

From *Corella eumyota* Transtedt
ELTANIN Cruise 12 station 1078, 61°27′ S-61°26′ S ; 41°55′ W-41°55′ W, 604 m, 5′ Blake Trawl, April 12, 1964, 1 female.

From *Molgula euplicata* Herdman
ELTANIN Cruise 27 station 1878, 72°57′ S-72°58′ S ; 171°35′ E-171°38′ E, 576-573 m, 5′ Blake Trawl, January 15, 1967, 1 female from esophagus of host.

We are indebted to M. C. Monniot for the indentification of the ascidians in the antarctic material listed just above. From his collections from the coasts of Europe he has also provided us with the following host records for

Ascidicola rosea : *Diazona violacea* Savigny. Banyuls-sur-Mer ; *Ascidia obliqua* O. F. Müller, Kristineberg ; *Polycarpa pomaria* (Savigny), Banyuls-sur-Mer ; *Styela partita* (Stimpson), Banyuls-sur-Mer. We have also :

From *Polycarpa obtecta* Traustedt
Gulf of Mexico, Alhatross Station 2405, 30 fathoms, USNM 452, March 15, 1885, 1 female.

From *Styela coriacea hemicaespitosa* Ritter :
Off Cerros Islands, Lover California, Mexico, Albatross Station 2838, USNM 92218, May 5, 1888, 2 females.

From *Ascidia paratropa* Huntsman :
Satellite Channel, British Columbia, Canada, August 7-10, 1963, 4 females.
Northwest coast of British Columbia, exact locality unknown, no date, 2 females.

Unidentified pyurid tunicate :

> Off coast of Southern California, University of California collections : " Channel Dredge, " June 18, 1901, 2 females.

Description :

Female : The overall length in a representative specimen, to the ends of the caudal rami is 3.6 mm. The body (fig. 1, a) has been frequently figured and described. It is markedly cylindrical with a slight posterior taper. The cephalosome has a strongly developed shield, which overlaps the first segment of the metasome. The composition of the metasome is complicated by the coalescence of the segments of the fifth legs and of the genital apertures and possibly one abdominal segment. The body articulation has been variously interpreted, but descriptively, the metasome can be stated to consist of 4 clearly delimited leg-bearing segments and a long complex region bearing the fifth legs and the genital apertures. The usual major body articulation is not formed. The urosome then consists of 3 clearly articulated segments, 2 lacking appendages and terminating with the anal somite and its caudal rami. It was only lately pointed out (Gotto, 1957 ; Monniot, 1965) that the anal somite bears at its anterolateral margin a wide transverse pad set profusely with cuticular projections (Gotto, 1957, fig. 1). This structure is not depicted in the figures here and is rarely observed on preserved material. Fixation causes a slight contraction, sufficient to telescope the urosomal articles and retract the pad. We were struck by the observation that a similar pad is developed on the dorsal surface of the urosome of *Styelicola lighti* (figs. 4a, 6e).

The antennule (fig. 1, b) is short, thick, 5-segmented, and the articles are heavily sclerotized. All the setae of the appendage are stiff and most are short. The armature of the 5 articles, I-IV, is as follows : I — 8 setae ; II — 7 setae ; III — 5 setae, 1 asthete ; IV — 3 setae, 1 aesthete ; V — 8 setae, 2 aesthetes. Further ornamentation consists of ridgings of the cuticle.

The antenna (figs 1, c, d) is trimerous, the articles decreasing in width distally. All the articles are heavily sclerotized. The basal article has a stout seta at the distal medial corner. The second article has a flattened spine on the surface ; there is a sclerotized lobe on the opposite surface at the proximal third. A row of spinules ornaments the distal medial corner. The terminal article is very narrow, its length about equals the combined lengths of the 2 basal articles. There is a seta in an emargination at the middle of the medial margin. Distally there is 1 spine with a slightly hooked end, 2 spinulose elements of the same length as the spine and 2 curved, stiffened setae, one about one third longer than the other. A curved row of spinules ornaments the face of the segment at the distal fourth.

The remaining cephalosome structures are described in the orientation of an *en face* view (fig. 3, b). The labrum has a more or less simple posterior margin, but bilaterally placed dorsal sclerotizations bear on either side a row of spiniform processes.

The mandible (figs. 1, e, f) consist of the unimerous protopodite and bimerous palp. The protopodite extends medially as an extremely large masticatory lamella, the medial margin of which is formed of a series of teeth of very characteristic form, some bipartite and some tripartite. The basal article of the palp bears no armature but is ornamented with a single row of spinules. The distal article has an emargination at the lateral fourth and below this there is articulated a long seta. The apex bears 2 setae and there is an additional seta at the distal medial fourth. The setae are graduated in length from medial to lateral around the apex. A row of spinules is set at the bases of the 2 terminal setae. A pair of small paragnaths (fig. 1, g) is set on a transverse postoral sclerotization at the bases of the mandibles. The paragnath is a lobe with sclerotizations at the base and along the lateral margin. The much thinner distal portion has a rounded contour.

The maxillule (fig. 1, g) is a bilobed structure, the segmental composition obscure. The medial lobe, probably the basal endite, bears 7 setae. The lateral, more ventrally placed lobe bears 7 spines and gives no indication of possible composition as to segments or rami.

The maxilla (fig. 1, h) is bimerous, the proximal article longer and very much wider than the distal. At the distal medial corner of the basal article there is a small endite. Distally this endite tapers as a spiniform process. There is a setule inserted at the base of the process. The distal article narrows into a slightly hooked process, at the base of which on the anterior face there is a closely appressed seta. Five small setules articulate on the ventral margin proximal to the hook.

The maxillipeds (fig. 1, i) are joined together by a medial plate so that the pair has a common articulation on the body. Each consists of a long, flat lobe, with three apical setae and three medial setae.

The first legs (fig., 2, a) are biramous with bimerous protopodites and rami. The coxopodites unite medially to form a common articulation with the body. There is a medial apparatus, consisting of an elongate bar distal to the common base. There are distinctive sclerotizations. Rows of spinules ornament the sclerotized and unsclerotized areas. The basipodite is much extended medially so that the bases of the rami are at markedly different levels. There is a long seta at the distal lateral corner of the basipodite, and a spine at the distal medial corner. The basal article of the exopodite bears a spine at the distal lateral corner. A patch of spinules is set just proximal to this. The distal article articulates obliquely on the basal and bears 3 lateral spines, 3 terminal spines and a small spine, set in front of 2 of the terminal spines. There are 2 spinules at the base of each spine. The basal article of the endopodite has no armature but is very spinulose. The terminal article has 3 apical spines. Articulating at the middle of the posterior face there is a single very long seta (.34 mm long in the specimen examined).

The second leg (fig. 2, b) is biramous with bimerous protopodite and rami. The protopodite, exopodite and basal article of the endopodite are as in the first leg except that the basipodite lacks the medial distal spine. The terminal article of the endopodite has 4 distal spines and 3 very long setae articulating on the posterior ace. The most proximal end medial of these setae is .97 mm long. The middle seta is .67 mm long, the lateral is .39 mm long.

The third leg (fig. 2, c) is biramous with bimerous protopodite and rami. It is just like the second leg. The very long setae measure .91 mm, .53 mm, and .4 mm, respectively, from medial to lateral.

The fourth leg (fig. 2, d) is biramous with bimerous protopodite and rami and the protopodite is much as in the preceding 2 pairs of legs. The basal article of the exopodite has a single spine at the distal lateral corner. The terminal article bears 2 lateral spines, 3 terminal spines and a short spine, articulating somewhat on the face. The basal article of the endopodite bears 1 extremely long seta at the distal medial corner. This measures 1.12 mm long. The terminal article has 2 terminal spines and 2 spiniform projections apically. Two long setae articulate on the posterior surface ; the more medial measures .98 mm, the other is .84 mm long.

The fifth leg (figs 2, e, g) is greatly enlarged and swollen and reaches to the end of the elongate genital-metasome complex. The rounded posterior margin bears a single seta. The 2 fifth legs overlap dorsally and each covers the whole side of the genital complex. The outer surface bears a general covering of raised rings (fig. 2, f). Ventral to the dorsal surface of each leg the extruded ovisac is accommodated in a dorsal concavity of the genital complex. There is a cuticular line ventrally, on the body proper apparently delimiting the segment of the fifth legs. Just posterior to this line there is on each side a complex of sclerotizations surrounding the oviducal aperture (fig. 2, h). There is 1 setule on a membrane at the margin of the aperture. The insemination pore is midventral just slightly posterior to the level of the oviducal apertures and diverging seminal tubes pass from the pore toward the apertures.

The caudal ramus (fig. 2, i) is shorter than the anal somite, and tapers slightly. There is a stiffened seta at the middle of the lateral margin, and 4 apical setae. The longest seta is about two-thirds the length of the ramus.

The copepod, as collected in the locations in British Columbia recorded above, is whitish but light rosy pink ova and embryos give a distinctive coloration to the oviducts or to the ovisacs. The pecific name indicates that most specimens observed in Europe were distinctly pink.

Detection of the paragnath is of substantial interest, as indicative that this structure can occur among the Ascidicolidae. It has been known since the original description that a paragnath occurs in *Enterognathus*. In this form and in *Ascidicola* the structure is substantially of the same form as found widespread among the Notodelphyidae. In notodelphyids with much modified mouthparts the paragnath often is still included. No such case has yet been reported for the more modified ascidicolids and we have not satisfactorily identified a paragnath in the wide sampling of representatives of all the subfamilies we have studied.

We call attention here to the specimens from the Antarctic we have listed above. We examined these in an attempt to confirm the existence of modified spines in the first legs, as invoked by Lang in his description of *A. aculeoretusa*. We failed to find any unusual development in our specimens and accordingly cannot support establishment of a separate species for the Antarctic population.

We have not had opportunity to study the male, but there is information concerning it in the literature. In the original description, Thorell included an account of what he considered to be a male. Canu (1892) made the supposition that Thorell's specimen was an immature female, as has turned out to be the case. Sars (1921, p. 65-66, pl. 31) briefly characterized the male and figures the habitus, the antennule, first and second legs and the caudal ramus. Monniot (1965, p. 158-159, figs. 43, h, c, j. l-n, q, s, t) treated the dimorphism of the species. Gage (1966) presented most interesting information on the incidence of adult males and subadult stages.

The male is remarkable in that while being much smaller and more cyclopoid in habitus than the female, it has the head appendages almost exactly similar to those of the female. In this regard it is distinctly different from all the other ascidicolid genera for which the male is known. It is interesting that in some of the notodelphyids (*Pygodelphys* spp., some *Doropygus* spp.) a similar correspondence of the head appendages in the two sexes occurs.

The legs of the male *Ascidicola* differ strongly from those of the female. It could be roughly said that they are entirely like the legs of some modified notodelphyids. There are discrepancies in the figures of Sars and Monniot, as to the setation of the first 2 legs, but there is a possibility of a considerable degree of individual variation. We have found such variation in the legs of male notodelphyids.

The fifth and sixth legs and caudal rami are remarkably like those of a number of notodelphyids.

In the dimorphism and in the characters of the head appendages of both sexes and the legs of the female, *Ascidicola* is a thoroughly distinctive copepod type. On the other hand, as we have pointed out above, most of the basic features of the appendages in *Ascidicola* show remarkable conformities to what might be considered prototypes in the Ascidicolidae in the wide sense, and often also in the Notodelphyidae. The dimorphism is remarkable in the light of the knowledge now available on the biology of the species (Gotto, 1957; Gage, 1966). The feeding process of the female has been thoroughly described. The anatomy of the male presents distinct problems in attempts to reconcile the feeding biology in the 2 sexes. Since the male has all the mouthparts developed to the same degree as in the female it seems reasonable to assume it feeds, and very likely, on food similar to that of the female. However, the male thoracic appendages totally lack the exaggerated development of the setae which is crucial to the highly characteristic feeding process of the female.

The species is now rather well known, as might be expected from its wide geographic range. Its occurrence has doubtless been missed in many additional localities because of its particular biology. Gotto (1957) and Gage (1966) present many details of the biology, development and seasonal cycles of this species in the British Isles, showing particularly a coordination of developmental stages in the copepod with stages of development of the ascidian hosts. These findings serve well as a hint as to the extremely interesting possibilities remaining in the study of the natural history of the ascicicole copepods, individually and as an assemblage.

STYELICOLA Lützen, 1968

Styelicola Lützen, 1968, p. 97 (type species, by monotypy, *S. bahusia* Lützen, 1968).

The type species of the genus, discovered by Lützen, is shown by the discovery of our new species to be a rather aberrant member of its genus, and of the subfamily. Our new species in preliminary superficial examination was listed as another record of *Ascidicola* cf. *rosea*. Closer inspection and ultimately, dissection disclosed a very good conformity to the generic characters of *Styelicola*, with a new, unsuspected set of very elaborate adaptations of the legs, but retaining an equivalent degree of development of the mouthparts. Our new anatomical data lead us to emend the generic diagnosis slightly.

Diagnosis :

Female : The body form is ascidicolin or short and with various tendencies to reduction in segmentation and development of the appendages. The antennules are short, compact, 7- or 8- segmented ; the antennae are trimerous, and the terminal article bears a hooked seta or claw. The mouthparts show reduced segmentation and ornamentation. The first 4 pairs of legs show distinctive adaptations, either toward prehensile modification, or by reduction of segmentation and ornamentation. The fifth pair of legs consist in part of an expanded structure which bears a free endopodite, this bearing several setae.

The male remains unknown.

KEY TO SPECIES, BASED ON FEMALES

1\. General body form trim, fusiform, forebody and hindbody of about equal length, hindbody with slight but regular posterior taper.............................. *lighti*, new species

1′. Body short, thick, broad, approaching eruciform habit, forebody much exceeding hindbody.. *bahusia* Lützen, 1968

STYELICOLA BAHUSIA Lützen, 1968

Styelicola bahusia Lützen, 1968, p. 97-102, figs. 1-2 (type locality, Skagerrack, Bohuslän coast, Sweden, in *Styela atlantica* (Van Name) and *S. gelatinosa* Traustedt).

STYELICOLA LIGHTI new species

(Figures 4, 5, 6)

Type : Holotypic female, USNM (type locality, Amoy, China, from *Hartmeyeria chinensis* Tokioka, 1967 (identified by T. TOKIOKA), collected by S. F. LIGHT).

Specimens examined : The holotype remains the only specimen so far discovered.

Female : The overall length of the single specimen, to the ends of the caudal rami is 3.4 mm. The body (figs. 4, a, c, d) remarkably resembles that of *Ascidicola rosea* ; it is subcylindrical, blunt apically, and with a slight posterior taper. The well-marked shield of the cephalosome is sharply delimited dorsally. It covers the head complex and this includes the segment of the maxillipeds. Each of the thoracic segments corresponding to legs 1-4 is well developed and strongly marked off. The segment bearing the fifth legs is very complex. At its anterior margin it is slightly narrower than the segment of the fourth legs. Laterally the unit (because it doubtless incorporates more than one segment) is involved in the large expansions which are the basal portions of the fifth legs and cover the proximal portions of the paired egg sacs. Posterior to the origins of the expansions the unit tapers to somewhat more than half of its anterior width by a series of 2 or 3 successive constrictions. Because the fifth legs clearly originate on this unit, which also supports the oviducal apertures, it is probably a fused complex of the last 2 thoracic segments. An interesting and unusual corollary feature is the apparent lack of the usual major body articulation between a forebody and the hindbody ; this arrangement is also typical of *Ascidicola rosea.* Four long urosomal articles apparently comprise 3 true abdominals seg-

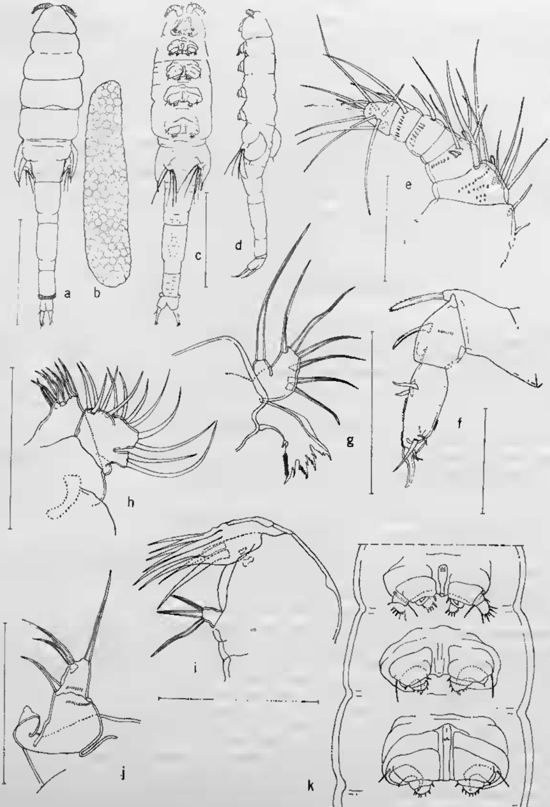

FIG. 4. — *Styelicola lighti*, new species, holotypic female : a, habitus, dorsal view ; b, egg sac ; c, habitus, ventral ; d, habitus, lateral ; e, antennule ; f, antenna ; g, mandible ; h, maxillule ; i, maxilla ; j, maxilliped ; k, legs 1 to 3, in place, ventral view. Scales for a and c = 1.0 mm ; other scales = 0.1 mm.

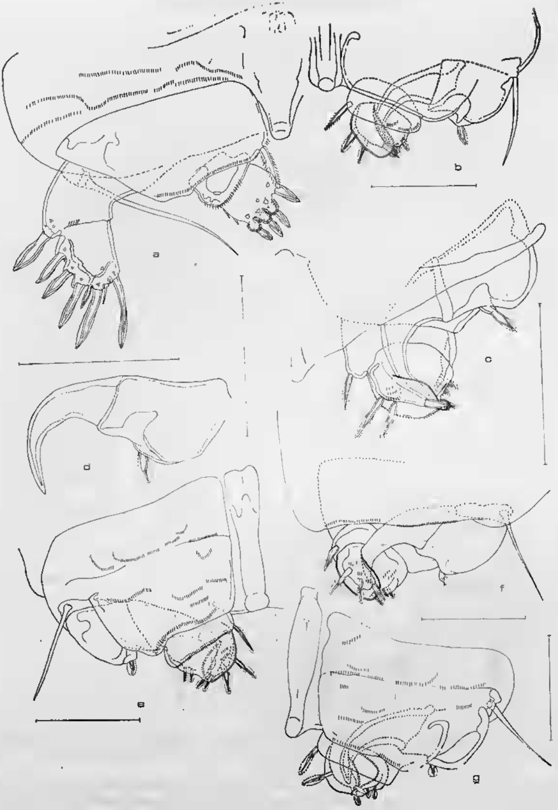

Fig. 5. — *Styelicola lighti*, new species, holotypic female : a, first leg ; b, second leg, anterior view ; c, second leg, posterior view ; d, second exopod ; e, third leg, anterior ; f, third leg, posterior ; g, fourth leg, anterior. Scales = 0.1 mm.

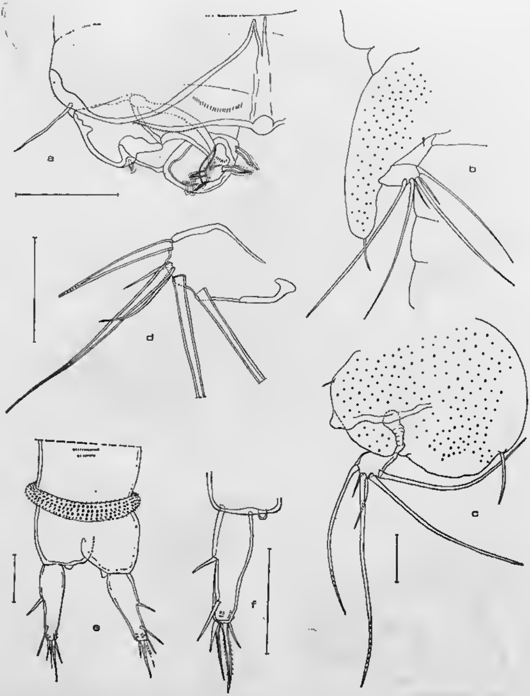

Fig. 6. — *Styelicola lighti*, new species, holotypic female : a, fourth leg, posterior view ; b, pediform projection-fifth leg, in position on body, ventral view ; c, fifth leg ; d, endopod of fifth leg ; e, anal somite and caudal ramus. Scales = 0.1 mm.

ments and the anal somite. The anterior articles are rather similar, participating in the general body taper. Each shows a constriction at about the posterior fifth. At the articulation of the anal somite there is borne on it a curious pad, located dorsally (figs. 4, a, 6, e). This shows a remarkable correspondence to the spinose pad of the abdomen of *Ascidicola rosea* but is dorsal rather than ventral. The many spinose elements arranged in a very regular pattern on the pad seem to differ basically from those of *Ascidicola.* The short anal somite supports the caudal rami, to be described and figured below. The anterior urosomal articles and the posterior portion of the fifth leg-genital complex are ornamented ventrally with regular rows of fine spinules. The elongate egg sacs are firmly attached to the oviducal apertures, each sac with its anterior end shielded by the flap-like expansion of the pediform projection. Each egg sac (fig. 4, b) is about 0.6 the length of the body and contains considerably over 200 eggs, these more or less arranged in about 10, or perhaps more, longitudinal rows.

The antennule (fig. 4, e) is stout and well sclerotized. It is composed of 7 articles; the articulation is somewhat weaker between articles 4-5 and 6-7. The setae are stiff and none is notably long. They seem in general to be lacking in plumosity but this feature could not be clearly made out owing to the state of our specimen. The presentation of the armature here must be regarded as an approximation, giving some minimal expectations, at least, for the 7 articles (I-VII) : I — 2 setae ; II — 7 setae and a short round-tipped element ; III — 3 setae and 2 short stout elements, one marginal and one on the surface of the article ; medial to this element a short row of spinules ; IV — 1 seta ; V — 1 seta ; row of spinules ; VI — 2 setae, row of spinules ; VII — 8 setae of various lengths made out on this specimen.

The antenna (fig. 4, f) is 3-segmented. The articles show the following ratio of lengths, proximal to distal : 1:1:2.5. The basal article bears a distal spiniform seta ; this element is stout and thick with distal fine spinose ornamentation. The second article bears a marginal short, stout spiniform element at about midway on its length. The terminal article bears proximally 2 short stout elements inserted close together near the margin ; there are 4 subapical elements : a long setule and 3 short, rather spiniform elements ; one of the latter takes origin on a stout tapered claw-like element broadly articulated on the apex of the article.

The mandible (fig. 4, g) much resembles that of *Ascidicola* in general configuration. The basal portion extends as a masticatory lamella. This is heavily sclerotized and the gnathal margin consists of 4 subequal tooth-like lobes, each acute terminally. The margins of these lobes are irregularly serrate. The palp appears to comprise a single element, although basally this is complicated by a large marginal lobe. The lobe bears a long seta, and there are 6 more setae inserted rather regularly along the apex and medial margin of the body of the palp.

The maxillule (fig. 4, h) is basically bipartite. A proximal element, conforming well to the usual endite, bears 7 stout marginal spiniform setae. An articulated palp, indicating by its lobing that some of the basic elements of the generalized maxillule are possibly represented, bears 5 setae on a medial lobe, 6 setae on a terminal lobe and 2 setae on a lateral lobe.

The maxilla (fig. 4, i) is tapered markedly and apparently is composed of 2 articles. The massive basal article bears a process basally which furnishes insertion apically for 3 subequal stout setae. Distally on the article 2 additional longer setae are inserted close together. The remainder of the appendage forms an unsegmented apical piece bearing 6 graduated setae ; not all of these are clearly articulated on the appendage.

The maxilliped (fig. 4, j) is flat with marginal sclerotization. It bears one stout seta about midway on the medial margin, 2 inserted together somewhat distal to this, and a single apical seta. There are some rows of spinules on the surface of the appendage.

The 4 pairs of legs of the metasome form a series showing an unusual prehensile adaptation (fig. 4, k). The first legs (fig. 5, a) are the least modified along this line, but are still far from generalized appendages. The protopodites are massive with sclerotizations and surface ornamentations of fine spinules. The coxopodites are linked by a lamella, but there is no medial coxal seta. The massive basipodites furnish insertions for the rami. Laterally each basipodite develops a prolonged base which supports a very long, basally stout, medially directed seta. On the distal medial corner the basipodite bears a short stout spine, as is usual among related copepods. The 2-segmented exopodite seems to be a broadened flattened plate. The basal segment bears a stout flanged spine at its distolateral corner. The distal article is about as massive as the basal, rounded apically. There are 3 large marginal spines inserted in emarginations ; a distolateral slightly longer spine with 2 small accompanying spinules, one inserted to either side of its base ; and a slender spine borne at the distal medial corner.

The endopodite is entirely distinctive. It is 2-segmented ; the basal article without spines or setae. The second article is wider than long, with its broad apex produced into 4 lobes, each furnished insertion for a short stout spine. Each of the 3 more lateral lobes has a characteristic flange enveloping the base of the spine. There are some characteristic cuticular ornaments on the surface of the ramus.

The second leg (fig. 5, b, anterior view) although highly modified is readily seen to be derivative from the basic plan of the first leg. The protopodite remains massive with almost complete fusion of coxopodite and basipodite. An exceptionally long seta is inserted laterally on the portion corresponding to the basipodite. The exopodite (fig. 5, d) takes a very complex articulation so that it can swing medially and fold against the basipodite and endopodite (fig. 5, c, posterior view). The basal segment of the 2-segmented exopodite furnishes the complex articulation of the ramus and its anatomically lateral surface bears a short stout spine which in the usual posture of the appendage is directed distally. The entire apical portion of the appendage is converted into a flat, curved, tapered claw with very heavily sclerotized margins. When the ramus is flexed the apical claw is enveloped in a fold formed in the endopodite. The endopodite remains bimerous, with the basal article broad and short. It supports a distolateral spine. The posterior surface of the terminal article participates in a longitudinal fold of the entire ramus which receives the claw of the exopodite. The lateral lobe of the terminal article bears 2 short spines inserted more or less apically on the lobe.

The succeeding third (figs. 5, e, anterior view ; 5, f, posterior view) and fourth (figs 5, g, anterior view ; 6, a, posterior view) legs show only slight deviations from the basic plan of the second legs.

The fifth legs somehow participate in the lamellate projections of the sixth thoracic segment (figs. 6, b, c ; 4, a, c, d). The expansions, which serve as covers for the anterior part of the egg sacs, show by the 2 marginal setae borne on each that there is probably an element of the appendage incorporated, or alternatively fully forming the projection. The medial and lateral setae could possibly be taken as indications of the representation of parts of a coxopodite and a basipodite. There is no very substantial evidence for assuming an exopodite is involved. The free segment (figs. 6, c, d), with its 6 setae could best be accounted for as a modified endopodite, as LÜTZEN concluded in the case of *S. bahusia*. Four of the setae are very long, subequal, with some indications of ornamentation on some of them. The second from the medial margin is accompanied by 2 subequal short setae inserted near its base.

The caudal ramus (figs. 6, e, f) is somewhat flattened dorsoventrally, with sclerotized margins. A relatively normal setal complement is accounted for by the 2 lateral and 4 apical elements, but these tend to be spiniform and shortened. The largest of the apical elements is only slightly more than half as long as the ramus.

Unfortunately, this most interesting species is known only from a single specimen. The discovery of the male could well provide some very suggestive information relative to the morphological sequence of adaptations in the Ascidicolidae.

SUBFAMILY BUPRORINAE Thorell, 1859

Buproridae Thorell, 1859, p. 340, 358-359 ; 1860, p. 119, 139-141 ; 1862, p. 7, 14, 17, 61. — Gerstaecker, 1870-1871, p. 719. — Kossmann, 1874, p. 281. — Brady, 1878, vol. 1, p. 18, 21, 30, 146-147 (part). — Aurivillius, 1882b, p. 108, 109 ; 1883, p. 104, 105. — Della Valle, 1883, p. 252. — Aurivillius, 1885a, vol. 4, p. 236. — Sars, 1921, p. 61. — Pesta, 1934, p. 8. — Lang, 1948, p. 6, 25, 26, 27. — Bocquet & Stock, 1961, p. 225. — Bresciani & Lützen, 1962, p. 373.

Buproriden Claus, 1875a, p. 351, 352 (part).

Ascidicolidae Canu, 1891a, p. 472, 475 (part) ; 1892, p. 107 (part).

Boporidae Bocquet & Stock, 1963, p. 293.

Notodelphyidae Claus, 1862, p. 102 (part).

Since this subfamily is monotypic, at least as far as including a single genus, its characters are those of *Buprorus*, discussed below.

Buprorus Thorell, 1859

Buprorus Thorell, 1859, p. 340, 359 (type, by monotypy, *B. loveni* Thorell, 1859) ; 1860, p. 119, 140 ; 1862, p. 7, 11, 13, 14, 61-63. — Claus, 1862, p. 102. — Gerstaecker, 1870-1871, p. 719. — Claus, 1872, p. 419. — Kossmann, 1874, p. 283, 289. — Claus, 1875, p. 351, 352. — Aurivillius, 1882a, p. 63, pl. 5, fig. 13 ; 1882b, p. 109, 110, 113 ; 1883, p. 105, 106, 109 ; 1885a, p. 236 ; 1885b, p. 282 ; 1886, p. 44. — Canu, 1891a, p. 475 ; 1892, p. 28. — Hartmeyer, 1911, p. 1735. — Sars, 1921, p. 61. — Schellenberg, 1922, p. 224. — Hansen, 1923, p. 23. — Wilson, 1932, p. 602. — Pesta, 1934, p. 8. — Neave, 1939, p. 502. — Sewell, 1949, p. 191, 192, 193 (part). — Bocquet & Stock, 1961, p. 225. —

not Buprorus Sewell, 1949, p. 192, for *Buprorus pranizoides* = *Anomopsyllus pranizoides* Sara, 1921.

The taxonomic characters of the genus are remarkably consistent through the component species, these being differentiated by rather minor features. The body form is very distinctive, with almost complete reduction of the urosome. The incubatory cavity strongly suggests affinity with the Notodelphyidae, but we would interpret this as a convergent feature and we feel that relationship with the other ascidicolids is more strongly indicated by the appendages. The antennule is distinctive for the genus in configuration, but the ornamentation and the segmentation show great resemblance to *Botryllophilus*. In *B. nordgaardi* the antennule is 7-segmented, with profuse setation, the exact details of which are not available from Sars' presentation. The pattern is not at all notodelphyid, but could serve as an approximate model of the prototype of the ingredient segments and setae of the whole series that we are proposing to include in the Ascidicolidae. In the antenna there are more setae than occur in any of the ascidicolids and, again, the segmentation and setation departs very definitely from the notodelphyid pattern. All the antennae in the whole series we consider as ascidicolids could derive from an appendage with very much this basic anatomy, which could also very possibly be found to occur among cyclopinids. The mandible, maxillule, and maxilla are all reduced appendages. In all cases they are very like the corresponding appendages of *Ascidicola*, which are in turn a bit more generalized. Among the ascidicolids probably the closest approaches to the most generalized representatives of these appendages occur in *Botryllophilus*. These, in turn could all derive from the most basic condition in the Notodelphyidae and very likely reflect a common ancestry with that family. The maxilliped of *Buprorus* is so reduced as to offer very little information to comparative morphology. It is, however, almost exactly like that of *Ascidicola*. Legs 1 to 4 strongly suggest those of either *Ascidicola* (in segmentation, not ornament) or *Botryllophilus*, but with some definite modifications from either condition.

Diagnosis :

The body form in the female is highly distinctive, with a fusion of the segments of the metasome, extension throughout the metasome of the incubatory cavity, and with strong suppression of the urosome, essentially eliminating the caudal rami. The antennules are flattened, of 3 to 7 segments, with many setae, these distributed along the anterior and terminal margines. The antennae are trimerous, non-prehensile. The mandible is reduced to a protopodite article with masticatory lamella and with the palp reduced to a small setiferous lobe or a single seta. The maxillule is reduced, the protopodite consisting of an article with a prominent endite with numerous marginal spines. The uniramous distal article bears 4 or 5 elements of armature. The maxilliped is bimerous or trimerous, the basal segment much exceeding the others and with a single distal endite. The terminal article or articles bear a medial hook and accompanying setae. The maxilliped is reduced to a simple lobe with 4 distal marginal setae. The first to fourth legs have bimerous protopodites, bimerous exopodites and unimerous endopodites. Setation varies in the species. The fifth legs are expanded lobes with 4 to 5 terminal and lateral setae.

The male is not known.

KEY TO FEMALES OF *BUPRORUS*

1. Antennule 7-segmented................................ *nordgaardi* Sars, 1921
1″. Antennule trimerous... 2
2. Urosome reduced, no setae or spines present........................ *loveni* Thorell, 1859
2′. Urosome reduced to anal somite tipped with three spines............... *caudatus*, new species

Excluded species : *Buprorus pranizoides* Sewell, 1949, p. 192, for *Anomopsyllus pranizoides*, Sars, 1921.

BUPRORUS LOVENI Thorell, 1859

Buprorus loveni Thorell, 1859, p. 342, 343, 358-359 (type locality, Swedish Coast in *Ascidia mentula*, *A. canina*, *A. aspersa*) ; 1860, p. 19, 122, 123, 139-141 ; 1862, p. 7, 8, 61, 63-64, pl. 10, fig. 14. — Gerstaecker, 1870-1871, p. 775, 776, 780, pl. xi, figs. 27-30. — Claus, 1872, p. 419. — Aurivilius, 1882a, p. 63, pl. 5, fig. 13 ; 1882b, p. 110, 113 ; 1883, p. 33, 106, 109, pl. 1, fig. 13 ; 1885a, p. 236 ; 1885b, p. 282 ; 1886, p. 44. — Hartmeyer, 1911, p. 1735. — Sars, 1921, p. 62-63, pl. 30. — Hansen, 1923, p. 23-24. — Lang, 1948, p. 3. — Sewell, 1949, p. 191, 192, 193. — Gotto, 1960, p. 225. — Bresciani & Lützen, 1962, p. 373.

Distribution : Swedish west coast, Bohüslan, Gullmarsfjord, N. Finmark, W. Finmark, Norway, Vestmanhavn, Faëroes, Smörkullen, Löken.

Hosts : (Names as recorded by the various authors ; we have not attempted to form a synonymy for the ascidians) : *Ascidia aspersa*, *A. canina*, *A. mentulo*, *A. obliqua* ; *Ascidiello aspersa* ; *Phallusia mentula*, *P. obliqua*.

BUPRORUS NORDGAARDI Sars, 1921

Buprorus nordgaardi Sars, 1921, p. 80-81, pl. 37, fig. 1 (type locality, Trondhjem Fjord, in *Amaroecium* sp.). — Sewell, 1949, p. 192. — Gotto, 1960, p. 225. — Bocquet & Stock, 1961, p. 225.
Distribution : Trondhjem Fjord, Norway.
Host : *Aplidium* sp.

BUPRORUS CAUDATUS new species
(Figure 7)

Types : Holotypic female, UNSM 92537 (type locality, off Southern California, Albatross Station 2972, 34°, 18′, 30″ N, 119°, 14″ W, 1889, from *Styela coriacea* (Alder & Hancock) (= *Styela hemicaespitosa* Ritter, cat. no. 5684) ; and paratypes below :

Specimens examined :

California : From *Styela coriacea* (Alder & Hancock) (= *S. hemicaespitosa* Ritter) off Southern California, 34°, 18′ 30″ N, 119° 41′ W, Albatross Station 2972, 1889, 4 adult females, holotype, one paratype dissected, 2 undissected paratypes.

Description :

Female : Overall length 1.1 mm. The habitus (fig. 7, a) is as previously figured for *B. lovein* by THORELL and by SARS an ovoid body with a projecting bead and ventral row of appendages. The

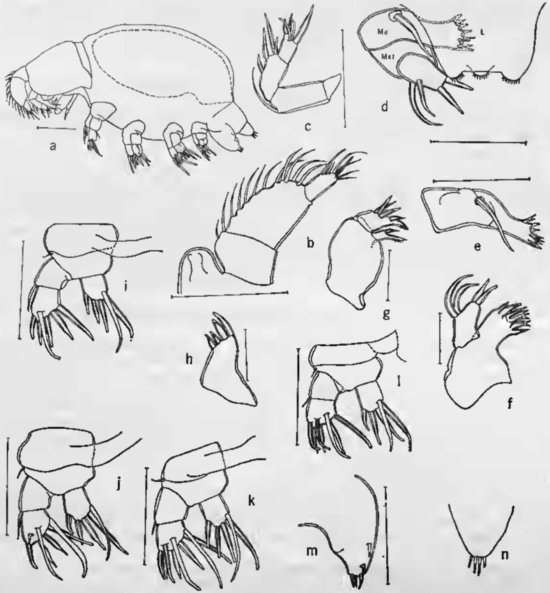

Fig. 7. — *Buprorus caudatus*, new species, paratypic female ; a, habitus, lateral ; b, antennule and rostrum ; c, antenna ; d, labrum (L), mandible (Md), and maxillule (Mx1) ; e, mandible ; f, maxillule ; g, maxilla ; h, maxilliped ; i, first leg ; j, second leg ; k, third leg ; 1, fourth leg ; m, fifth leg, lateral ; n, urosome. Scales = 0.1 mm.

incubatory cavity can be seen to extend throughout the metasome. The body regions are a cephalosome, bearing as its last appendages, the maxillipeds ; unsegmented metasome bearing 4 pairs of legs ; and much modified and reduced urosome bearing the large fifth legs and terminating in a conical anal somite tipped with 4 spines and lacking caudal rami. All the appendages are heavily sclerotized.

The rostrum (fig. 7, b) is a simple lobe, somewhat sclerotized.

The antennule (fig. 7, b) is trimerous, flattened, and with a single row of setae along its anterior and terminal margins. The basal 2 articles are markedly wider than the terminal article. The middle article is much the longest. The armature is as follows : I-2 setae ; II-10 or 11 setae ; III-7 setae, 1 aesthete.

The antenna (fig. 7, c) is trimerous, with the basal article nearly equalling the combined lengths of the terminal 2. The basal article has a single seta at the medial distal corner. The second article bears 4 heavily sclerotized spines on the medial margin along the distal half. The terminal article is modified in outline by a small medial terminal projection. On this there are inserted 2 heavily sclerotized spines. At its base are 2 curved, stiffened seta. Laterally, at the apex, there is a stout spine considerably longer than the article.

The labrum (fig. 7, d [L]) terminates in 3 lobes bearing fine setules.

The mandible (figs. 7, d [Md]; 7, e) consists of a protopodite drawn out medially as a toothed lamella. From the middle of the appendage there emerges from a pit a conspicuous seta which is the only remnant of the palp.

The maxillule (fig. 7, f) is bimerous. The protopodite is drawn out medially into a toothed endite, bearing 6 spiniform projections, possibly homologuous with the setae of other forms. The distal article, possibly representing the palp, has a medial terminal lobe bearing 2 short, stout spines. At the lateral distal corner there are 2 curved, sclerotized spines, longer than the medial spines.

The maxilla (fig. 7, g) is bimerous. The basal article is about 3 times longer than the distal and about twice as wide. At the distal medial corner of this article there is an endite which terminates in a spinulose, spiniform process. At the base of this process there is a small articulated spine. The distal article is contracted terminally by 3 emarginations and terminates medially in a curved hook. In the emarginations there are articulated spines, 1 in the first, 2 in the second, 1 in the third at the base of the hook.

The maxilliped (fig. 7, h) is a unimerous tapered lobe. Four spines form a row beyond the middle of the medial margin.

The first legs (fig. 7, i) are biramous, with bimerous protopodite, bimerous exopodite and unimerous endopodite. The coxopodites are united by a band of cuticle which is not developed as strongly as the usual intercoxal lamella. There is a small setule on the lateral margin of each basipodite, which is trapezoidal in outline, so that the articulation of the exopodite is lateral. The basal article of the exopodite has a seta at the distal lateral corner. The terminal article has 3 terminal spines, 2 medial spines and 1 curved, stiffened seta, articulated on the posterior surface at the distal fourth. The endopodite is short, about as long as the basal article of the exopodite. It bears 1 distal lateral spine, 2 apical spines, and 1 distal medial curved spine. A long, curved, stiffened seta articulates on the posterior face near the articulation of the distal medial spine.

The second legs (fig. j) are biramous, with bimerous protopodite. bimerous exopodite and unimerous endopodite. The protopodites and endopodites are as in leg 1. The basal article of the exopodite has a seta at the distal lateral corner. The second article bears 1 apical spine, 3 medial spines, 1 medial curved, long seta, a setule and a long curved seta, the latter 2 articulated on the distal posterior face.

The third legs (fig. 7, k) resemble the second exactly except for the exopodites. The basal article of the exopodite bears a setule at the distal lateral corner. The distal article bears 3 terminal spines, 2 medial spines, a medial, long, curved seta, 1 spine and 1 long curved seta, the latter 2 articulating on the distal posterior face.

The fourth legs (fig. 7, 1) are biramous, with bimerous protopodites, bimerous exopodites and unimerous endopodite. The coxopodites are united by a relatively poorly developed lamella. On the anterior surface the articulation between the coxopodite and the basipodite are like those of the third leg, except the second article of the exopodite lacks the long curved medial seta.

The fifth leg (fig. 7, m) is a large, swollen lobe, actually larger than the other legs. Its armature consists of 3 terminal spines and 2 lateral spines spaced beyond the middle. Caudal rami are lacking but the body terminates in a conical anal somite tipped with 4 spines (figs. 7, a, n). The anus is subterminal.

In almost all its features, this species conforms very well with the figures presented by Sars for *B. loveni*, except that the fifth legs and the urosome are much more developed and offer a diagnostic difference. Sars' figures of the head appendages are somewhat generalized, so it is entirely possible that restudy of the European form will offer substantial differences. In the legs the exopodites are shown by Sars to have many more elements of armature than are found on our species. *Buprorus nordgaardi* is markedly distinct from both species. The name of our species is derived from the fact of substantially greater representation of the urosome than in the other species.

SUBFAMILY ENTEROCOLINA Della Valle, 1883

Famille de lernéens, Tribu des dichélestiens van Beneden, 1860, p. 160 (part) (for *Enterocola* n. g.). — *Dichelesthiina* Kossmann, 1874, p. 288-289 (part). — Family *Holotmeta* Kossman, 1874, p. 285, 288-289 (part).

Ergasilina Claus, 1875, p. 352 (part).

Buproriden, Claus, 1875, p. 350-351 (part). — Buproridae, Brady, 1878, v. 1, p. 18-19, 21, 30, 146-147 (part).

Ascidicolidae, Gerstaecker, 1870-1871, p. 719 (part). — Giard, 1888, p. 505 (part). — Canu, 1891a, p. 472 (part) ; 1892, p. 186 (part). — T. Scott, 1901, p. 351-352 (part). — Calman, 1908, p. 177, 182 (part). — Chatton & Brément, 1909c, p. 223 (part). — Smith, 1909, p. 66 (part). — Chatton & Brément, 1915, p. 143-144, 148 (part).

Ascidicolinae, Chatton & Brément, 1915, p. 143-144, 148 (part). — Schellenberg, 1922, p. 219-220 (part). — Brehm, 1927, p. 490 (part). — Barnard, 1955, p. 237 (part).

Enterocolidi Della Valle, 1883, p. 252.

Enterocolidés, Canu, 1892, p. 107.

Enterocoliens, Canu, 1886, p. 373-374 ; 1892, p. 117. — Chatton & Harant, 1922c, p. 245, 249-251 ; 1924e, p. 417-418.

Enterocolidae, Sars, 1921, p. 73-74 (part). — Blake, 1933, p. 226 (part). — Gray, 1933, p. 523 (part). — Pesta, 1934, p. 8 (part). — Lang, 1948, p. 23, 25-27 (part). — Rose & Vaissière, 1953, p. 91 (part). — Gotto, 1954, p. 659 (part). — Bresciani & Lützen, 1962, p. 376 (part). — Monniot, 1965, p. 160 (part). — Dudley, 1966, p. 155 (part). — Gotto, 1966a, p. 193 (part). — Stock, 1967a, p. 9 (part). — Lützen, 1968, p. 101.

Enterocolinae, Chatton & Harant, 1924a, p. 352-353 ; 1924b, p. 360-363. — Gotto, 1962a, p. 541.

Notodelphyidae, Norman & Scott, 1906, p. 201 (part). — Barnard, 1955, p. 237 (part).

Chatton & Harant (1924h, p. 360-363) concluded that the three genera so thoroughly studied by them, *Enterocola* van Beneden, *Enterocolides* Chatton & Harant, and *Lequerrea* Chatton & Harant, should form the nucleus of a distinct subfamily, Enterocolinae, in the family Ascidicolidae. They provided an excellent diagnosis and we are essentially adopting this, adding characters derived from our comparative studies of previously known and new forms. We propose to exclude from this subfamily, the genera mentioned tentatively by Chatton & Harant as possibly of eventual inclusion : *Zanclopus* Calman ; *Enterognathus* Giesbrecht ; *Bactropus* Gravier ; *Entobius* Dogiel ; and *Ventriculina* Bassett-Smith. They based their definition on the females of the genera and pointed out that the characters of males must eventually be considered, but were not available at the time. We must also acknowledge this necessity, but have little additional information concerning males, so the diagnosis must still rest on characters of females. We have a few comments on males below (see p. 46).

The enterocolin body is cruciform in the female but there is no exactly diagnostic detail derivable from the general habitus. Other ascidicolids and some other cyclopoids have the same approximate construction.

The cephalosome is broad, approaching semicircular outline, the convexity anterior and dorsal. The cephalosome lacks pleural folds, apical plaque or rostrum. There are 4 or less pairs of cephalosomal appendages, the mandibles and maxilliped always are lacking. The labrum is present, not particularly salient and characteristically displaced anteriorly. A very consistent feature of the labrum is the occurrence of 2 spinulose setae at the lateral corners.

The metasome may have the 5 component thoracic segments (which must commence with the second segment ; the thoracic segment corresponding with the missing maxillipeds is apart of the head complex) clearly demarcated, but there are considerable modifications and fusions. The sixth thoracic segment is frequently coalesced with the fifth, and may further participate in a fusion with the urosome. There may be paired pterostegites on any of the segments and the pediform processes of the last segment are probably in part homologous.

The urosome is shorter than the metasome, stumpy, and its outward appearance may vary from segmented to coalesced. The caudal rami are reduced, usually not clearly articulated with the urosome, or may be totally lacking.

The antennule is reduced, tending to indistinct segmentation and sparse setation ; in *Lequerrea* the appendage is possibly absent (alteratively, it is present and the antenna is lacking).

The antenna is long and often much expanded. It is uniramous and mostly clearly bimerous. There are no indications of prehensile function in the female and the setae tend to be reduced in number and concentrated apically. Copepodids and the male of at least *Enterocola fulgens* have the antenna prehensile.

The mandible is absent in all copepodid stages.

The maxillule is massive and articulates on the head in a very complicated way. It appears to be composed of a base and a palp but development and comparative morphology indicate the appendage may be biramous. The protopodite and presumed endopodite are fused to form the lamelliform, heavily sclerotized base, which is produced medially with a lobed apex. There is an articulated seta inserted on the surface. The free article is a setigerous lamella articulated on the base ; the apex of this is entire to bilobed, with 5 or 6 setae, these variously grouped on the lobes.

The maxilla is uniramous, heavily sclerotized and with the apex produced medially as a hook-process. There is always a complicated articulation of the base of the hook with the terminal part of the appendage suggesting the composition is bimerous. There is a spinulose endite distal on the basal segment, and a seta on the ventral margin of the hook.

The maxilliped is absent.

There are 4 pairs of subequidistantly spaced legs. These are subequal, always obscurely articulated on the body, and biramous. To a considerable degree the patterns of structure and oramentation of the legs are generic characters. The protopodites tend to articulate obscurely on the body. The endopodites vary from unimerous to bimerous, setiferous to not so, the setae when present apical and not exceeding 2 in number. The exopodites are unimerous to bimerous, of a characteristic outline, not bearing proper setae, but with a variety of curiously developed spine-like elements.

The sixth thoracic segment always bears pediform projections which may be setiforous or not. When present, the setae are minute. The projections tend to be larger than any of the pterostegites when these are present and are always salient features in the general aspect of the animal.

KEY TO GENERA, BASED ON FEMALES

1. Three pairs of cephalic appendages ; antennules or antennae missing...... *Lequerrea* (p. 37)
1′. Four pairs of cephalic appendages ; antennules and antennae both present............. 2
2. Endopodites 1 to 4 without setae.................................... *Enterocolides* (p. 42)
2′. Endopodites 1 to 4 with 2 setae, terminal or subterminal................. *Enterocola* (p. 45)

ENTEROCOLINAE sp. *incertae* sedis

Enterocolidae indet., Monniot, 1965, p. 160 (from Banyuls-sur-Mer, Golfe du Lion, France, from *Cratostigma gravellophila*).

LEQUERREA Chatton & Harant, 1924

Lequerrea Chatton & Harant, 1924a, p. 349 (Type species, by monotypy, L. *perezi* Chatton & Harant, 1924) ; 1924b, p. 362-363. — Wilson, 1932, p. 601. — Neave, 1939, p. 923. — Gotto, 1960, p. 226.

In adding a new species we extend somewhat the diagnosis of the authors of the genus. As pointed out by CHATTON & HARANT, most of the appendages and the general features of the habitus conform with the diagnostic characters of the subfamily Enterocolinae.

The general aspect is much like that of species of *Enterocola*, but the present form is a very large copepod. The size may be a reflection of the occurrence in solitary ascidians, both known species so far found to occur in species of *Polycarpa*.

The urosome is markedly shorter than the remainder of the body, unsegmented, with the anus dorsal, but at the end of the body.

Either the antennule or the antenna is missing, and the exact determination will have to await evidence from development. By comparison with the series of species of enterocolins, we tend to concur with the surmise of the authors that the antennule is missing. There are 5 setae on the exopodite of the maxillule, in contrast to the 6 setae usual in species of *Enterocola* and *Enterocolides*.

The first to fourth legs are all biramous, and it is characteristic, as in *Enterocolides*, that the endopodite lacks any articulated elements of armature. Proportions of the rami are not distinctive, since the endopodite may be longer or shorter than the exopodite. The pediform projections of the sixth thoracic segment lack setae, but some species of *Enterocola* correspond in this feature.

The anatomical characters not specifically mentioned above can be assumed, as far as the 2 species now known are concerned, to conform to the general features of the Enterocolinae.

The 2 species can be readily distinguished by the relative proportions of the rami of the legs. In *L. perezi*, the exopodite slightly exceeds the endopodite ; in *L. canui*, the endopodite greatly exceeds the exopodite.

LEQUERREA PEREZI Chatton & Harant, 1924
(Figure 8)

Lequerrea perezi Chatton & Harant, 1924a, p. 347, 349-352, fig. 1 (type locality, La Rade de Brest, France, in *Polycarpa* sp., from intestine) ; 1924b, p. 363. — Harant, 1931, p. 371. — Gotto, 1960, p. 226.

Distribution : Atlantic coast of France ; Plymouth, England.

Host : *Polycarpa* sp., probably restricted to *Polycarpa gracilis* Heller.

Specimens examined :

Host undetermined : Brest, France, Chatton number 263, (possibly holotypic specimen).
1 female.
Host undetermined, probably *Polycarpa* sp..:
Duke Rock, Plymouth Bay, Plymouth, England, 6 fathoms., September 8, 1958, P. L. Dudley, 1 female.
From *Polycarpa gracilis* Heller :
Duke Rock, Plymouth, England, 1 female.

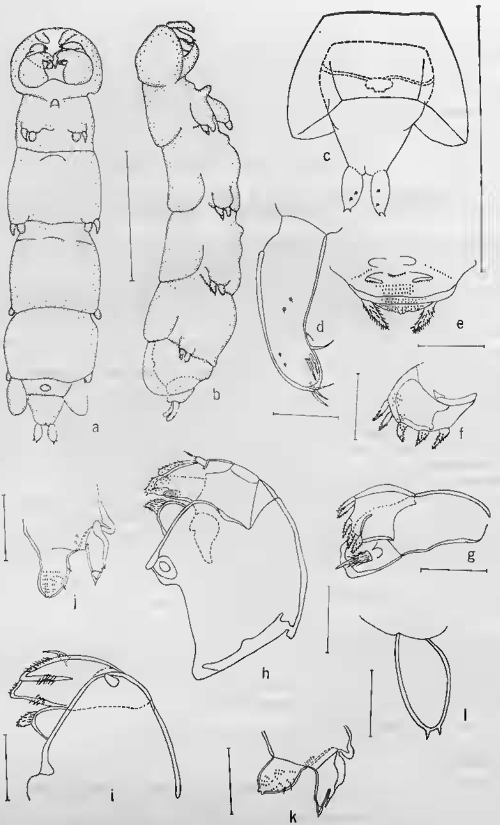

Fig. 8. — *Lequerrea perezi* Chatton & Harant, female : a, habitus, ventral view ; b, habitus, lateral ; c, urosome, ventral ; d, antenna (?) ; e, labrum ; f, palp of maxillule ; g, maxillule, ventral ; h, maxilla, posterior ; i, maxilla, anterior ; j, first leg ; k, third leg ; 1, caudal ramus. Scales for a, b, c, = 1.0 mm ; other scales = 0.1 mm.

Description :

Female (figs. 8, a-l), supplementing the original description :

Body (figs. 8, a, b), 3.17 mm total length, measured from anterior margin to the end of the caudal rami. The body is somewhat sclerotized, relatively slender, with segmentation indicated ventrally by constrictions. Dorsally there are paired pterostegites on the second through fifth thoracic segments. This feature departs from the statement of Chatton and Harant to the effect that there are no dorsal duplicatures, except as involved in the fifth pedigerous projections. In frontal view the cephalosome and thoracic segments are of about equal width, contrasting to the somewhat narrower, tapering urosome. On the second thoracic (first leg-bearing) segment there is a sclerotized projection anterior on the ventral midline, projecting somewhat anteriorly. The fifth pedigerous segment is expanded laterally into conspicuous curved lamellae, unarticulated, and continuous ventrally as an apron-like sheath covering the anterior part of the urosome (fig. 8, c). The insemination pore is covered by this sheath. The lamellae bear no setae.

We use the orientation of an *en face* preparation to refer to the features of the head appendages.

Chatton & Harant considered that most likely the antennules were absent. We concur in this conjecture, but developmental evidence will be necessary to provide definitive information.

The antenna (?) (fig. 8, d) is rather elongate but there is no clear indication of ingredient segmentation. There is some feeble sclerotization and the setation is weak and apparently reduced.

The labrum (fig. 8, e) as we illustrate it, corresponds to the original description.

The maxillule (figs. 8, f, g) and the maxilla (figs. 8, h, i) correspond to the original description, and we herewith present the first illustrations of them.

We find the legs as described in the original description. The first (fig. 8, j) and second are similar. The third (fig. 8, k) and fourth differ somewhat from the former and are similar to each other, in bearing a long process with an articulated spine on the lateral margin of the basal segment of the exopodite. In a similar locus on the first 2 legs there is a minute spinule. The caudal rami (fig. 8, l) were described generally in the original description but on our specimen each bears 2 terminal projections.

The remarkably precise description of the original authors leaves us in little doubt of the identity of our specimens. We have been able to furnish some supplementary illustration and the distribution is slightly extended by our records. For the first time a specific identification for the host can be provided, namely *Polycarpa gracilis*, which is an interesting discovery in view of our procuring specimens of a new species of *Lequerrea*, described below, from *Polycarpa rustica* from approximately the same locality. In our specimens the body was yellow and the embryos in the ovisacs were bright orange.

Lequerrea canui, new species
(Figures 9, 10)

Types : Holotypic female (type locality, Salcombe, near Plymouth, England, intertidal, from *Polycarpa rustica* (Linnaeus), August, 1958, paratypes, specimens listed below.

Specimens examined :

From *Polycarpa rustica* (Linnaeus) : Salcombe near Plymouth, England, intertidal, August, 1958, holotypic female and 1 other female.

Duke Rock, Plymouth Bay, England, 6 fathoms, September 9, 1958, 1 female.

Duke Rock, Plymouth Bay, England, 5-6 fathoms, September 12, 1958, 1 female.

Description :

Female (figs. 9, a-k, 10, a-e) :

Body (fig. 9, a) 5.78 mm total length, measured from anterior margin to the end of the caudal rami of one specimen. The shape is eruciform, somewhat curved, with the segmentation obscured,

Fig. 9. — *Lequerrea canui*, new species, paratypic female : a, habitus, lateral view ; b, urosome and pediform projections, ventral ; c, urosome and pediform projections, dorsal ; d, antenna (?) ; e, labrum ; f, postoral sclerotizations ; g, maxillule ; h, basal portion of maxillule ; i, palp of maxillule ; j, maxilla, posterior ; k, maxilla, anterior. Scales for a, b, c = 1.0 mm ; other scales = 0.1 mm.

Source : MNHN, Paris

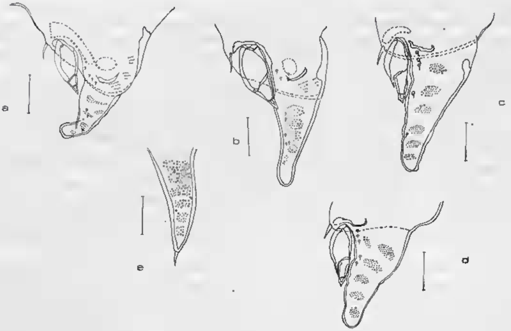

Fig. 10. — *Lequerrea canui*, new species, paratypic female : a, first leg ; b, second leg ; c, third leg ; d, fourth leg ; e, caudal ramus. Scales = 0.1 mm.

indicated only by slight indentations. There are no apparent pterostegites. The body is more swollen than in *L. perezi*, and as in the latter the third legs are separated so each is displaced somewhat dorsally, the fourth legs are markedly lateral. The pediform projections perhaps corresponding to fifth legs are markedly smaller than those of *L. perezi*. They are appressed to the proximal portion of the ovisacs which are elongate and curved. The urosome (figs. 9, h, c) as in *L. perezi*, is unsegmented, and there is no delimiting articulative line ventrally, although a dorsal articulation is present. The anus is dorsal near the end of the urosome.

The insemination pore is exposed on the ventral anterior surface of the urosome, since there is no apron-like sheath, as in *L. perezi*. Diverging seminal canals pass from the pore dorsolaterally to the vicinity of the oviducal apertures.

We use the orientation of an *en face* preparation to refer to the features of the head appendages. There is no rostrum and apparently the antennule is absent.

The antenna (?) (fig. 9, d) is elongate, with indication that there are 2 ingredient segments, since a strong sclerotization on the ventral face at the distal third perhaps represents an articulation, which is incomplete dorsally. There are no setae proximal to the sclerotization. Terminally and medially there are 10 short setae surrounding the distal margin. The dorsal face bears 6 rows of fine spinules at about the distal third.

The labrum (fig. 9, e), as in *L. perezi* is displaced far anteriorly on the cephalosome to a position at the bases of the antennae. As in the congener there is a terminal piece which is triangular and somewhat denticulate, but without elaborate tooth-like structures. Rows of fine spinules ornament the surface of this piece. On the anterior surface of the labrum there are medial rows of somewhat coarser spinules. The usual lateral terminal setae of the labrum are covered with coarse spinules. Posterior to the mouth on the surface of the cephalosome is a complex of sclerotization, including raised medial lobes (fig. 9, f). This is emarginated by the heavy sclerotized ridges surrounding the bases of the mouthparts. At the anterior lateral margin of the central sclerotization there is on each side a lobe bearing a circular patch of heavy spinules.

The maxillule (figs. 9, g, b, i) is very heavily sclerotized, and there is evidently a fusion of the usual elements with the protopodite. The palp portion is also probably incompletely articulated, but it is represented by a flattened lobe-like element, which projects ventrally over the remainder of the appendage. It bears 5 marginal setae, in groups of 2 and 3. All the setae are spinulose and there are patches of spinules on the surface at the bases of the setae. The basal portion is massive and heavily sclerotized. Apically it is somewhat bilobed. On the anterior face there is inserted a very strong seta covered with coarse spinules.

The maxilla (figs. 9, j, k) is apparently trimerous and very heavily sclerotized. The basal segment is massive, somewhat truncate and with a distal medial protuberance that possibly represents one of the endites. This protuberance is dome-like and terminates in a spinulose thumb-like process. The articulation of the second probable segment is very complicated. On one surface it is very evident, cutting directly across the appendage. The corresponding continuation on the opposite surface appears to be obscured by a distal greatly extended expansion of the basal segment. There is no seta or derivative on the second segment. The terminal segment is triangular in outline, but is actually anteroposteriorly flattened, and comprises 2 subequal appressed lobes. The lobes bear patches of spinules. A seta, with a somewhat expanded base, is set on an emargination at about the basal fourth of the external margin. A circular sclerotization on the basal segment is possibly representative of the aperture of a glandular duct.

The first to fourth thoracic legs (figs. 10, a-d) are all biramous, with the endopodites consistently longer than the exopodites ; the reverse is the case in *L. perezi*. The articulations of the legs with the body are not delimited. The exopodites are distinctly articulated with the protopodites, but the articulations of the endopodites are obscure. Each protopodite bears a seta at the lateral distal corner, a feature lacking in *L. perezi*. There are patches of fine spinules on the anterior surface of each protopodite, and a row of 3 or 4 heavy spinules is found between the exopodite and endopodite on each leg. Internally there are complex sclerotized skeletal pieces which serve as attachments for muscles. The exopodites are very heavily sclerotized, short, conical, trimerous. In the first and second legs (figs. 10, a, b) there is no lateral armature and the terminal element is regularly conical. In the third and fourth legs (figs. 10, c. d), the basal segment is drawn out laterally as an elongate, unarticulated, spinose process. The terminal element is modified in outline from a regular cone to a dome sharply constricted terminally to a pointed apex. There is no surface ornamentation on the exopodites. The endopodites are from 1 1/2 to 2 times longer than the exopodites and are digitiform, lacking articulations and armature. There is a faint indentation on the posterior surface of each leg between the protopodite and the endopodite. The anterior surfaces of the endopodites bear oval patches of fine spinules, and there are a few heavier spinules on these surfaces near the lateral margins.

The pediform processes of the sixth thoracic segment are unarmed (figs. 9, b, c) and it is possible that fifth legs are lacking. The processes cover the oviducal apertures which have accompanying complex sclerotizations and are heavily muscularized.

The caudal ramus (fig. 10, e) is elongate, conical and bears a single terminal spiniform projection. The surface is ornamented with patches of fine spinules and scattered, isolated, heavier spinules. This ramus differs markedly from the ellipsoidal ramus of *L. perezi*.

Two of the 3 females collected were ovigerous. The animals were removed from the gut of the host in each instance. The ova in the oviducts were purplish pink, the embryos in the ovisacs had a mixture of orange and pink yolk. No males have been found.

ENTEROCOLIDES Chatton & Harant, 1922

Enterocolides Chatton & Harant, 1922c, p. 246-252 (type species, by monotypy, *E. ecaudatus* Chatton & Harant, 1922) ; 1924a, p. 353. — Wilson, 1932, p. 598. — Neave, 1939, p. 241.

The characters of the one species of this genus serve also to furnish the generic diagnosis.

ENTEROCOLIDES ECAUDATUS Chatton & Harant, 1922
(Figure 11)

Enterocolides ecaudatus Chatton & Harant, 1922c, p. 246-252, fig. 1 (type locality, Port Vendres, Golfe du Lion, France, from " un Distomide blanc " [subsequently identified as " *Didemnopsis crassa* " Daumezon] ; Chatton & Harant, 1924a, p. 353) ; 1924b, p. 363. — Harant, 1931, p. 137. — Gotto, 1957, p. 288 ; 1960, p. 226.

Distribution : Golfe du Lion, France.

Host : *Didemnopsis crassa*, now known as *Trididemnum inarmatum.*

Specimens examined :

From *D. inarmata* Drasche :

" distomide blanc, glob. " (Tunicate identified by M. Harant).
Near Port Vendres, near Banyuls-sur-Mer, France, November 11, 1910, Chatton number 151, 1 female. (Topotypic specimen, possibly holotype.)

From " *Distaplia* sp. " :

Near Port Vendres, near Banyuls-sur-Mer, France, 50-100 m, January 10, 1912, Chatton number 58, 8 females.

We offer what we consider to be pertinent supplementary information to the description of CHATTON & HARANT and illustrate our specimens for comparison. The specimen, an adult female, measured 1.42 mm, overall length, as compared with the range of 1.5 to 1.7 mm of the authors. The proportions of our specimen, cephalosome : metasome : urosome, are 3 : 14 : 4, as compared with the published ratio 1 : 5, 2.

The habitus (figs. 11 a, b) corresponds well to the figure and description of the authors. The only additional feature shown by us is the insemination pore on the urosome, with one of the diverging seminal tubes, leading to the oviducal aperture under the pediform process, called the " oostegite " by the authors. The antennule (fig. 11, c) agrees very well with the original with the exception that basal rows of spinules were not seen, but we saw additional scattered spinules on the surface of the basal article. The antenna (fig. 11, d) agrees well with the illustration but is unimerous, contrary to the statement of the authors that it is bimerous . The labrum (fig. 11, e) not figured by the authors, but described, is a trapezoidal plate bearing rows of spinules on the ventral surface and a spinulose seta at each distolateral corner. The maxillule (figs. 11, f, g) is bilobed. In the specimen we examined the palp portion has only 4 terminal setae ; a knob in the center may indicate a vestigial seta. The authors state the " exopodite " bears 3 setae on the distal margin of the external lobe and 1 on the external margin of the external lobe and 2 on an internal lobe. The basal element is massive, strongly sclerotized, bifid apically, and with a seta and a setule on the anterior margin. The maxilla, not previously illustrated (fig. 11, h) is bimerous, with the basal article much longer and wider than the terminal. An endite bearing a distinctly and articulated terminal claw protrudes medially from the distal medial corner of the basal article. The terminal article is large, claw-shaped, and extends parallel with the endite but somewhat exceeds it. There is a small seta on the anterior face of the terminal claw and no other surface ornamentation on the appendage. The 4 pairs of legs are biramous, each with a large base carrying rows of spinules and with a single seta at the distal lateral corner. In all the legs (figs. 11, i, j, k, l) the conical endopodite is unarmed and bears rows of spinules. The exopodite of the first leg (fig. 11, i) is unimerous, has a patch of spinules at the middle of the lateral margin, a small hook-like projection of the cuticle at the distal fourth and is pointed apically. The exopodite of the second leg (fig. 11, j), also unimerous, has spinules at the proximal fifth, a patch of spinules approximately at the middle on a protuberance, a spinule at the distal fourth, and an apical cuticular minute claw accompanied by a small spine. In the third leg (fig. 11, k) the exopodite strongly shows the basic distinctive structure characteristic of the entire subfamily. The ramus is a very heavily cuticularized, curved stylet ; it is specifically distinctive in bearing a patch of spinules on a projection at the middle of the

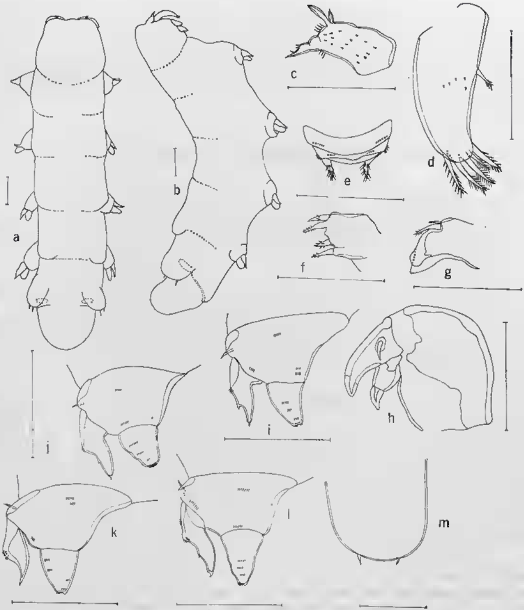

FIG. 11. — *Enterocolides ecaudatus* Chatton & Harant, female : a, habitus, dorsal view ; b, habitus, lateral ; c, antennule ; d, antenna ; e, labrum ; f, palp of maxillule ; g, medial process of basal portion of maxillule ; h, maxilla ; i, first leg ; j, second leg ; k, third leg ; 1, fourth leg ; m, pediform projection. Scales = 0.1 mm.

lateral margin. The exopodite of the fourth leg (fig. 11, 1) is very similar to that of the first leg. The pediform process (fig. 11, m) is a cupped plate with a curved terminal outline, so that it is somewhat longer than broad. The authors show a single seta at the middle of the margin. We find 2 setules, the more dorsal somewhat longer than the other.

The species has not been reported since the time of CHATTON and his colleagues. All the specimens available for our study were from the CHATTON collections.

There is some question about the host, but the authors seem to have settled on " *Didemnopsis crassa* " which is now known as *Trididemnum inarmatum* von Drasche.

ENTEROCOLA van Beneden, 1860

Enterocola van Beneden, 1860, p. 155-160 (type species, by monotypy, *E. fulgens* van Beneden, 1860). — Gerstaecker, 1870-1871, p. 719. — Kossmann, 1874, p. 288-289. — Claus, 1875, p. 351-352. — Brady, 1878, p. 21, 30, 147 (part). — Aurivillius, 1882a, p. 8, 92, 96 ; 1882b, p. 92 ; 1883, p. 88. — Della Valle, 1883, p. 245-247, 251. — Canu, 1886, p. 309, 311. — Giard, 1888, p. 505. — Canu, 1891a, p. 468-475 ; 1892, p. 25, 29, 33, 39, 48, 50, 51. 54, 58, 66, 87, 88, 90, 91, 92, 93, 108, 117, 118, 119, 127, 130, 131, 133, 209, 213-218. — T. Scott, 1900, p. 386 ; 1901a, p. 352. — Norman & Scott, 1906, p. 203. — T. Scott, 1907, p. 368-369. — Calman, 1908, p. 182. — Chatton & Brément, 1909c, p. 223-225. — Smith, 1909, p. 67. — Chatton & Brément, 1915, p. 144, 145, 148, 149, 153, 154. — Sars, 1921, p. 76-77. — Chatton & Harant, 1922a, p. 148-149 ; 1922c, p. 245, 249-251 ; 1924a, p. 348, 349, 353-354. — Schellenberg, 1922, p. 287-288. — Chatton & Harant, 1924b, p. 361, 362, 363. — Brehm, 1927, p. 490. — Wilson, 1932, p. 599, 600. — Neave, 1939, p. 241. — Barnard, 1955, p. 237, 241. — Gotto, 1960, p. 216 ; 1962, p. 541 ; 1966a, p. 193. — Dudley, 1966, p. 155, 157, 159, 160.

Entorocola Norman, 1868, p. 300 (part).

Intercola Hesse, 1862, p. 349, 354 ; 1865, p. 355.

non Enterocola Norman, 1868, p. 300.

non Enterocola Brady, 1878, p. 147. — T. Scott, 1892a, p. 301 ; 1892b, p. 203-205. — T. Scott and A., 1895, p. 359-360.

Biocryptus g. n. Hesse, 1865, p. 242-247, 256 (type species not designated). — Canu, 1892, 216 (uncertain species ; actually much resemblance to *Enterocola*). — Chatton & Harant, 1924b, p. 363 (*Enterocolinae*, but unidentifiable as to genus or species). — Neave, 1939, p. 430.

When CHATTON & HARANT (1924, p. 361-362) formulated their subfamily Enterocolinae, they already had so many species of *Enterocola* to account for that their generic definition is a very general one, with few particulars. Since that time still more species have been added. In order to obtain first-hand information about the male in the genus, we have studied some collections made from compound ascidians at Plymouth, England. We have found an amount of variation that leaves a definite question in our minds as to just where species limits lie in the series of *Enterocola* forms coming from closely related compound ascidians. To avoid designating our material as host forms, which we would not feel able to do in the absence of substantial suites of specimens for comparative study, we are, with definite misgiving, designating new species from our material. This experience of ours points up to us the close-knit nature of the relationship of the bulk of species so far described in the genus. We find the major discontinuity in the group to be that separating out *E. bilamellata* Sars, *E. setifera* Hansen, and *E. laticeps*, described below, and we must point out that the state of knowledge concerning SARS' and HANSEN's species is unsatisfactory.

As a result of CANU's excellent presentation on development (1892), the description of additional species of *Enterocola*, by CHATTON and his associates have employed an appropriate terminology for the head appendages, which procedure has been followed by other authors right to the present (c.f. GUILLE, 1964).

The body is cruciform, with 3 distinct regions. The cephalosome forms a head, and the maxillules and prominent maxillae tend to delimit the region ventrally. In the metasome the component segments are somewhat variably delimited and frequently feature dorsal duplicatures, termed pterostegites by CHATTON and his associates. These may not occur at all or may be borne only on some of the segments. The articulation of the legs with their body segments tends to considerable suppression. In most species there are lamelliform or mammiform processes between the protopodites of some or all of the pairs of legs. These are absent in some species. The sixth thoracic segment is characterised by enlarged pediform projections which envelop much of the dorsal and lateral portions of the urosome.

These usually are unarmed, but in some cases are setiferous, with at most 2 minute setae. The caudal rami are somewhat variable in proportions and extent of articulation with the urosome ; they are not setiferous. The antennule varies from unsegmented to vaguely bimerous ; SARS states that in *E. bilamellata* there are 4 segments. HANSEN shows a multiarticulate appendage. The setation is reduced. The antenna is vaguely to clearly bimerous, with the second segment equal to or much longer than the basal. The second segment is flattened, wide and always bears at least 6 setae, these of varying proportions. The labrum is always prominent, its surface variously ornamented with spinules, and there is characteristically at the posterolateral corners a pair of spinulose setae. These are absent in *E. megalova*, according to the original description, and the situation is not known for *E. setifera* or *E. bilamellata*. Some early statements that mandibular vestiges were present in species of *Enterocola* were possibly based on misidentification of these labral structures. CHATTON and HARANT did point out (1924a, p. 351) that if mandibular vestiges occur this would have to be verified by study of development. We feel, from our own study of ascidicolids and reexamination of CANU's findings, that there are no such mandibular vestiges after the first or second copepodid and that the conspicuous structures are involved with the labrum.

The maxillule is characteristic, essentially on a subfamilial pattern, remaining bilobed but with much suppression of segmentation. The lamellate palp portion tends to be lobed, with 6 setae distributed on the lobes and on the external margin. *Enterocola bilamellata* is reported to have only 5 such setae.

The maxilla is bimerous and heavily sclerotized. The basal segment supports a medially extended lobe which may appear even to form an articulation. The distal segment is subacute at the apex, with a hook-or claw-like aspect. There may be 1 or more small elements of ornamentation set basal to the distalmost hook-process.

There is no maxilliped.

The first to fourth legs are reduced, biramous. There are no setae on the protopodites. The exopodites tend to have a characteristic termination, this usually with a demarcated apex, often of very distinctive outline, consisting of a dome with an emerging tip, particularly on legs 1, 2 and 4. Very consistently the third leg will have the exopodite with the margin uninterrupted and forming in outline a stylet-like aspect. The endopodites may be clearly unsegmented ranging to obscurely bimerous and always bear at least 2 terminal setae. For all species for which the host relation is recorded, the copepod occurs in the stomach or nearby in the alimentary canal, and hosts previously recorded were compound ascidians. One new species, described below, p. 91, is from a solitary ascidian and furnishes a hint that such problematical species as *E. setifera* and *E. bilamellata* possibly also come from solitary ascidian hosts. Most species so far known come from hosts of the family Polyclinidae ; 2 are known from the Didemnidae.

THE MALE OF ENTEROCOLA

CANU (1892, p. 216, 218, pl. 18, figs. 3-8), described the male of *Enterocola fulgens* and we have been able to make out some features of the male fifth copepodid in our material of *E. pterophora*. With this basis we can present a short sketch of the diagnostic features.

The body is cyclopoid, the division into forebody and urosome well demarcated. The cephalosome of the adult male, as described by CANU, is notable in the formation of well-developed pleural folds. The ventral portions of these folds are covered with fine hairs, disposed in regular series. The cephalosome bears a rostrum and 4 pairs of appendages. The mandibles and maxillipeds are absent. There is also a distinctive modification of all the appendages. The metasome consists of 4 segments, each bearing a pair of biramous swimming legs. The urosome is 6-segmented, with the first segment bearing rudimentary fifth legs and the second with indications of sixth legs. Paired spermatophoral sacs lie in the second urosomal segment. The caudal rami bear elongate terminal setae.

The antennules are 7- or 8-segmented. The setation is well developed and the terminal article bears an aesthete as well as several setae.

The antenna is trimerous and bears an articulated terminal prehensile hook, accompanied by several setae. The basal article bears a single distal outer seta.

We have no positive information about the labrum.

The maxillule in the adult has some resemblance to that of the female, but the basal portion is reduced, while the palp, which is clearly articulated, bears 6 elongate plumose setae, rather than the short, hooked setae of the female.

The maxilla consists of 2 articles, the basal much exceeding the distal in length and somewhat in width. The basal article has no endite and does not develop the massive expansion and sclerotization characteristic of the female. The distal article is directly and simply articulated on the basal and does not at all form a hook-process. The armature of the terminal article is a long, plumose seta, laterally directed. This seta is very possibly the homologue of the very small, but consistently present, seta of the external face of the distal article of the females of all the species. Between the bases of the maxillae, but not directly joined with them, is a small ventral protuberance. These 2 mouthparts and the relatively elongate prehensile antenna and the general habitus of this male appear to us to form an interesting parallel in modification, following a pattern of reduction which, when it occurs in notodelphyids, leads to the formation of what might be called the “agnathaner” male type. The modifications consist of reduction of all gnathal parts of head appendages, with accompanying general lengthening of such appendages and of their setae.

By and large all the swimming legs conform very well to a general cyclopoid pattern, with perhaps a distinctive feature in the segmentation of the first exopodites. All the protopodites are bimerous, the coxopodites united by lamellae but lacking armature. The basipodites have lateral setae and in the first leg there is the medial spine which occurs so widely through species of gnathostomes. The endopodites are all trimerous and they tend somewhat to lack of setae on some of the basal articles. The exopodites of the first legs are bimerous, all the others are trimerous. There are some setae lost on basal articles. There are strong indications of correspondence with males of the Enteropsinae and equally definite trends to differ from males of *Ascidicola*, which might be said to conform even more to a general cyclopoid pattern, and of *Botryllophilus*, which has distinctive supplementary modifications.

The fifth leg is definitely much reduced, with indications of 2 articles, but the basal one is completely coalesced with the body. There is retained a small lobe, bearing a seta. The distal article is small, somewhat bilobed and bears a single short seta. The position of the fifth leg at the posterior margin of the first urosomal segment is a very generally occurring cyclopoid trait for males.

The so-called sixth leg is at the posterior margin of the second urosomal segment. There is no articulated appendage, but a bilobed prominence at either side of the segment is set with 2 setae at the lateral distal margin.

The caudal rami have a very cyclopoid aspect, both in general shape and arrangement and in the armature of 4 terminal plumose setae and of single dorsal and single lateral reduced setae.

KEY TO SPECIES OF ENTEROCOLA BASED ON FEMALES

1. With mammiform processes at the bases of some or all of the thoracic legs.............. 5

1′. Thoracic legs without mammiform processes.. 2

2. Pediform projection-fifth leg with very long setae............ *setifera* Hansen, 1923, p. 49

2′. Pediform projection-fifth leg with very short or barely visible setae or without setae.... 3

3. Dorsal surface of metasome produced into pairs of conspicuous overlapping folds..........
pterophora Chatton & Brément, 1909, p. 50

3′. Dorsal surface without conspicuous overlapping dorsal metasomal folds................ 4

4. Urosome lacking visible segmentation........................ *megalova* Gotto, 1962, p. 49

4′. Urosome clearly segmented.................................... *laticeps*, n. sp., p. 91

5. Setae of antenna short, hooked, clawlike, length of longest seta less than half greatest width of appendage.................................... *fulgens* van Beneden, 1860, p. 63

5′. Setae of antenna normal, flexible, length of longest seta considerably more than half greatest width of appendage.................................... 6

6. With distinct mammiform processes between all leg pairs.................................... 10

6′. Mammiform processes missing or very indistinct between one or more pairs of legs........ 7

7. Setae of antenna arranged so that an apical pair is set off on a distinctive lobe............ *clavelinae*, n. sp., p. 66

7′. Setae of antenna include 4 or more arranged in a compact apical row.................... 8

8. Setae of endopods 1-4 set close together apically on ramus.......................... 9

8′. Lateralmost of 2 apical setae of each endopod set more on the lateral surface than apical, and diverging from the axis of the ramus................ *hessei* Chatton & Harant, 1924, p. 49

9. Third endopod modified, outline more lobate than styliform; setae of endopods 1-4 about as long or shorter than ramus.................................... *precaria*, n. sp., p. 72

9′. Third endopod with usual styliform outline; setae of endopods 1-4 distinctly longer than the rami *ianthina*, n. sp., p. 74

10. Antenna with apex long, narrow, bearing 7 setae.............. *bilamellata* Sars, 1921, p. 49

10′. Antenna with apex broad, bearing 6 setae.................................... 11

11. Antennule lacking setae.................... *mammifera* Chatton & Harant, 1922, p. 49

11′. Antennule with setae.................................... 12

12. With caudal rami fairly developed, set off to some degree from the anal somite.......... 13

12′. Caudal rami simply indicated by terminal bilobing of body, not definitely demarcated...... *sydnii* Chatton & Harant, 1924, p. 76

13. Antenna clearly unimerous.............................. *petiti* Guille, 1964, p. 80

13′. Antenna completely or partially bimerous.................................... 14

14. Endopods 1-4 subrectangular, with more or less parallel margins, elongate; apical setae well separated at bases.................................... *brementi*, n. sp., p. 82

14′. Endopods 1-4 with medial margin curved more or less strongly, short; apical setae set close together.................................... *fertilis*, n. sp., p. 85

non Enterocola spp.:

Enterocola beaumonti Scott & Scott, 1895

Enterocola beaumonti, T. & A. Scott, 1895, p. 359-360, pl. 16, fig. 9, pl. 17, figs. 9-12 (from Valentia, Ireland, from an ascidian).
Placed in *Haplostoma* — (*Aplostoma*) by Chatton & Brément, 1909c, p. 228.
Placed in *Haplostomides* by Chatton & Harant, 1924d, p. 406-407.
Haplostominae, sp. incertae sedis, Ooishi & Illg, 1977, p. 79.

Entorocola (sic) eruca Norman, 1868

Entorocola eruca Norman, 1868, p. 300 (from Shetland Islands, from *Ascidia intestinalis*).
Removed from *Enterocola*, suggested as belonging to *Aplostoma* by Canu, 1886, p. 372. — Placed in *Aplostoma* by Brément, 1909, p. 83-85, 87.

Haplostoma eruca, Chatton & Harant, 1922e, p. 419. — Ooishi & Illg, 1977, p. 12 (see for additional citations).

Enterocola hibernica, Scott & Scott, 1895

Enterocola hibernica, T. & A. Scott, 1895, p. 360, pl. XVII, figs. 3-8 (from Valentia, Ireland, from an ascidian).
Placed in *Haplostomides* by Chatton & Harant, 1924d, p. 405-406, 407.
Haplostomides hibernicus Ooishi & Illg, 1977, p. 78 (see for additional citations).

SPECIES OF *ENTEROCOLA*

Enterocola bilamellata Sars, 1921

Enterocola bilamellata Sars, 1921, p. 77-78, pl. 36 (type locality, Norway Coast, host unknown). — Sewell, 1949, p. 191. — Gotto, 1960, p. 225 ; 1962a, p. 544. — Guille, 1964, p. 289.
Distribution : Coast of Norway.
Host : unknown.

Enterocola hessei Chatton & Harant, 1924

Enterocola hessei Chatton & Harant, 1924b, p. 358-360, 363, fig. 3 (type locality, Baie de Morlaix, France, from compound ascidians). — Harant, 1931, p. 371. — Gotto, 1960, p. 226 ; 1962a, p. 544. — Guille, 1964, p. 289.
Distribution : France, Channel Coast.
Host : Unknown.

Enterocola mammifera Chatton & Harant, 1922

Enterocola mammifera Chatton & Harant, 1922a, p. 153-154, 156, fig. 3 (type locality, Golfe du Lion, France, from *Aplidium asperum* Drasche). — Chatton & Harant, 1922c, p. 245, 248, 249 ; 1924b, p. 363. — Harant, 1931, p. 371. — Gotto, 1960, p. 226 ; 1962a, p. 544. — Guille, 1964, p. 289.
Distribution : Golfe du Lion, Mediterranean.
Host : *Aplidium asperum* Drasche.

Enterocola megalova Gotto, 1962

Enterocola megalova Gotto, 1962, p. 541-543, fig. 1 (type locality Strangford Lough, Ireland, from *Polyclinum aurantium* Milne Edwards). — Guille, 1964, p. 290. — Gotto, 1966a, p. 193.
Distribution : Ireland.
Host : *Polyclinum aurantium* Milne Edwards.

Enterocola setifera Hansen, 1923

Enterocola setifera Hansen, 1923, p. 27-28, pl. III, fig. 3a-3i (type locality, S. W. of Iceland, from bottom sample). — Sewell, 1949, p. 194. Guille, 1964, p. 289, did not accept the species. In a footnote be stated " ... Je ne pense pas que cette espèce appartienne au genre *Enterocola*... " Very rightly he pointed out the antenna was unlike anything to be expected in *Enterocola* and seemed more related to structures found in the Notodelphyidae. He also noted discrepancies between other appendages as described by HANSEN and the standard characters for the genus. Having accepted his opinion we were inclined to exclude the species from *Enterocola*. However, our study of the whole family Ascidicolidae and our noting of the range of variation in some appendages have led us to alter our opinion. There are clearly some ambiguities and the situation demands that the species be recollected and redescribed. HANSEN himself stated he was dissatisfied with his depiction of some of the important appendages. The animal is without doubt an ascidicolid and conforms, very roughly, but sufficiently, to be placed as a species of *Enterocola*, with the description unsatisfactory. The strange antenna depicted by HANSEN now is more acceptable to us in the light of our study of species of *Styelicola*. In these there is a prehensile apical claw on the antenna. Further, on the basal segment of the antenna of *S. bahusia* there is a process, doubtless a much modified spine or seta, of appearance remarkably similar to the element depicted by HANSEN.

Distribution : Iceland.

Host : Unknown.

Enterocola sp. Claus, 1875

Enterocola sp. Claus, 1875, p. 351-352, 360, pl. xxiv, fig. 31 (locality not given, from an ascidian). — Della Valle, 1883, p. 252. — Chatton & Harant, 1922a, p. 149.

Enterocola betencourti, Canu, 1891a, p. 474, 475 ; 1892a, p. 218. — Chatton & Brément, 1909c, p. 228.

Enterocola sp. A Chatton & Brément, 1909

Enterocola fulgens, Della Valle, 1883, p. 245-247, pl. 1, fig. 3-10 (from Naples, from *Aplidium crystallinum*, *A. gibbulosum* and didemnids).

Enterocola fulgens, Canu, 1892, p. 216.

Enterocola sp. A, Chatton & Brément, 1909c, p. 228. — Chatton & Harant, 1922a, p. 156.

Enterocola sp. Chatton & Harant, 1924b, p. 363.

Enterocola sp. B Chatton & Brément, 1909

Enterocola ? fulgens, T. Scott, 1900, p. 386-387, pl. XIII, fig. 21-27, (from Scotland, from an unidentified ascidian).

Enterocola sp. B, Chatton & Brément, 1909c, p. 228. — Chatton & Harant, 1922a, p. 156.

Enterocola sp., Chatton & Harant, 1924b, p. 363.

Enterocola sp. Schellenberg, 1922

Enterocola sp., Schellenberg, 1922, p. 294 (from Plattenberg Bucht, South Africa, from *Polycitor renieri* Hartmeyer).

Enterocola pterophora Chatton & Brément, 1909

(Figures 12, 13, 14, 15, 16, 17, 18, 19)

Enterocola pterophora Chatton & Brément, 1909b, p. 225-227, fig. 1-5, (type locality, Banyuls-sur-Mer, Golfe du Lion, France, from "*Leptoclinum commune*" ; 1911, p. 70 ; 1915, p. 145, 149, 153,

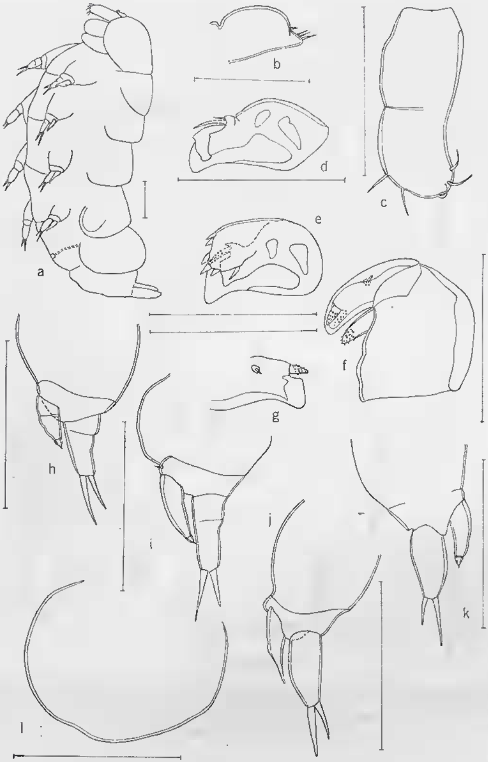

FIG. 12. — *Enterocola pterophora* Chatton & Harant, female : a, habitus, lateral view ; b, antennule ; c, antenna ; d, basal portion of maxillule ; e, maxillule ; f, maxilla ; g, apex of maxilla, anterior view ; h, first leg ; i, second leg ; j, third leg ; k, fourth leg ; l, pediform projection. All scales = 0.1 mm.

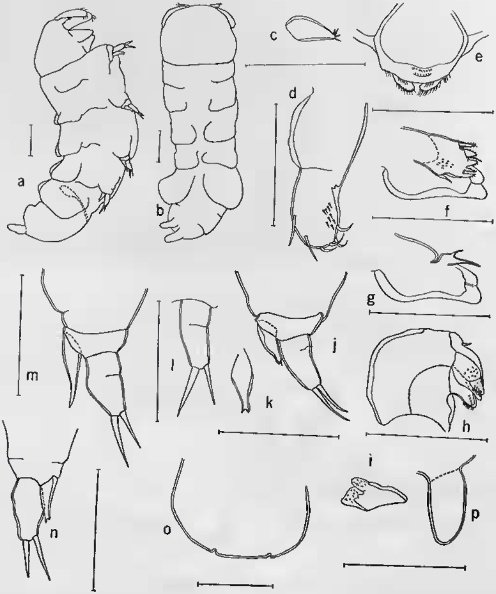

FIG. 13. — *Enterocola pterophora* Chatton & Harant, *Trididemnum* form, female : a, habitus, lateral view ; b, habitus, dorsal ; c, antennule ; d, antenna ; e, labrum ; f, maxillule ; g, basal portion of maxillule ; h, maxilla ; i, apex of maxilla, posterior view ; j, first leg ; k, exopodite of first leg ; l, endopodite of second leg ; m, third leg ; n, fourth leg ; o, pediform projection ; p. caudal ramus. Scales = 0.1 mm.

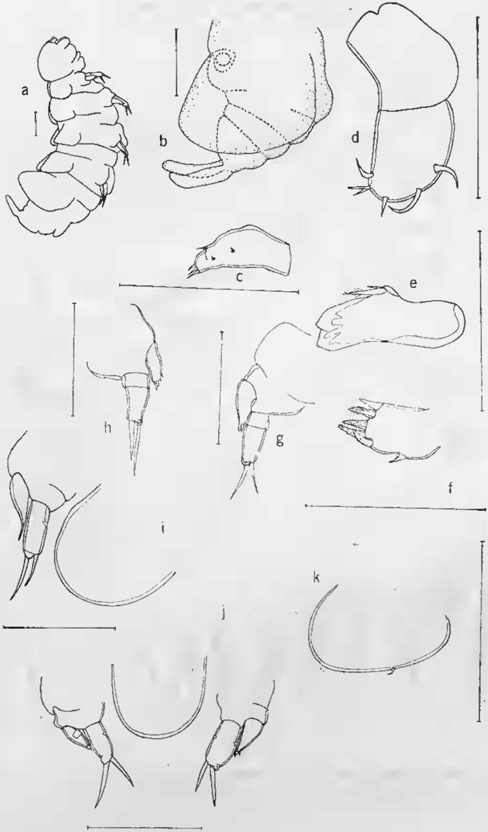

FIG. 14. — *Enterocola pterophora* Chatton & Harant, *Trididemnum* form, female : a, habitus, lateral view ; b, urosome, lateral ; c, antennule ; d, antenna ; e, maxillule, basal portion ; f, maxillule, palp ; g, first leg ; h, second leg ; i, third leg and medial ventral protrusion ; j, fourth leg, ventral protrusion ; k, margin, pediform projection. Scales = 0.1 mm.

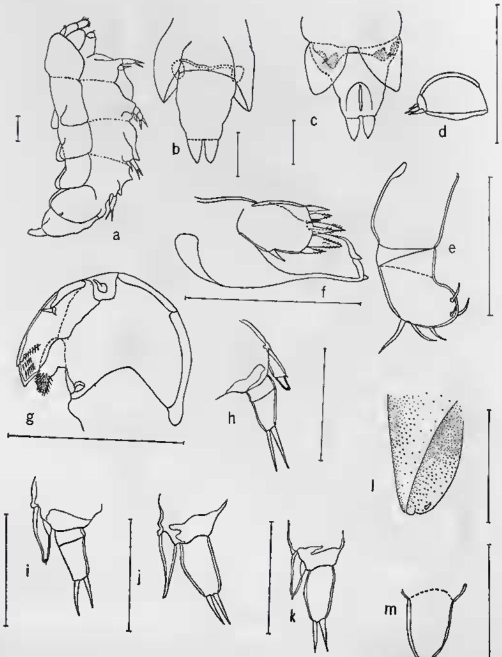

FIG. 15. — *Enterocola pterophora* Chatton & Harant, *Tridideamnum* form, female : a, habitus, lateral view ; b, urosome, ventral view ; c, urosome, dorsal ; d, antennule ; e, antenna ; f, maxillule ; g, maxilla ; h, first leg ; i, second leg ; j, third leg ; k, fourth leg ; 1, pediform projection ; m, caudal ramus. Scales = 0.1 mm.

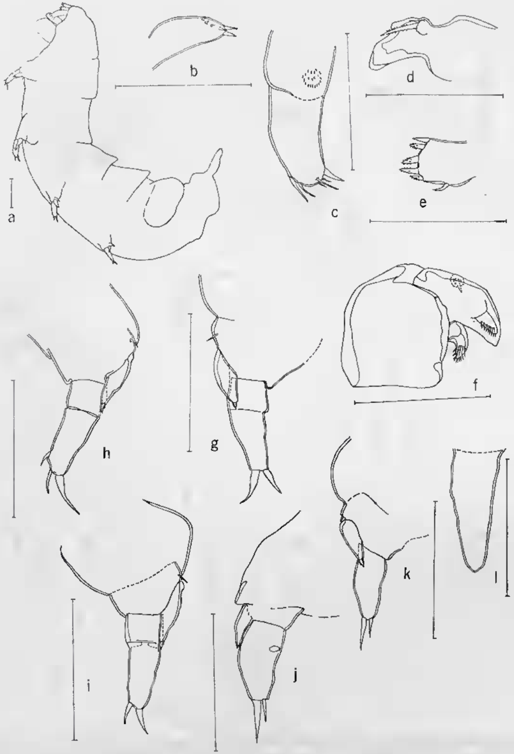

FIG. 16. — *Enterocola pterophora* Chatton & Harant, *Diplosoma* form, female : a, habitus, lateral view ; b, antennule ; c, antenna ; d, basal portion of maxillule ; e, palp of maxillule ; f, maxilla ; g, first leg, right ; h, first leg, left ; i, second leg, left ; j, third leg, right ; k, fourth leg, right ; 1, caudal ramus. Scales = 0.1 mm.

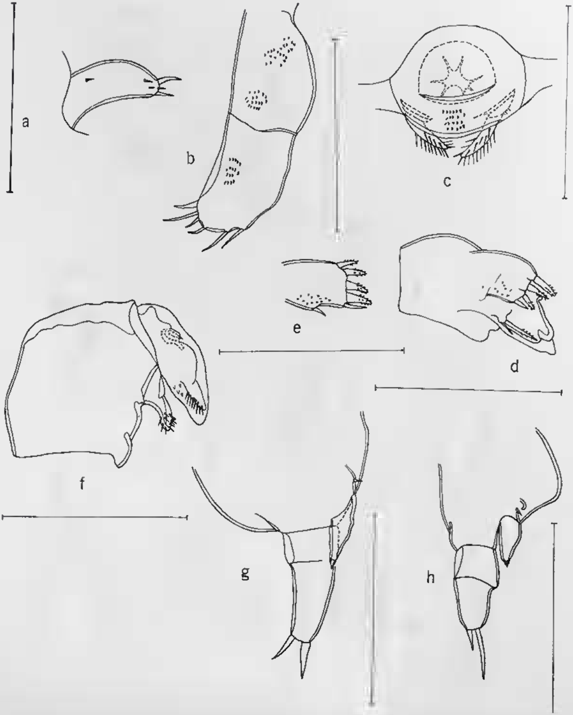

FIG. 17. — *Enterocola pterophora* Chatton & Harant, *Diplosoma* form, female : a, antennule ; b, antenna ; c, labrum ; d, maxillule ; e, palp of maxillule ; f, maxilla ; g, second leg ; h, fourth leg. Scales = 0.1 mm.

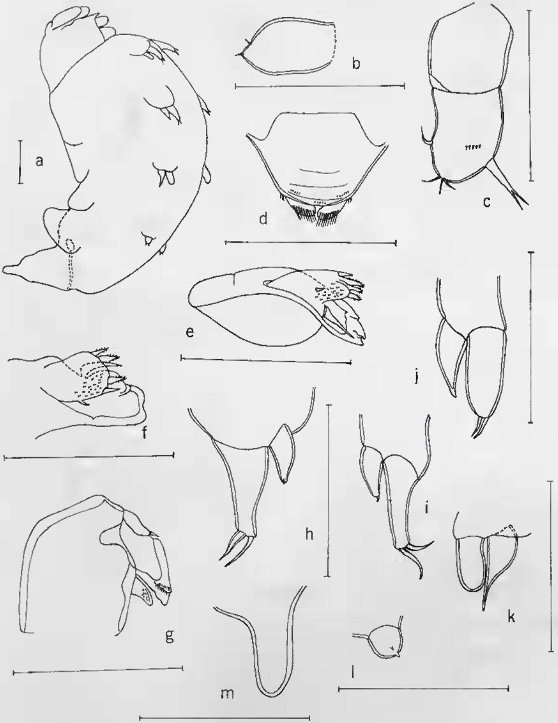

FIG. 18. — *Enterocola pterophora* Chatton & Harant, *Diplosoma* form, Banyuls, female : a, habitus, lateral view ; b, antennule ; c, antenna ; d, labrum ; e, maxillule ; f, maxillule ; g, maxilla ; h, first leg ; i, first leg ; j, second leg ; k, third leg ; 1, fourth leg ; m, caudal ramus. Scales = 0.1 mm.

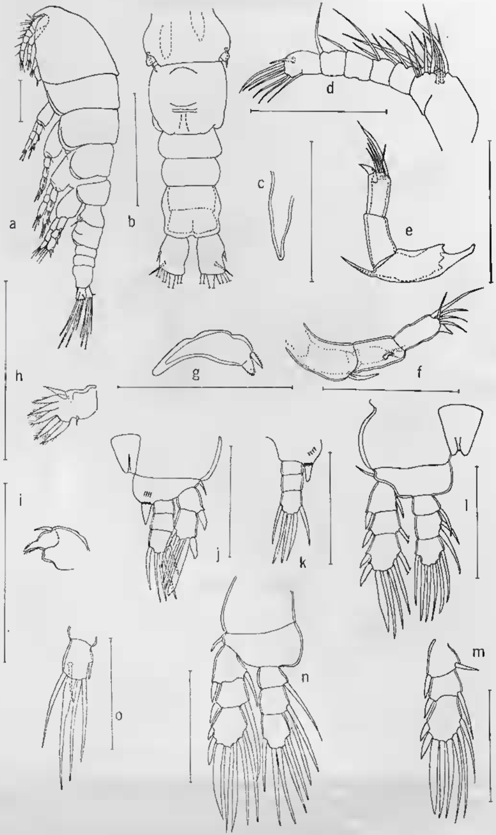

FIG. 19. — *Enterocola pterophora* Chatton & Harant, male fifth copepodid : a, habitus, laterodorsal view ; b, urosome, ventral view ; c, rostrum ; d, antennule ; e, f, antenna ; g, maxillule, basal portion ; h, maxillule, palp portion ; i, maxilla ; j, first leg ; k, first leg, part of basipodite and endopodite ; l, second leg ; m, third leg, exopodite ; n, fourth leg ; o, caudal ramus, ventral view. Scales = 0.1 mm.

fig. 1. — Chatton & Harant, 1922a, p. 151-152, 154, fig. 2 ; 1922c, p. 245. — Schellenberg, 1922, p. 294. — Chatton & Harant, 1924b, p. 363. — Harant, 1931, p. 371. — Sewell, 1949, p. 183. — Gotto, 1952, p. 674 ; 1954, p. 665 ; 1960, p. 221 ; 1962a, p. 544. — Guille, 1964, p. 289. — Gotto, 1966a, p. 193.

Distribution : Mediterranean, especially Golfe du Lion.

Hosts : *Didemnum commune* (Della Valle), *D. asperum maculatum* (Milne Edwards), *D. fulgens* (Milne Edwards), *Diplosoma listerianum* (Milne Edwards), *Parascidia flava* Milne Edwards, *Cystodites* sp.

Specimens examined :

From *Didemnum fulgens* Milne Edwards :

Northeast of Port Vendres, and near Cap Béar, near Banyuls-sur-Mer, France, 90 m, 60 m, mixed trawl, May 14, 1958, 1 female.

Near Banyuls-sur-Mer, 60-100 m, April 25, 1958, 1 female.

Northeast of Port Vendres, mixed trawl, 70, m, 30-60 m, May 6, 1958, 6 females, 1 male fifth copepodid.

Cap Doune, near Banyuls-sur-Mer, France, 50 m, May 2, 1958, 1 female.

Near Port Vendres, 50 25 m, May 13, 1958, 6 females.

" *Leptoclinum fulgidum* (*L. commune* Della Valle) " :

Banyuls, September 26, 1910, Chatton number 44, 1 female, 1 male.

" *Leptoc. fulgidum* " :

Aquarium, Banyuls, September 27, 1910, Chatton number 67, 1 female, 1 male, 2 fourth copepodids.

From *Didemnum maculosum* Milne Edwards :

Northeast of Port Vendres, and near Cap Béar, 90 m, 60 m, mixed trawl, May 14, 1958, 6 females.

North of Port Vendres and off Cap Béar, in Anse de Paulilles, 70-30 m, 20-50 m, mixed trawl, May 28, 1958, 3 females.

Gaiola, Bay of Naples, 25 m, March 13, 1958, 1 male.

" *Leptoclinum asperum — maculosum* " :

Banyuls, October 17, 1910, Chatton number 117, 3 females.

" *Leptoclinum mascul. coriac* " :

Port Vendres, 100 m, January 10, 1912, Chatton number 157, 15 females, 1 male, 1 developmental stage.

From *Polysyncraton lacazei* Giard :

Cap Doune, 50 m, May 2, 1958, 1 female.

From " *Leptoclinum* sp. " :

« Chalut au large de Cerbère, » September 25, 1912, Chatton number 162, 2 females.

From *Trididemnum tenerum* (Verrill) :

North and northeast of Port Vendres, 70 m, 30-60 m, mixed trawl, May 6, 1958, 1 female.

Duke Rock, near Plymouth, England 6 fm, September 8, 1958, 1 female.

Duke Rock, near Plymouth, England, 6 fm, September 9, 1958, 1 female. 1 male fifth copepodid.

From *Trididemnum niveum* Giard :

Troc l'Abeille, Banyuls, October 24, 1910, Chatton number 140, 1 female.

From *Diplosoma gelatinosum* var. *listerianum* Milne Edwards :

Near Port Vendres, 50-35 m, May 13, 1958, 1 female, teratological.

From " *D. spongiforme* " :

Chalut, nord Argelès — Canet, January 10, 1912, Chatton number 166, 10 females.

From " *Diplosoma listeri*, var *Kollerianum* Int-d'oscanius " :

September, 1912, Chatton number 155, 1 developmental stage.

Our suite of specimens includes material collected by Chatton, at least one with a tentative identification by him, and extends the roster of host species. Material from the typical host, as best as we can identify it from the old accounts, establishes a sufficient range of variation that we have felt confident in assigning material from additional ascidian species to this form. Our discussion below attempts to account for the range of variation we encountered. We would point out it has only been very rarely that such an extensive sampling of any species of ascidicolid has been similarly available for study. We offer what we consider to be pertinent supplementary information to the original description and figure a specimen from the probably typical host, *Didemnum fulgens*, collected by us from the region of the type locality, 2 females and a male fifth copepoidid from *Trididemnum tenerum* from Plymouth, and a female from *Trididemnum tenerum* from the type area, 2 females from *Diplosoma gelatinosum* from the type locality, collected by us.

Specimen from *Didemnum fulgens* (fig. 12) : Overall measurement 0.82 mm, as compared with the lengths of 0.8 to 1.0 mm given by the authors. The proportions, cephalosome : metasome ; urosome, are 1: 4: 2, corresponding to the authors ; ratio of 1: 5.5: 1 plus, but their figure, when measured, presents approximately a ratio of 1: 4: 2. The habitus (fig. 12, a) is in agreement with the original description with the slight exception that the animal has a somewhat greater measurement dorsal to ventral. The antennule (fig. 12, b) is somewhat more narrowed apically than shown by the authors. We see 4 setules rather than the 2 they discerned. The antenna (fig. 12, c) is very characteristic in this species. It appears to be bimerous but the articulation is somewhat incomplete. The distal article is rather flat and plate-like with a definite curve of the axis toward the midline. There are 2 small setae on the distal lateral margina and a group of 3 curved setae on the distal medial margin. The authors saw 4 small setae in the latter position. The maxillule (figs. 12, d, e) is bilobed. We agree with the author's description but the anterior margin of the basal portion bears a seta and a setule not mentioned by them. The maxilla (figs. 12, f, g) conforms to the original account. The 4 pairs of legs (figs. 12, h, i, j, k) are all biramous and the protopodites are bimerous. The endopodites of the first leg (fig. 12, h) and the second (fig. 12, i) are obscurely bimerous, those of the third leg (fig. 12, j) and the fourth (fig. 12, k) unimerous. Each of the endopodites bears 2 apical setae, both shorter than the ramus, with the lateral seta about one-third longer than the medial. The exopodite of the first leg is obscurely bimerous, with at least an interruption in the cuticle on one surface. There is a characteristic terminal element with the shape of a pointed dome. The exopodites of the second leg and the fourth leg are unimerous and each has a similar pointed dome-like endpiece. The exopodite of the third leg (fig. 12, j) is characteristic of the genus and consists of a curved stylet. The pediform projection (fig. 12, l) is a subcircular plate which bears no elements of armature. The urosome and caudal rami are similar to those shown by the authors but in this specimen the strongly differentiated segmentation shown by them does not appear.

Female specimens from *Trididemnum tenerum* (figs. 13, 14, 15) : The overall measurements are 0.81, 0.75, 0.99 mm, measured along the curve of the body to the tip of the caudal ramus. The habitus (figs. 13, a, b ; 14, a ; 15, a) in each corresponds well to those of Chatton & Brément and the specimen discussed above, from *Didemnum*. We present additional details for the urosomes (figs. 14, b ; 15, b, c). The antennules vary from a simple tapering lobe with 4 terminal setules (fig. 13, c) to a somewhat longer appendage with 3 small terminal setules and a marginal setule (fig. 14, d), and to a lobe with 3 terminal setules (fig. 15, d). The antenna has a characteristic form for the species, but the proportions and the setation vary slightly (figs. 13, d ; 14, d ; 15, e). Two of the specimens have exactly the pattern of setation shown by the authors. The labrum (fig. 13, e), not previously illustrated, consists of a flattened lobe with rows of spinules on the surface and with 2 digitiform spinulose palps emerging from the distal lateral corners. The maxillules (figs. 13, f, g ; 14, e, f : 15, f) are as described for the specimen from *Didemnum* above. The maxilla (fig. 13, h ; 15, g) corresponds to the original description. The legs show a great degree of minor variation within a consistent basic pattern. They conform throughout in biramous construction with bimerous protopodites. In all cases the endopodite bears 2 terminal setae, always shorter than the ramus, but the relative lengths of these vary somewhat. The endopodite of the first leg varies from unimerous (fig. 13, j) to obscurely bimerous (figs. 14, g ; 15, h). The exopodite also varies from unimerous (figs. 13, j, k ; 14, g) to bimerous (figs. 15, b). In all specimens there is a subterminal cuticular point, but in one specimen (fig. 15, b) there is an additional spinule at the distal third of the lateral margin. In the second legs the endopodite may vary from obscurely bimerous (fig. 13, 1) to distinctly bimerous (figs. 14, h ; 15, i). The exopodites are all unimerous. In 2 specimens there is no differentiated element except a minute subterminal cuticular point. In the remaining specimen (fig. 14, h) there is a diffentiated dome-like apex bearing a small subterminal spine. In the third legs the endopodite varies from obscurely bimerous (figs. 13, m ; 14, i) to unimerous (fig. 15, j). The exopodite in all specimens is a curved pointed unimerous stylet. In all specimens the fourth leg has unimerous rami. The armature of the exopodite varies from a subterminal cuticular point (fig. 13, n) to a terminal cuticular point (fig. 15, k) to a differentiated dome-like element with a terminal point (fig. 14, j). There are never mammiform processes between the legs, but there may be a conspicuous single medial sclerotized lobe (figs. 14, i, j). The pediform projection is always a large subcircular plate. As minor variations there may appear slight marginal indentations (fig. 13, o) and there may be present a single marginal or submarginal seta, facing internally (figs. 14, k ; 15, 1). The caudal ramus (figs. 13, p ; 15, m) varies somewhat in length relative to the urosome and indeed may become extremely elongate (fig. 14, b).

In one collection color features were noted ; the ova in the oviducts were bright pink and the embryos in the ovisacs had cherry-red yolk.

Three female specimens from *Diplosoma gelatinosum* (figs. 16, 17, 18) that we dissected indicated a strong differentiation from the material discussed above, but the series presented so much internal variation that we cannot on the basis of the present suite offer a clear-cut differentiation of these as a separate taxonomic entity. Further, more extensive study may demonstrate a separation. The specimens were relatively large, a representative specimen measuring 1.23 mm overall. The proportions cephalosome : metasome : urosome were 1: 4: 2. The dorsal plates are not as well differentiated as in our other specimens (fig. 16, a) but they are clearly indicated and the pediform process is similar in size and form to the typical specimens. The body shows a greater curvature than we saw in other material. The antennule (figs. 16, b ; 17, a) is long, conical, with only a slight taper and with 2 or 3 apical setules. There may be additional setules on the surface. The antenna (figs. 16, b ; 17, c) is indistinctly bimerous, and although the appendage is long and narrow, the axial curvature is slight. The pattern of setation is the same as in typical specimens. The labrum (fig. 17, c) conforms. The maxillule (figs. 16, d, e ; 17, d, e) and the maxilla (figs. 16, f ; 17, f) also conform. The first leg is rather distinctive (figs. 16, g, h). There is a setule on the protopodite near the articulation of the exopodite. The endopodite is bimerous and unusually long. The right leg of the specimen dissected had the usual 2 apical setae, but the left had an additional seta, probably an abnormality The exopodite is unimerous, with the usual apical structure. The second leg (figs. 16, i ; 17, g) also has the seta on the protopodite and has a bimerous endopodite, exceptionally long. The third leg (fig. 16, j) as in the other specimens studied, has the endopodite unimerous, but there is a differentiated area in the cuticle perhaps indicating a suppressed segmentation. The exopodite is particularly short and departs somewhat from the usual styliform outline found throughout the genus. The fourth leg (figs. 16, k ; 17, h) may have the endopodite unimerous or bimerous ; the exopodite is unimerous with the usual differentiated apical elements. There is a setule on the protopodite which we have not seen on fourth legs of other specimens. The caudal ramus (fig. 16, l) is elongate, conical.

The only specimen of *E. pterophora* from *Diplosoma gelatinosum* from our own collecting, and the only one recently taken from this host, therefore, is a female which we can only interpret as a teratological example (fig. 18). The body shape is distorted, and the length measurement probably would not be significant. It does have the usual indications of dorsal plates and the pediform projections conform to the other specimens from the same host. There is good correspondence with other specimens in the labrum (fig. 18, d), maxillule (figs. 18, e, f), maxilla (fig. 18, g) and the caudal ramus (fig. 18, m). The antennule (fig. 18, b) is swollen although it has the usual setation. The antenna (fig. 18, c), although it has the usual outline, has aberrant setae. The first legs (figs. 18, h, i) are recognizable as those of the species and would fall within the range of variation of the other specimens. The second leg (fig. 18, j), however, has an exopodite which has a form more reminiscent of the typical third exopodite. The third leg (fig. 18, k), although it has the typical exopodite, has a very reduced endopodite with no terminal setae. The fourth leg (fig. 18, 1) is reduced to a uniramous unimerous, lobe, with 2 setules.

Such aberrant specimens are seldom observed among the ascidicolids, doubtless because of the relative rarity of almost all the species. It is interesting to observe that although this specimen possesses obviously monstrous features, it does conform to the basic generic and specific diagnoses. It emphasizes the variability of the leg structure in this particular species.

We did not dissect the specimens from *Polysyncraton lacazei* or from *Didemnum maculosum*, but feel a reasonably secure identification could be made by superficial examination in connection with observations made on the whole suite of material. For some of his specimens from *D. maculosum* (CHATTON No. 157) CHATTON recorded that the body was pale rose, with " ovarics " and ovisacs violet.

The male fifth copepodid (from *Trididemnum tenerum*, Plymouth) (figs. 19, a-o) : the body form (fig. 19, a) is cyclopoid, with the qualification that the habitus is distinctly copepodid. The overall length, measured from the apex of the head to the end of a cuadal ramus, is 0.70 mm. The segmentation is well defined. The individual was almost ready to molt into the adult and some of the features of that stage can be made out through the cuticle. The body is demarcated into 3 regions. The cephalosome doubtless incorporates the body regions corresponding to appendages through the maxillipeds, but the latter, and the mandibles, are lacking. There are 4 free thoracic segments bearing the swimming legs. The urosome (fig. 19, b) is 5-segmented. The first segment bears the minute fifth legs and developing spermatophores can be discerned within this segment. The second urosomal segment has some ventral cuticular folds and indications of the spermatophoral sacs which will be present in the adult stage. The remaining 3 segments of the urosome are somewhat narrower than the first 2. The last segment is approximately equal in length to the combined lengths of the preceding 2 segments, and internally there are indications that this segment will divide into 2 upon molting, producing a urosome of 6 segment in the adult male.

The rostrum (fig. 19, c) is elongate, tapering and unornamented.

The antennule (fig. 19, d) is 6-segmented. The basal article is about equal in length to the combined lengths of articles 2, 3, 4 and approximately 2 times wider than all the remaining articles. There is little taper in articles 2 through 6. The setation is as follows : I — 10 setae ; II — 2 ; III — 2 ; IV — 1 ; V — 1 ; VI — 7 setae, 1 aesthete. It can be observed that article IV will divide into 2 articles in the adult, producing in the adult male an antennule of presumably 7 articles.

The antenna (figs. 19, e, f) is trimerous, the articles having the proportional lengths of approximately 2 : 1: 1. The basal article has a long setiform projection at the distal inner corner. The second article is unarmed. The terminal article bears an articulated pointed element which contains the developing articulated hook of the adult male (the outlines of the latter are dotted in Fig. 19, e). In addition there are 4 subequal setae on the terminal margin and 1 seta, which is at least one-third longer than the others, in an emargination slightly proximal to the apex on the outer margin.

The labrum was not made out in our preparation.

The maxillule is bilobed and has some resemblance to that of the female. The basal element, perhaps derived by fusion of the protopodite and parts of the palp, forms a lamella (fig. 19, g) produced medially and terminating in 2 spinulose processes, one of these articulated and bearing heavier spinules than the other. The seta and setule of the anterior margin in the female are absent in this male copepodid, and the sclerotization of the apex of the lamella is much weaker in the male copepodid. The free palp (fig. 19, h) is lamellate, weakly sclerotized, and distinctly articulated. Across the truncate apex there is a row of 5 subequal long setae bearing fine hairs. The 2 internal setae are clearly articulated, the other 3 are not articulated. On the external margin at the distal fourth there is an unornamented articulated seta as long as the terminal setae. Proximal to this the margin of the ramus is sclerotized. On the internal margin at the distal third there is a small setule, unornamented. This setule is not represented in the female. Judging from our specimen, in E. CANU's presentation for *E. fulgens* (1892, pl. 18) we would expect that the apical and external elements will persist in the adult male and will show increased length and plumosity.

The maxilla (fig. 19, i) is obscurely bimerous. The endite of the basal article present in the female is absent here, although there is some lobing of the distal medial margin. The terminal article is produced apically as 2 setiform processes ornamented with fine hairs. An unornamented seta articulates on the outer margin. From an adult male and CANU's figure, it is probable that the latter seta may be an elongate plumose seta in the adult, and that the medial processes will disappear. The appendage is not so heavily sclerotized as in the female and possibly differs functionally as well.

The first leg (figs. 19, j, k) is biramous, with bimerous protopodite, trimerous endopodite and bimerous exopodite. There is a bilobed subtriangular intercoxal lamella. The coxopodite lacks elements of armature and ornamentation. The basipodite bears a short seta on the lateral margin and a distal medial spine which reaches almost to the distal margin of the second article of the endopodite. Rows of spinules are found on the surface of the basipodite and at the base of the medial spine. The 2 basal articles of the endopodite (fig. 19, k) are unarmed and unornamented. The distal article bears 1 lateral seta, 3 terminal setae and a medial seta. The basal article of the exopodite has a distal lateral spine. The second article has a distal lateral spine, a terminal spine, a terminal seta and 2 medial setae.

The second leg (fig. 19, l) is biramous, with bimerous protopodite, trimerous rami. The coxopodites are joined by a bilobed subtriangular lamella. The basipodite bears a seta on the lateral margin. The basal article of the endopodite bears a distal medial seta. The second article bears 2 medial setae. The terminal article bears a lateral seta, 3 terminal setae and 2 medial setae. The 2 basal articles of the exopodite each bears a lateral spine and a medial seta. The terminal article bears 2 lateral spines, a terminal spine, a terminal seta, and 3 medial setae.

The third leg is just like the second except that the exopodite (fig. 19, m) has an additional medial seta on the terminal article.

The fourth leg (fig. 19, n) is similar to the 2 preceding, except that there are only 5 setae on the terminal article of the endopodite rather than 6, and the exopodite is as in the second leg.

The fifth leg (fig. 19, b) consists of a simple, unornamented lobe well articulated at the distal margin of the first urosomal segment, accompanied by a seta inserted dorsally at the base of the lobe. The sixth legs are indicated by bilobed unornamented protrusions at the distal ventrolateral margin of the second urosomal segment.

The caudal ramus (fig. 19, o) is broad and flat, about two-thirds as long as the anal somite. There are 4 setae on the truncate terminal margin, these at least twice as long as the ramus. There is a short dorsal seta just beyond the middle and a short seta set in an emargination at the middle of the lateral margin.

We find that Canu's description of the male and the account of development in *Enterocola* copepodids are strongly confirmed by the details of anatomy in this specimen. We have remarked upon the remarkable correspondences with notodelphyids above.

Enterocola fulgens van Beneden, 1860
(Figures 20, 21, 22)

Enterocola fulgens van Beneden, 1860, p. 155-160, 1 pl., 7 figs., (type locality, coast of Belgium, from *Aplidium* sp.). — Gerstaecker, 1870-1871, p. 774, 801. — Aurivillius, 1882b, p. 92-93 ; 1883, p. 88-89. — Canu, 1890, p. 758 ; 1891a, p. 468-469 ; 1892, p. 29, 37, 48, 49, 59, 66, 67, 85-88, 105, 143, 214, 215, 216-218, pl. 18, figs. 1-12, pl. 19, figs. 12, 13. — Norman & Scott, 1906, p. 203. — T. Scott, 1907, p. 368-369. — Chatton & Brément, 1909c, p. 227. — Hartmeyer, 1911, p. 1736. — Chatton & Brément, 1915, p. 146, fig. 1, c. — Schellenberg, 1922, p. 287-288, 294. — Chatton & Harant, 1924b, p. 363. — Harant, 1931, p. 370. — Leigh-Sharpe, 1935, p. 48. — Lang, 1948, p. 17. — Sewell, 1949, p. 183, 188. — Gotto, 1952, p. 674 ; 1954, p. 666. — Barnard, 1955, p. 241. — Gotto, 1957, p. 259 ; 1960, p. 216, 221 ; 1962a, p. 544. — Guille, 1964, p. 290. — Gotto, 1966a, p. 193. — Hamond, 1973, p. 350.

non Enterocola fulgens, Della Valle, 1883, p. 245-248, 251, figs. 3-10 (Naples, from *Aplidium cristallinum* della Valle, *A. gibbulosum* della Valle, didemniens).

non Enterocola fulgens, T. Scott, 1900, p. 386 (Scotland, from unidentified ascidian) ; 1901a, p. 352.

Interocola fulgens, Hesse, 1862, p. 349, 354 ; 1864, p. 335.

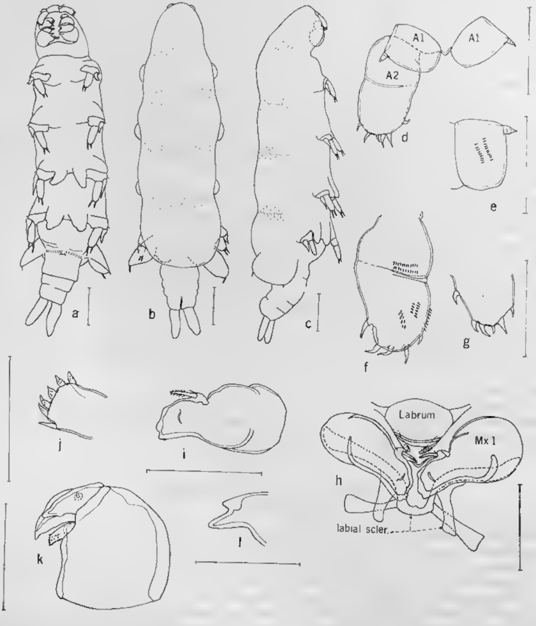

Fig. 20. — *Enterocola fulgens* van Beneden, female I : a, habitus, ventral view ; b, habitus, dorsal view ; c, habitus, lateral view ; d, antennules (A1) and antenna (A2) ; e, antennule ; f, antenna ; g, apex of antenna ; h, labrum, maxillule (Mx1) and post-oral labial sclerotization (labial scler.) ; i, basal portion of maxillule ; j, palp of maxillule ; k, maxilla ; l, apex of maxilla, posterior view. Scales for a, b, c, = 0.2 mm ; other scales = 0.1 mm.

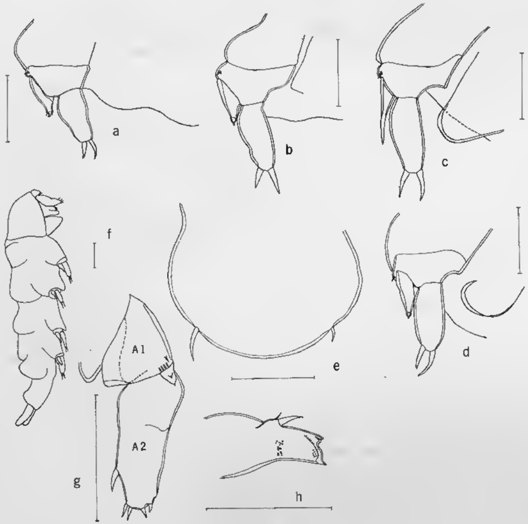

FIG. 21. — *Enterocola fulgens* van Beneden, female I : a, first leg ; b, second leg ; c, third leg ; d, fourth leg ; e, pediform projection ; f, *Enterocola fulgens*, female II, habitus, lateral view ; g, antennule (A1) and antenna (A2) ; h, basal portion of maxillule. Scales = 0.1 mm.

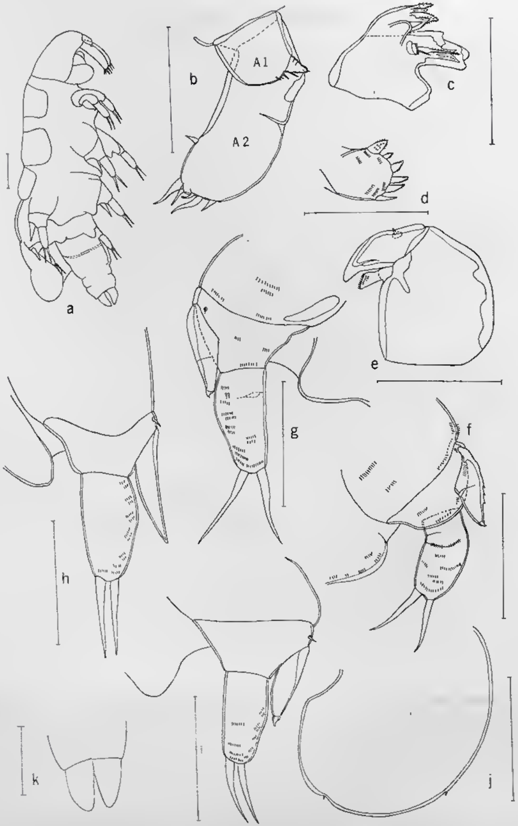

FIG. 22. — *Enterocola fulgens* van Beneden, female from *Polyclinum* sp. : a, habitus, lateral view ; b, antennule (A1) and antenna (A2) ; c, maxillule ; d, palp of maxillule ; e, maxilla ; f, first leg ; g, second leg ; h, third leg ; i, fourth leg ; j, pediform projection ; k, caudal rami. Scales = 0.1 mm.

Enterocola betencourti Canu, 1891a, p. 474-475 (type localities, near Boulogne, from *Polyclinum succineum*, and Brittany, from *Aplidium zostericola*); 1892, p. 49, 67, 143, 218, pls. 18, figs. 13, 14, pl. 20, figs. 1-4. — Chatton & Brément, 1909c, p. 228. — Hartmeyer, 1911, p. 1736. — Schellenberg, 1922, p. 294. — Chatton & Harant, 1922a, p. 149-151, 154, fig. 1. — Sewell, 1949, p. 183, 184, 188.

Distribution : Mediterranean, West coast of Europe, British Isles, Tafelbucht, S. Africa.

Hosts : *Amaroucium erythraeum* Michaelsen, *A. gibbulosum* Savigny, *A. mediterraneum*, *Aplidium ficoides* van Beneden, *A. ficus* Savigny, *A. pallidus* Verrill, *A. zostericola* Giard, *A. sp.*, *Botryllus schlosseri* (Pallas), *B. sp.*, *Glossoforum luteum* Giard, *Glossophorum* (*?sabulosum*), *Macroclinum pulmonaria* (Ellis & Solander), *Polyclinum aurantium* Milne Edwards, *P. luteum* (Giard), *P. succineum* Milne Edwards, *Sidnyum turbinatum* Savigny, *Synoicum pulmonaria* (Ellis & Solander).

Specimens examined :

From *Polyclinum aurantium* Milne Edwards var. *luteum* (Giard) :
" *Glossophorum luteum* ", Tatihou, April, 1911, CHATTON number 8, 1 female.
" *Glossophorum* ", La Hougue, June 5, 1911, CHATTON number 50, 2 females.
From *Polyclinum* sp. :
La Vieille, near Roscoff, France, 20 m, 1958, coll. E. BINDER, 1 female.

As indicated above, the bulk of our material is from the CHATTON collection, and indeed the specimen in CHATTON number 8 bore the manuscript identification to this species. It very probably is one of the three adult females collected by BRÉMENT at Tatihou and referred to as *E. betencourti* in connection with a description and illustrations by CHATTON & HARANT (1922a, p. 149-151, fig. 1). All these CHATTON specimens conform rather well to this characterization of the species.

The lengths of 2 specimens measured were 1.78 and 0.95 mm, the latter a specimen which had obviously been subjected to drying at one time. The authors give the lengths as ranging from 1.3 to 1.7 mm. The proportions of our specimens, cephalosome : metasome : urosome, were 1 : 4 : 1 or 1.5. The corresponding formula of the authors was 1 : 3.5 : 1.

The habitus (figs. 20, a, b, c ; 21, c) corresponds well with figures by the authors and those of CANU. Indentations at least indicate the segmental composition of the body and this was not shown by CHATTON & HARANT.

The antennules (figs. 20, d : A1, e ; 21, g : Al) do not correspond well with the illustration of CHATTON & HARANT, but we believe that this can be explained by the presentation of different views. They probably did not observe the appendages in place on the animal. It is difficult to determine whether there is an actual terminal segment on the appendage. On 1 specimen (fig. 21, g) there would appear to be a minute conical terminal segment set at the distal lateral corner of the large subquadrangular basal segment. Spinules ornament this protuberance and at least 1 spinule is found on the basal segment. A row of spinules illustrated by CHATTON & HARANT on the basal segment in reality consists of a corrugation of the cuticle. In the other specimen (figs. 20, d, e) the apical element is so small and spinulose that it resembles a modified seta but we believe it is probably homologous to the terminal article.

The antenna (figs. 20, f, g) or one specimen is very broad, obscurely bimerous, and bears 5 to 6 short, clawlike setae around the distal margin. The longest of these is as long as about one fourth of the greatest width of the appendage. Rows of spinules ornament the surfaces of the articles. In the second specimen (fig. 21, g) the antenna is narrower, but this may be an artefact of fixation. There are 4 apical clawed setae and a medial clawed seta. The longest of these is about one-third the greatest width of the appendage. These figures correspond well with that of the apex of the antenna shown by CHATTON & HARANT, although they apparently found 6 setae consistently.

The labrum (fig. 20, b) has not previously been illustrated.

The maxillule (figs. 20, h, i, j ; 21, h) is set above a complex labial sclerotization (fig. 21, h). It is bilobed ; the basal portion is lamelliform and heavily sclerotized. On a lobe of the anterior margin there is born a seta and accompanying setule. The palp portion carries 5 uncinate, spinulose setae on its distal margin and an unornamented normal seta on the outer margin at the distal third. Our illustrations of the palp correspond to that of the " exopodite " of Chatton & Harant.

The maxilla (figs. 20, k, l) is bimerous and heavily sclerotized. At the distal medial corner of the basal segment there is a digitiform spinulose endite with a truncate distal margin. The terminal segment terminates in 2 unarticulated hooks, one somewhat shorter than the other. On the surface in an interruption in the cuticle there is set a small conical seta.

The legs (figs. 21, a, b, c, d) are biramous, with bimerous protopodites and unimerous rami. The coxopodites are unarmed; each basipodite bears a small seta at the distal lateral corner. The exopodites of the first, second and fourth legs have differentiated pointed apical dome-like elements. The expodite of the third leg has the styliform outline characteristic of most species of the genus. The endopodites are longer than the exopodites and each bears 2 short setae, these much shorter than the ramus in each case. The medial of the 2 is slightly longer. Between the legs of the third and fourth pairs there are pairs of pronouncedly developed mammiform processes. Although there are sinuous lines in the cuticle between the legs of the first and second pairs there are no differentiated mammiform processes. Canu and Chatton & Harant never referred to the presence of these processes, although they are consistently present in our specimens. This oversight has led to confusion in subsequent treatments of the species and the genus.

The pediform projection (fig. 21, e) is a curved plate of circular outline. There are 2 widely spaced marginal setae. The more dorsal of these is more conspicuous than in any other species of *Entercola*. Although Chatton & Harant refer to this seta they did not see the more ventral seta.

The caudal rami are long, conical and apparently articulate with the body. In our specimens they were approximately 3 times as long as wide and about half the length of the urosome.

Our specimen from *Polyclinum* sp. (collected by Binder, 1958) has presented difficulties (fig. 22). It conforms generally in habitus (fig. 22, a), it is 1.72 mm long and has the proportions cephalosome ; metasome : urosome, 1 : 3 : 1.5. It should be noted that this specimen was somewhat contracted and distorted when extracted from the preserved tunicate host. The antennule (fig. 22, b : A1) corresponds to the second specimen discussed above. The terminal element here appears even more like a typical article. It bears more setules on the basal segment also. The obscurely bimerous antenna (fig. 22, b : A2) is flattened and very broad and bears 6 setae. The longest is half the greatest width of the appendage. Others are very short and claw-like. The overall configuration conforms reasonably well to the diagnostic condition, although there is a strong trend toward a more generalized aspect. The maxillule (figs. 22, c, d) and the maxilla (fig. 22, e) are as described above. The legs (figs. 22, f, g, h, i) do not conform very well to the previously described specimens, since the setae of each coxopodite are longer, although they are still shorter than the ramus. The exopodites are proportionately longer and the first 2 legs have slightly differentiated mammiform processes. The exopodite of the third leg (fig. 22, h) is narrow, elongate and triangular and does not have the characteristic styliform aspect. The pediform projection has 2 tiny setules, both of these much shorter than in the other specimens (fig. 22, j). The caudal rami (fig. 22, k) are only twice as long as wide and about a third as long as the urosome. They still articulate clearly. Thus, in the habitus, size, head appendages this specimen conforms well with typical *E. fulgens*. The legs appear to depart to a considerable degree.

Enterocola clavelinae Chatton & Harant, 1924
(Figures 23, 24, 25)

Enterocola clavelinae Chatton & Harant, 1924b, p. 354-356, 363, fig. 1 (type locality, Baie de Morlaix, France, from *Clavelina nana* Lahille). — Harant, 1931, p. 360. — Gotto, 1960, p. 226; 1962, p. 544. — Guille, 1964, p. 289.

Distribution : Channel coasts of France; Mediterranean.

Hosts : ***Polycitor* (*Clavelina*) *nana*** (Lahille).

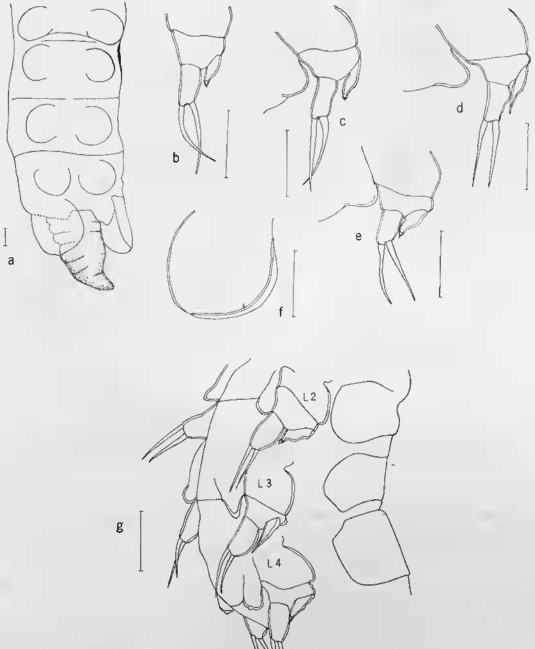

Fig. 23. — Remnant of holotype of *Enterocola clavelinae* Chatton & Harant (a-f) and *Enterocola sydnii* Chatton & Harant (g) : a, *E. clavelinae*, metasome and urosome, dorsal view ; b, first leg ; c, second leg ; d, third leg ; e, fourth leg ; f, pediform projection ; g, *E. sydnii*, remnant of metasome, lateral view showing second through fourth legs and mammiform processes and dorsal processes. Scales = 0.1 mm.

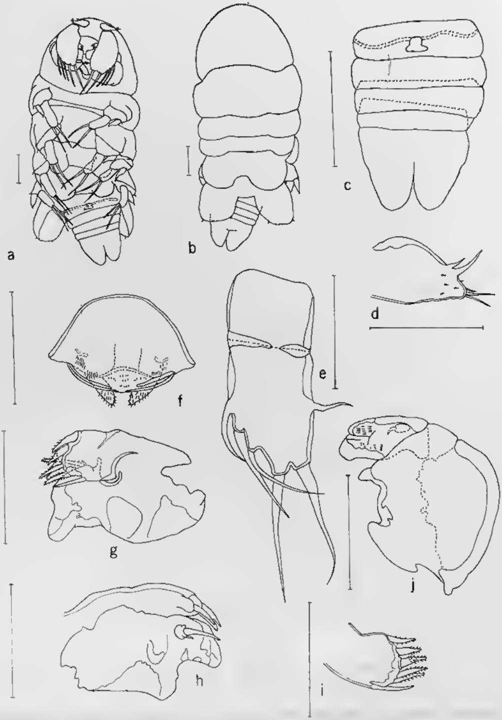

FIG. 24. — *Enterocola clavelinae* Chatton & Harant, female : a, habitus, ventral view ; b, habitus, dorsal view ; c, urosome ; d, antennule ; e, antenna ; f, labrum ; g, maxillule ; h, maxillule ; i, palp of maxillule ; j, maxilla. Scales = 0.1 mm.

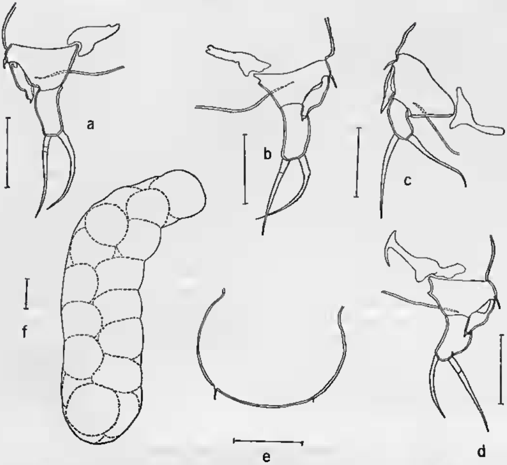

Fig. 25. — *Enterocola clavelinae* Chatton & Harant, female : a, first leg ; b, second leg ; c, third leg ; d, fourth leg ; e, pediform projection ; f, ovisac with contained embryos. Scales = 0.1 mm.

Specimens examined :

" *Clavelina nana* ", Chatton number 239, one partially dissected specimen, female, (possibly holotype).
From *Polycitor* (*Clavelina*) *nana* :

Cap l'Abeille, near Banyuls-sur-Mer, France, 25 m, June 3, 1958, 1 female.

Remarks :

From the Chatton specimen, which is very possibly the holotype of the species, although it is only a fragment, we can offer some further characters. We present a dorsal view of the entire remnant (fig. 23, a) to show the paired dorsal duplicatures mentioned by the authors. We were able to dissect off all 4 swimming legs. Although the authors mentioned that paired mammiform processes were present only between the third and fourth legs, we saw partially differentiated processes between the second legs (fig. 23, c). All the legs have bimerous protopodites and unimerous rami. The exopodites of the first (fig. 23, b), second (fig. 23, c) and fourth (fig. 23, e) legs have typical differentiated pointed dome-like apical elements. The exopodite of the third leg (fig. 23, d) has the characteristic styliform outline of most *Enterocola* species. All of the endopodites have 2 apical setae, these longer than the ramus itself. Rather characteristic is the placement of the lateral seta somewhat more proximally than the medial seta. The apical margin of the endopodite is thus somewhat inclined. The pediform projection (fig. 23, f) is a circular, curved plate, with a single small setule on the margin but facing internally. The authors said that this process, which they termed the oostegite, was asetigerous. The caudal rami, as indicated by the authors, are not delimited from the urosome. The urosome is shown in lateral view in figure 23, a, because of the distortion of the specimen.

Our specimen from Banyuls (figs. 24, 25) was strongly contracted so the habitus (figs. 24, a, b) is not really representative of the normal individual. The length is 0.93 mm, in this contracted state. The urosome (fig. 24, c) appears segmented, but it is possible that the contraction has produced the strongly indicated folds. There is a midventral insemination pore and seminal tubes diverge toward the oviducal apertures far laterally. The antennule (fig. 24, d) is a conical, unsegmented lobe, with 2 anterior setae and 3 smaller terminal setae. Spinules ornament the surface near the apex. The antenna (fig. 24, e) is strongly bimerous, with the terminal segment longer than the basal. The basal article is unarmed. There is a short seta at the middle of the medial margin of the terminal segment. Set apically there are 2 setae which are about 1.3 times as long as the greatest width of the appendage. Both of these setae are set on low lobes. Separated from the apex, on the lateral margin there are 3 graduated setae which are shorter than the apical setae. CHATTON & HARANT also noticed that there are emarginations between all the setae and a very marked emargination on the lateral margin beween the group of 3 lateral setae and the 2 apical setae. The labrum (fig. 24, f) has not previously been figured. The maxillule (figs. 24, g, h, i) is bilobed ; the basal portion is lamellate and bears a seta and a setule on a lobe on the anterior margin. The palp bears 5 distal setae and a seta on the external margin. The maxilla (fig. 24, j) is bimerous and is heavily sclerotized. At the distal medial corner of the massive basal segment there is an unornamented digitiform endite. The distal segment is bifid apically, has some spinulose ornamentation and there is a seta set in an anterior cuticular interruption. The legs (figs. 25, a, b,c, d) agree very closely with those we illustrate from the CHATTON specimen with the exception that we saw a seta on the lateral margin of each basipodite and the mammiform processes were not apparent in this highly contracted specimen. The pediform projection (fig. 25, e) bears a salient minute dorsal marginal setule and a more ventral marginal exceedingly minute setule. The ovisac (fig. 25, f) is distinctly curved anterioly.

ENTEROCOLA PRECARIA new species
(Figure 26)

TYPES :

Holotypic female (type locality Gaiola, Bay of Naples, Italy, from *Polycitor* (*Eudistoma*) *mucosus* (Drasche) and paratype listed below.

Specimens examined :

From *Polycitor* (*Eudistoma*) *mucosus* (Drasche) :
Gaiola, Bay of Naples, Italy, 35-40 m, January 2, 1958, holotypic female and female paratype.

Description :

Female (fig. 26) :

The body (figs. 26, a, b) measures 0.85 mm ; the specimen is rather contracted. The proportions, cephalosome : metasome : urosome, are 1 : 3 : 1. Paired dorsal duplicatures are only indicated on the surface and are not salient. The urosome (fig. 26, c) appears segmented, but because of the contraction of the specimen, the appearance may be due merely to folding of the integument. The antennule (fig. 26, d) is unimerous with a strong distal taper from about the basal third. There are about 8 small setules concentrated at the distal third on the anterior and apical margins. The antenna (fig. 26, 3) is unimerous, subrectangular. There is a short medial seta at the distal fourth, 4 equispaced setae on the rather truncate distal margin and a shorter seta at the distal of the lateral margin. The longest seta is 4/5 the greatest width of the appendage. The labrum (fig. 26, f) is an unornamented semicircular plate with a spinulose palp extending posteriorly from each posterior lateral corner. The

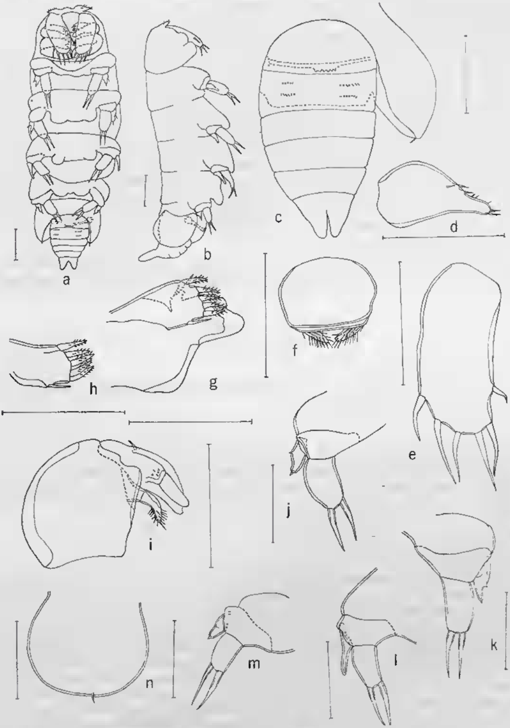

Fig. 26. — *Enterocola precaria*, new species, paratypic female : a, habitus, ventral view ; b, habitus, lateral view ; c, urosome and pediform projection ; d, antennule ; e, antenna ; f, labrum ; g, maxillule ; h, palp of maxillule ; i, maxilla j, first leg ; k, second leg ; 1, third leg ; m, fourth leg ; n, pediform projection. Scales = 0.1 mm.

maxillule (figs. 26, g, h) is bilobed. The basal portion is lamellate and bifid distally. On the anterior margin there is a lobe set with a seta and accompanying setule. The palp bears 5 spinulose setae on the distal truncate margin and 1 unornamented seta at the middle of the external margin. The maxilla (fig. 26, i) is bimerous, with the basal segment massive, heavily sclerotized and bearing at the distal medial corner a curved articulated spinulose digitiform endite. The distal segment has a terminal massive hook and a second long narrow digitiform process articulated on a lobe on its surface. A small seta is set in a cuticular interruption on the anterior margin. All the legs (figs. 26, j, k, l) have bimerous protopodites and unimerous rami. The protopodites are unarmed. The expodites of the first and second legs end in a pointed cuticular specialization and each has a pointed cuticular deflection at the middle of the lateral margin. The expodite of the third leg has a distinctive outline, lobate distally rather than styliform (fig. 26, 1). The exopodite of the fourth leg (fig. 26, m) is like that of the first and second except that it lacks the lateral cuticular point. The endopodites on the whole are very short, just slightly exceeding the lengths of the exopodites. The 2 setae of each are set apically. In the first 3 legs these setae are approximately as long as the endopodite and they slightly exceed it in the fourth leg. The pediform projection (fig. 26, n) is a curved plate with circular margin. It bears a single setule in the middle. The caudal rami (fig. 26, c) are simple conical lobate extensions of the urosome without apparent articulations.

This is very possibly a host form of *Enterocola fulgens*, but it does possess distinctive morphological characters, particularly of the maxilla and the third leg. The name is derived from the Latin term for uncertain.

ENTEROCOLA IANTHINA new species
(Figure 27)

Types :

Holotypic female USNM (type locality vicinity of Jolo, Philippine Islands, from *Polycitor (Eudistoma) ianthinus* Sluiter), and paratype.

Specimens examined :

From *Polycitor (Eudistoma) ianthinus* Sluiter :
Vincinity of Jolo, Philippine Islands, USNM 6029, Accession No. 53256, Station 5139, Albatross Philippine Expedition, 20 fathoms, February 14, 1908, holotypic female, 1 paratypic female.

Description :

Female (fig. 27) :

Body (figs. 27, a, b) measures 1.08 mm. Proportions, cephalosome : metasome : urosome : are 1 : 3 : 1. Dorsal duplicatures are only indicated and are not salient. The antennule (fig. 27, c) is obscurely bimerous, with the portion corresponding to a distal segment about 1/3 as wide as the widest part of the basal segment. There are about 7 setules concentrated on the distal half of the anterior margin and on the apex. The antenna (fig. 27, d) is bimerous, with the apical segment longer. The basal segment is unarmed. On the apex of the second segment there are 4 subequal equispaced setae. At the distal fifth of the medial margin there is a shorter seta. At the distal fifth of the lateral margin there is inserted the longest seta of the appendage. This seta is longer than the greatest width of the distal segment of the appendage. The labrum (fig. 27, e) is a semicircular plate with a spinose lobe extending posteriorly from each posterior lateral corner. A row of spinules ornaments the distal margin. The maxillule (figs. 27, f, g) is bilobed. The base is lamellate and bifid distally. Set on the surface near the anterior margin is a seta and an accompanying setule. The palp bears 5 spinulose setae on the curved distal margin and a spinulose seta at the distal third of the external margin. A patch of spinules ornaments the surface. The maxilla (fig. 27, h) is bimerous. At the distal medial corner of the massive basal segment there is an articulated endite which is somewhat bifid apically

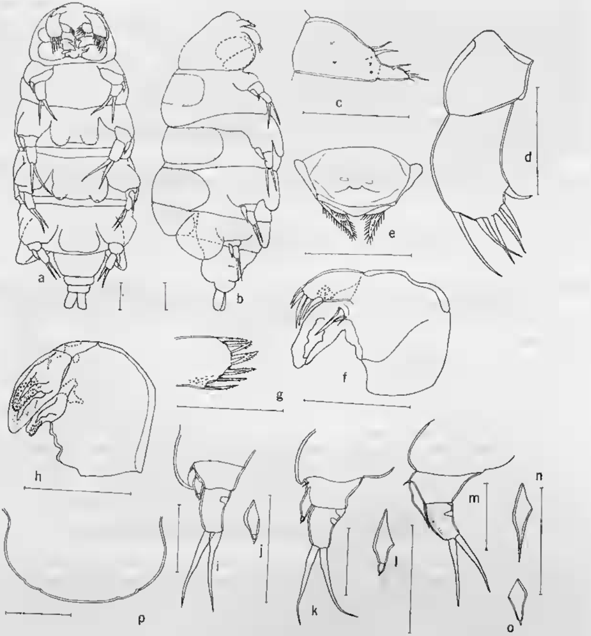

Fig. 27. — *Enterocola ianthina*, new species, holotypic female : a, habitus, ventral view ; b, habitus, lateral view ; c, antennule ; d, antenna ; e, labrum ; f, maxillule ; g, palp of maxillule ; h, maxilla ; i, first leg ; j, exopodite of first leg ; k, second leg ; l, exopodite of second leg ; m, third leg ; n, exopodite of third leg ; o. exopodite of fourth leg ; p. pediform projection. Scales = 0.1 mm.

and bears a patch of spinules near the apex. The distal segment has a massive terminal hook and a second articulated shorter hook on the surface. The latter hook is ornamented with spinules. A small seta is inserted on the anterior margin. All the legs (figs. 27, i, j, k, l, m, n, o) have bimerous protopodites and unimerous rami. There are pronounced mammiform processes between the legs of the second and third pairs, none in the first pair, and a single slightly bilobed plate in the fourth pair. Although the endopodites have a marginal interruption in the cuticle there is no well-developed articulation on either major surface. In all legs the basipodites bear a seta at the distal lateral corner.

Source : MNHN, Paris

The exopodites of the first legs (figs. 27, i, f) and the second legs (figs. 27, k, l) are shorter than the endopodites and each has a differentiated pointed dome-like element. The exopodite of the third leg (figs. 27, m, n) has the characteristic styliform outline of most species of *Enterocola* and is longer than the endopodite. The exopodite of the fourth leg (fig. 27, o) ends in a simple pointed element and does not have the articulated dome-like structure. The endopodites taper somewhat distally and the 2 setae on each endopodite are subequal and longer than the ramus. The pediform projection (fig. 27, p) is a semicircular curved plate which has no element of armature although there are 4 very shallow emarginations on each, these delimiting 2 very shallow lobes, 1 dorsal and 1 ventral. The caudal ramus (figs. 27, a, h) is subrectangular in form and has no elements of armature. It articulates distinctly with the urosome.

The specific name derives directly from that of the host. The species is not a strongly differentiated one ; it is very similar to *E. fulgens*. The key above indicates differentiating characters.

ENTEROCOLA SYDNII Chatton & Harant, 1924
(Figures 28, 29)

Enterocola sydnii Chatton & Harant, 1924b, p. 354, 356-358, 363, (type locality Locquirec [Côtes-du-Nord] France, from *Sydnium concrescens* Giard). — Harant, 1931, p. 371. — Gotto, 1960, p. 226 ; 1961, p. 153 ; 1962a, p. 544. — Guille, 1964, p. 289. — Gotto, 1966a, p. 193.

Distribution : Channel coasts of France and England.

Hosts : *Sidnyum turbinatum* (Savigny) and *S. elegans*.

Specimens examined :

From *Sidnyum turbinatum* (Savigny) :
" *Circinalium concrescens* " : from Locquirec, France, CHATTON number 246, 1 partially dissected specimen, female. Possibly the holotype.
From *Sidnyum elegans* (Giard) :
" *Fragarium elegans* ", Roscoff, France, 1922, CHATTON number 26, 1 female.
From *Morchellium argus* (Milne Edwards) :
From Duke Rock, near Plymouth, England, 6 m, September 9, 1958, 1 female.

From the CHATTON specimen, number 246 which is very possibly the holotype of the species, although it is only a fragment of the thorax, we can illustrate some further characters beyond those originally described. The authors pointed out there were dorsal duplicatures on segments 3 and 4 (corresponding to the third and fourth legs). Our fragment shows similar processes also on the segment of the second legs. The original description stated there were mammiform projections between the legs of all pairs, those of the fourth legs mucronate. We illustrate the projections of the second through fourth legs (fig. 28, a ; 29, a). We cannot verify the authors' statement that the endopodites are twice as long as the exopodites ; the specimen shows the endopodites slightly longer than the exopodites, but we feel sure that the true articulations of these rami were not properly taken into consideration in the original description. The illustration presented by CHATTON & HARANT of the second leg shows the outlines almost exactly as we see them, but the articulation of the exopodite was not shown at all and that of the endopodite was probably taken from the wrong surface. We cannot account for the apparent exaggeration of the lengths of the setae in the authors' illustration. We illustrate the third and fourth legs of the species for the first time.

Female from *Sidnyum elegans* (fig. 28) : Overall measurement 1.5 mm. This is somewhat longer than the authors gave for the type material, namely 1.2 mm. The proportions, cephalosome : metasome : urosome, are 1 : 4 : 1.5 ; the corresponding formula from the original description of CHATTON

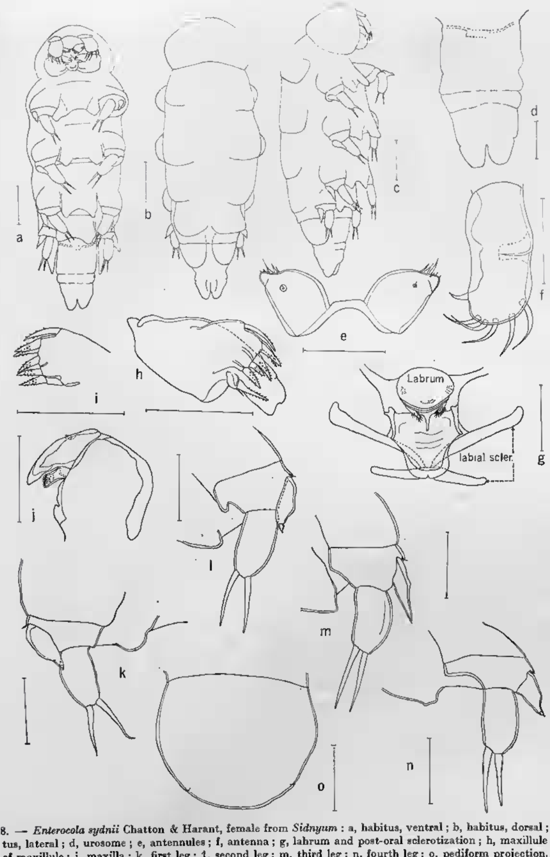

FIG. 28. — *Enterocola sydnii* Chatton & Harant, female from *Sidnyum* : a, habitus, ventral ; b, habitus, dorsal ; c, habitus, lateral ; d, urosome ; e, antennules ; f, antenna ; g, labrum and post-oral sclerotization ; h, maxillule ; i, palp of maxillule ; j, maxilla ; k, first leg ; l, second leg ; m, third leg ; n, fourth leg ; o, pediform projection. Scales for a, b, c = 0.2 mm, other scales = 0.1 mm.

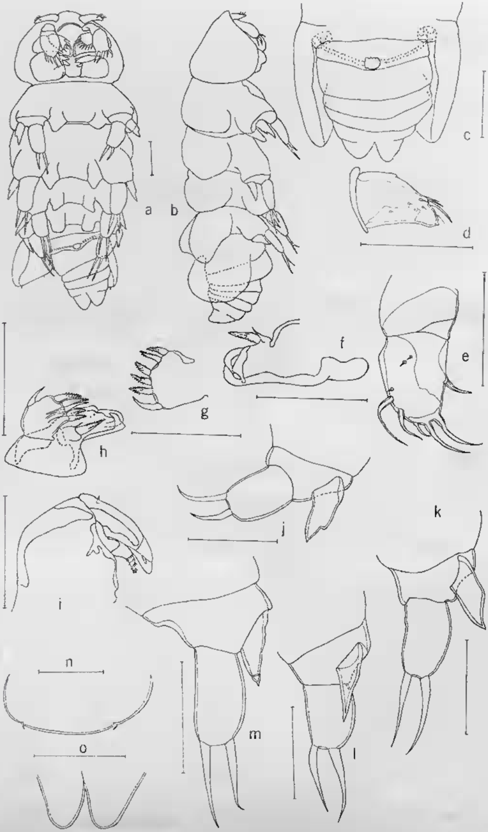

FIG. 29. — *Enterocola sydnii* Chatton & Harant, female from *Morchellium* : a, habitus, ventral ; b, habitus, lateral ; c, urosome ; d, antennule ; e, antenna ; f, maxillule, basal portion ; g, maxillule, palp ; h, maxillule, ventral view ; i, maxilla ; j, first leg ; k, second leg ; l, third leg ; m, fourth leg ; n, margin of pediform projection of sixth thoracic segment ; o, caudal rami. Scales = 0.1 mm.

& **Harant** was 1 : 3.5 : 1.5. The habitus (figs. 28, a, b, c) agrees fairly well with the original description, although our specimen is somewhat bulkier and does not show the flexure shown. We illustrate the urosome (fig. 28, d) and show the midventral insemination pore and diverging seminal tubes.

The antennule (fig. 28, e) is unimerous with a slightly differentiated apex, which suggests a short segment. There are 3 short setae and several setules on the anterior margin. This appendage does not conform closely to the appendage illustrated by **Chatton** & **Harant** but we feel that their illustration is from an anterior view and thus could actually be interpreted to conform to the structure we viewed in place on the specimen. The antenna (fig. 28, f) is obscurely bimerous and has a short seta at the distal third of the medial margin of the portion of the appendage corresponding to the terminal article. On the curved apex there are arranged 5 short setae. The longest seta is slightly shorter than the greatest width of the appendage, so the setae are somewhat shorter than those illustrated by the authors. The labrum (fig. 28, g) has not been previously illustrated. There is a complex labial sclerotization in the integument of the ventral body surface. The maxillule (figs. 28, h, i) is bilobed and conforms generally to the original description ; it has not been previously illustrated. The maxilla (fig. 28, j) is bimerous. At the distal medial corner of the massive heavily sclerotized basal segment there is an articulated, subrectangular endite which bears rows of spinules both on the distal margin and on the surface. The distal segment is prolonged medially as two unarmed unarticulated hooks, one somewhat shorter. On the anterior margin there is a short stiff seta inserted in an interruption in the cuticle.

The first legs (fig. 28, k) have not previously been illustrated. The protopodites are bimerous and the rami are unimerous. There is a short lateral seta at the distal lateral corner of the basipodite. The endopodite is only slightly longer than the endopodite, and the 2 apical setae are slightly shorter than the ramus. The exopodite bears a terminal differentiated small hook. The remaining legs (figs. 28, l, m, n) correspond well with our observation on the partial specimen from *Sidnyum turbinatum*. Paired mammiform processes occur between the legs of each pair. These between the third and fourth legs are more prominent than the others ; however, the processes of the fourth legs have a truncate apex rather than the mucronate condition. The pediform projection (fig. 28, o) is as described except that there are 2 tiny setules on the margin. The caudal rami (fig. 28, d) are not demarcated and appear to be simple prolongations of the urosome.

Female from *Morchellium argus* : The body of this specimen was rather contracted ; it measured overall 0.92 mm. The habitus (figs. 29, a, b) corresponds fairly well to the specimen from *Sidnyum elegans*. Possibly it is the contracted state which is responsible for the more salient dorsal processes. Because of the contracted state, the urosome (fig. 29, c) appears to be segmented. There are no real articulations. The genital apparatus on the first segment of the urosome consists of a midventral protrusion supporting an insemination pore ; diverging internal seminal canals proceed toward the oviducal apertures which have accompanying complicated sclerotizations, each with a setule, at the base of the pediform projections.

The antennule (fig. 29, d) compares well with our other specimens, except that it appears to be somewhat more heavily sclerotized. The antenna (fig. 29, e) is more clearly bimerous than in our other material, and the medial seta is found at the middle of the margin rather than at the distal third. The apical armature is similar, except that the central seta is shorter. The appendage has heavy sclerotizations and some spinules on the surface. The maxillule (figs 29, f, g, h) is very similar to the other specimens. The maxilla (fig. 29, i) has the same general form but the endite is a curved digitform process and bears circular rows of spinules. The first two pairs of legs (figs. 29, j, k) have a somewhat different appearance from those of the other specimens. Although the protopodites are bimerous, there is no lateral seta on the basipodite. The endopodites are similar in outline, but the endopodite of the first leg has the 2 terminal setae considerably shorter than the ramus. The exopodite of the first leg (fig. 29, j) terminates in a point and there is an emargination at the distal lateral fourth. There is no differentiated apical element. The exopodite of the second leg (fig. 29, k) although constricted at the distal third, lacks the emarginations of the first leg, and also lacks the usual apical element. The third leg (fig. 29, l) is similar to the other specimens in the protopodite and the exopodite, but the endopodite is much shorter. The fourth leg (fig. 29, m) is very similar to that of the specimen from *Sidnyum turbinatum.* Mammiform processes are developed between the legs of each pair but we did not determine whether those of the fourth pair were mucronate. The pediform projection (fig. 29, n) and the caudal rami (fig. 29, o) are very similar to those of our other specimen.

The specimen last described, from *Morchellium argus* has some slight differences from the other material, as pointed out, and so may actually represent a host form, or alternatively, may be a distinct species. Since we had only a single specimen to study we were unable to explore these possibilities further. We found the taxonomic references to the tunicate hosts involved completely chaotic and have used a terminology which we hope will keep our records of collection clear. It seems from what we can best make out that our specimens all came from closely related hosts.

ENTEROCOLA PETITI Guille, 1964
(Figure 30)

Enterocola petiti Guille, 1964, p. 283-288, 289, fig. 1-3 (type locality, Banyuls-sur-Mer, Golfe du Lion, France, from *Amaroucium densum* Giard).

Specimens examined :

From *Polycitor* (*Paradistoma*) *cristallinus* Renier : identification uncertain.
Cap l'Abeille, near Banyuls-sur-Mer, France, 25 m, May 7, 1958, 1 female 1 developmental stage.

We have found one adult female (figs. 30, a, b, c) which appears to us to correspond reasonably well to the description of this species. The overall length is 1.09 mm, compared with the range of 1.0 to 1.2 mm of the original material of GUILLE. The proportions, cephalosome : metasome : urosome, are 1 : 4 : 1, as compared with 1 : 2.7 : 1 of the original description. The author does not depict dorsal plates ; on our specimen there are slight indications of duplicatures (figs. 30, b, c). The antennule (fig. 30, d) is unimerous, and does not show the number of setae and setules found by the author but it is very possible our specimen is somewhat deformed in this regard. The antenna (fig. 30, e) labrum (fig. 30, f), and maxillule (figs. 30, g, h, i) correspond well to the original description. The maxilla (fig. 30, j) is a reasonably typical appendage for the genus but does not quite correspond with the original description and figure. It consists of a massive basal segment with a digitiform spinulose endite at the distal medial corner. The clearly articulated distal segment terminates in 2 hook-like extensions, one unornamented and considerably longer than the other, which is spinulose. There is a short seta set in an interruption of the cuticle near the anterior margin. The legs (figs. 30, k, l, m, n) have bimerous protopodites, rather than unimerous as indicated in the original descriptions and the basipodite bears a short seta at the distal lateral corner. The exopodites of the first legs (fig. 30, k), the second legs (fig. 30, 1), and the fourth legs (fig. 30, n) are very similar in outline to those illustrated in the original description and each bears a pointed dome-like articulated element as was shown in the figure 3B′. The only exception seems to be the presence of an interruption in the cuticle of the exopodite of the second leg, possibly indicating an incipient bimerous condition. The exopodite of the third leg (fig. 30, m) although similar in outline to that illustrated by the author, shows an apparent articulation of the distal styliform process. The endopodites of all the legs are also similar in outline to the illustrations, with a characteristic bulging curvature of the lateral margins. The apex of each is thus somewhat narrower than the base and the 2 setae of each, which are longer than the ramus, are set with their bases close together. The author illustrated many patches of spinules on the legs, which we saw but did not depict in our figures. The pedifgom projection (fig. 30, o) which the author said was acbaetous we found to carry 2 minute marginal setae. The urosome in our specimen (fig. 30, p) does not show the distinct segments depicted by the author. The caudal rami are very short lobes, each set on the end of the urosome with a pronounced articulation. At the center of the urosome near the anterior end there is located the insemination pore with diverging internal seminal tubes.

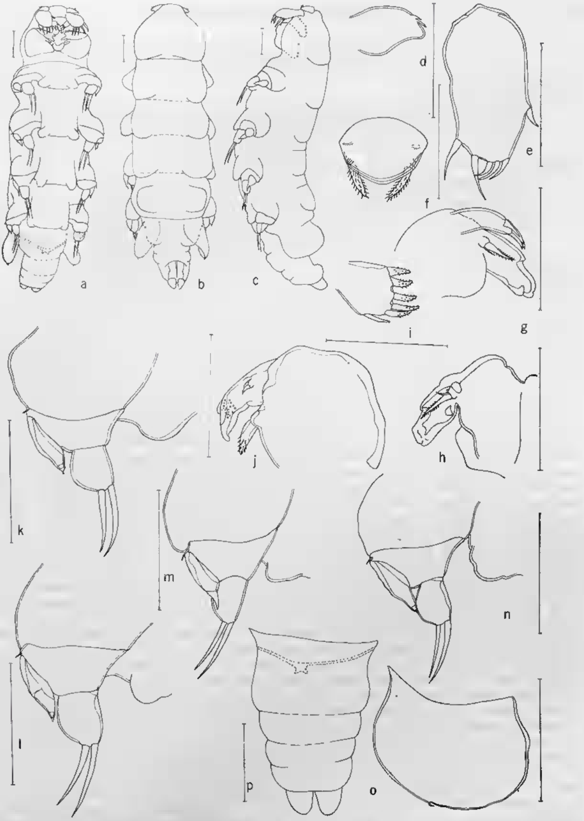

Fig. 30. — *Enterocola petiti* Guille, female ; a, habitus, ventral ; b, habitus, dorsal ; c, habitus, lateral ; d, antennule ; e, antenna ; f, labrum ; g, maxillule ; h, basal portion of maxillule ; i, palp of maxillule ; j, maxilla ; k, first leg ; l, second leg ; m, third leg ; n, fourth leg ; o, pediform projection ; p, urosome. Scales = 0.1 mm.

ENTEROCOLA BREMENTI new species
(Figures 31, 32)

Types :

Holotypic female (type locality, Callot, Channel coast of France, from *Aplidium pallidum* (Verrill) ; and paratypes from the same collection and from Tatihou, listed below.

Specimens examined :

From *Aplidium pallidum* (Verrill) :

" *Aplidium zostericola* ", Callot, France, CHATTON number 254, holotypic female and 2 female paratypes.

" *Aplidium zostericola* ", Tatihou, France, May, 1911, CHATTON number 46, female paratype.

Description :

Female (fig. 31, 32) :

The body (fig. 31, a, b ; 32, a, b) measures 1.4 mm overall length and .98 mm in a contracted specimen. The proportions of the uncontracted specimen, cephalosome : metasome : urosome, are 1 : 6 : 1.3. In the uncontracted specimen there is no evidence of dorsal duplicatures. In the contracted individual folds of the dorsal surface simulated dorsal duplicatures. In the contracted specimen the urosome (fig. 32, a, b) is folded and drawn into the segment of the pediform projections. In the uncontracted specimen, the urosome (fig. 31, c) does not show complete segments. Near the anterior end of the urosome there is a midventral insemination pore and internal seminal tubes diverge from this toward the oviducal apertures. The antennule (fig. 31, d ; 32, c) shows almost no taper. It is a single lobe with a few setules on the anterior and apical margins. A few spinules may ornament the surface. The antenna (fig. 31, e ; 32, d) is obscurely bimerous, with the portion corresponding to an apical segment longer than the remainder. There is a short seta at the middle of the medial margin of the portion corresponding to the apical segment and 3 setae of intermediate length on the apex. Two additional somewhat longer setae insert on the lateral margin at the distal third and fourth. The longest seta of the appendage is just slightly shorter than the greatest width of the appendage. The maxillule (fig. 31, e, f, g ; 32, e, f) is bilobed. The lamellate basal portion has a projecting lobe (fig. 31, f ; 32, e) ornamented with spinules at about the middle of the anterior margin. Near the insertion of the palp there is a prominence set with a seta and a setule. The apex of the medially directed lobe of the basal portion, seen on an *en face* preparation (fig. 32, e) has a slightly bifid character, because of the development of fairly strongly developed anterior and posterior tooth-like processes. There is a row of spinules at the base of each tooth. The palp bears 5 spinulose setae on its distal margin, separated into an internal group of 2 and a more external group of 3. At the distal third of the external margin there is a long, narrower, unornamented seta, approximately twice as long as the longest apical seta. The maxilla (figs. 31, h ; 32, g) is bimerous, with the basal segment massive, heavily sclerotized and bearing at the distal medial corner a curved articulated spinulose digitiform endite. The distal segment is bifid apically, ending in 2 hook-like processes. These are unornamented, with 1 of the hooks somewhat shorter than the other. A small seta is set in an interruption of the cuticle near the anterior margin. The legs (figs. 31, i, j, k, l ; 32, h, i, j, k) have bimerous protopodites and unimerous rami. Each basipodite has a small seta at the distal lateral corner. The exopodite of the first leg (figs. 31, i ; 32, h) the second leg (figs. 31, j ; 32, i) and the fourth leg (figs. 31, l ; 32, k) ends in a differentiated pointed dome-like element. The exopodite of the third leg (figs. 31, k ; 32, j) has the characteristic styliform outline of most species of the genus. In 1 specimen (fig. 32, j) the styliform apex is set off by a line in the cuticle. The endopodites of the legs are subrectangular and the 2 apical setae of each are rather widely separated from each other. The setae are consistently shorter than the rami. The first and second legs of the endopodites are considerably longer than the exopodites. However, in the third and fourth legs the rami are approximately equal. Paired mammiform processes

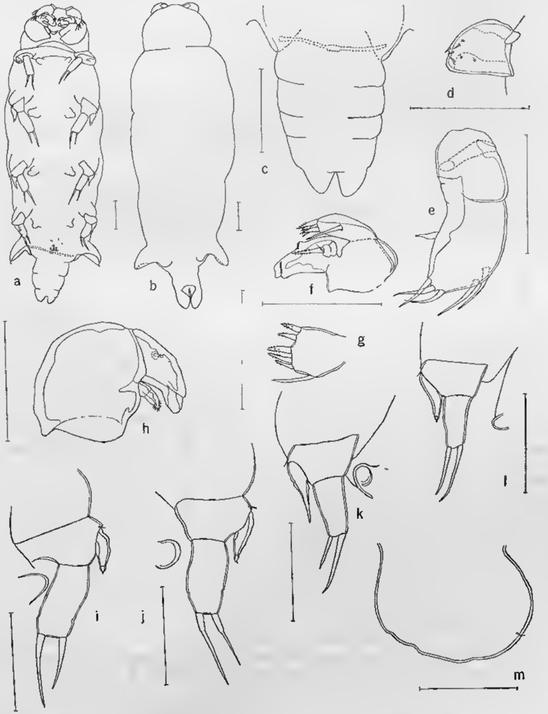

Fig. 31. — ***Enterocola brementi***, new species, holotypic female : a, habitus, ventral ; b, habitus, dorsal ; c, urosome, ventral ; d, antennule, e, antenna ; f, maxillule ; g, palp of maxillule ; h, maxilla ; i, first leg ; j, second leg ; k, third leg ; 1, fourth leg ; m, pediform projection. Scales = 0.1 mm.

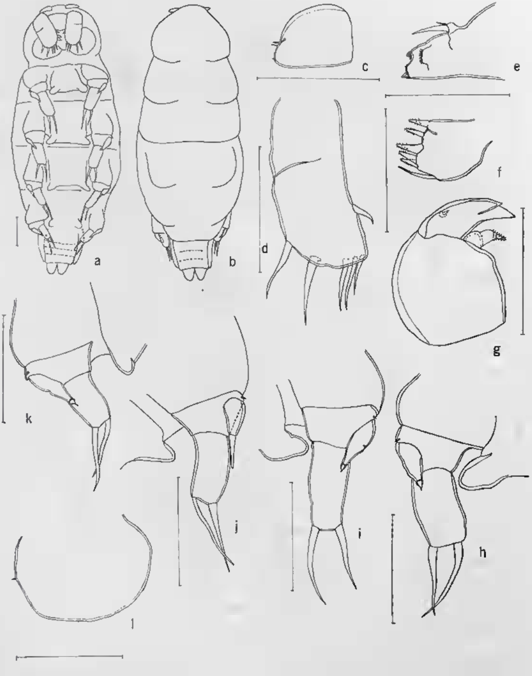

FIG. 32. — *Enterocola brementi*, new species, paratypic female : a, habitus, ventral ; b, habitus, dorsal ; c, antennule ; d, antenna ; e, basal portion of maxillule ; f, palp of maxillule ; g, maxilla ; h, first leg ; i, second leg ; j, third leg ; k, fourth leg ; l, pediform projection. Scales = 0.1 mm.

are found on the legs of each pair in both specimens. The pediform projection (figs, 31, m ; 32, l) is a curved plate with a circular margin. It bears a minute dorsal setule on the margin. The caudal rami (fig. 31, c) are simple conical lobate extensions of the urosome without evident articulations.

It should be noted that all specimens studied were from the CHATTON collections and we have not collected this species ourselves. The species bears a great resemblance to *E. petiti*, also typically from a species of *Amaroucium* but it differs considerably in the form of the rami of the legs and in the length of the external seta of the maxillular palp and the form of the antenna.

ENTEROCOLA FERTILIS new species
(Figures 33, 34, 35, 36)

Types :

Holotypic female (type locality, near Port Vendres, from *Amaroucium* (*Parascidia*) *areolata* Chiaje.

Near Banyuls-sur-Mer, France, holotypic female, allotypic male, paratypic females and female paratypes listed below.

Specimens examined :

From *Amaroucium* (*Parascidia*) *areolata* Chiaje :

Near Port Vendres, near Banyuls-sur-Mer, France, 50-25 m, May 13, 1958, 5 females, 1 male, including holotype, allotype, and paratypes.

" *Parasc. flavum* ", Argelès, near Banyuls, July 10, 1910, CHATTON number 100, 7 females paratypes.

Description :

Female (figs. 33, 34) :

The body (figs. 33, a, b, c ; 34, a, m) measures 1.76, 1.37 and 0.8 in a very contracted specimen. Paired dorsal duplicatures are only indicated on the surface and are not salient. The proportions, cephalosome ; metasome : urosome, are 1 : 5 : 2 or 1.7, in the uncontracted specimens. The urosome (figs. 33, d ; 34, b) has folds simulating segments. Near the anterior end there is a midventral insemination pore and diverging internal seminal tubes. The antennule (figs. 33, e ; 34, c) is a lobe terminating subacutely, set with small setules. The antennule of the contracted specimen (fig. 34, n) is slightly more developed. The antenna (figs. 33, f ; 34, d) is obscurely bimerous There is a short medial seta at the middle of the medial margin of the portion corresponding to an apical segment. Apically there are 3 closely-set setae of intermediate length ; 2 somewhat longer setae articulate on the curving lateral margin at the distal fourth and fifth ; the longest seta is only slightly shorter than the greatest width of the appendage. The labrum (fig. 33, g) is an unornamented plate with 2 spinose lobes extending posteriorly from dorsal insertions just anterior to the posterior margin. The maxillule (figs. 33, h, i) (34, e, f) is bilobed with the base extending directly medially. The palp is lamellate, somewhat bifid distally. At the distal third of the anterior margin of the portion of the appendage directed medially there is an unornamented lobe. Near the articulation of the palp there is a prominence bearing a setae and a setule. The palp bears 5 spinulose setae on its distal truncate margin, grouped as 2 external and 3 internal setae. At the distal third of the external margin there is an unornamented seta which is about one and a half times as long as the longest apical seta. The maxilla (figs. 33, j ; 34, g) has a massive basal segment which bears at its distal medial corner an articulated digitiform, spinulose endite. The apical segment, which is narrower than the basal segment but also heavily sclerotized is bifid distally, with one process somewhat shorter than the other. Set in an interruption of the cuticle near the anterior margin there is a very short seta.

All of the legs (figs. 33, k, l, m, n ; 34, h, i, j, k, o, p) have bimerous protopodites and the basipodite of each bears a small seta at the distal lateral corner. The exopodite of the first legs (figs. 33, k ; 34, h, o), the second legs (figs. 33, m ; 34, j) has the characteristic styliform outline of most species of the genus, but there is a subapical line in the cuticle setting off the apex of the process. The endopodites are consistently shorter than the exopodites. The ramus has a more curved lateral margin than the medial margin. The 2 apical setae of each endopodite are set closely together and are longer than the ramus. Between the legs of each pair there is a pair of well-developed mammiform processes.

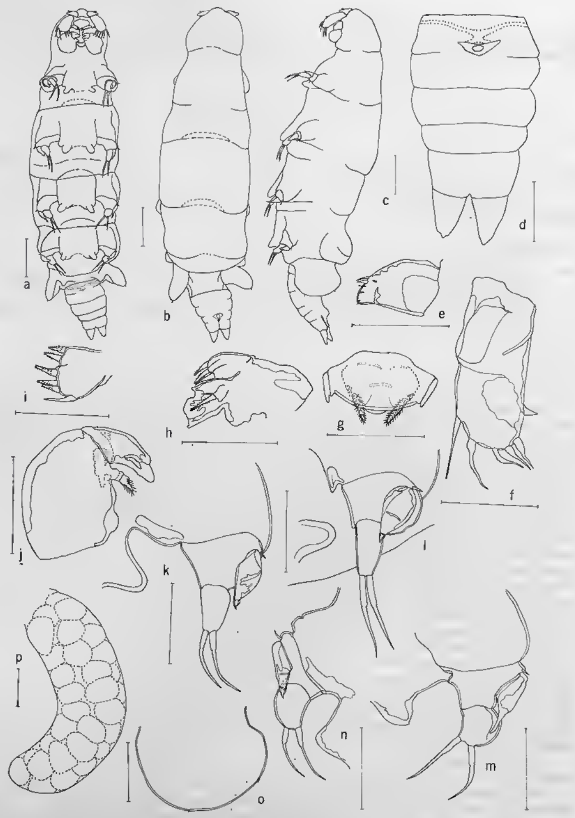

Fig. 33. — *Enterocola fertilis*, new species, holotypic female : a, habitus, ventral ; b, habitus, dorsal ; c, habitus, lateral ; d, urosome, ventral ; e, antennule ; f, antenna ; g, labrum ; h, maxillule ; i, palp of maxillule ; j, maxilla ; k, first leg ; l, second leg ; m, third leg ; n, fourth leg ; o, pediform projection ; p, ovisac with embryos. Scales for a, b, c, p = 0.2 mm ; other scales = 0.1 mm.

Source : MNHN, Paris

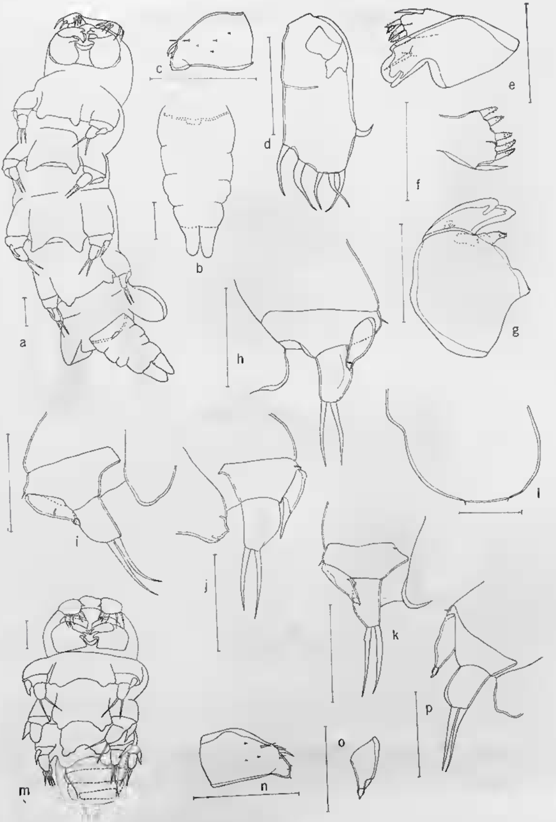

FIG. 34. — *Enterocola fertilis*, new species, paratypic female 2 (a-l), paratypic female 3 (m-p) : a, habitus, ventral ; b, urosome ; c, antennule ; d, antenna ; e, maxillule ; f, palp of maxillule ; g, maxilla ; h, first leg ; i, second leg ; j, third leg ; k, fourth leg ; l, pediform projection ; m, habitus, ventral ; n, antennule ; o, first leg ; exopodite ; p, second leg. Scales = 0.1 mm.

Source : MNHN, Paris

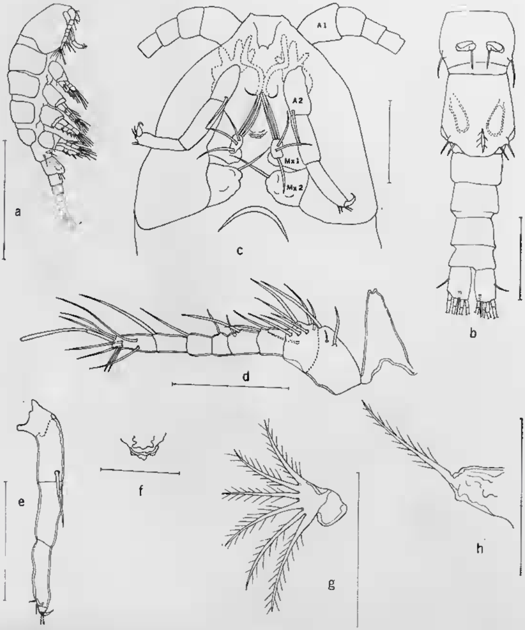

Fig. 35. — *Enterocola fertilis*, new species, allotypic male : a, habitus, lateral ; b, cephalosome, ventral view : A1 = antennule ; A2 = antenna, Mx1 = maxillule, Mx2 = maxilla ; c, urosome, ventral ; d, antennule and rostrum ; e, antenna ; f, remnant of labrum ; g, maxillule ; h, maxilla. Scale for a = 0.5 mm ; scale for f = 0.2 mm ; other scales = 0.1 mm.

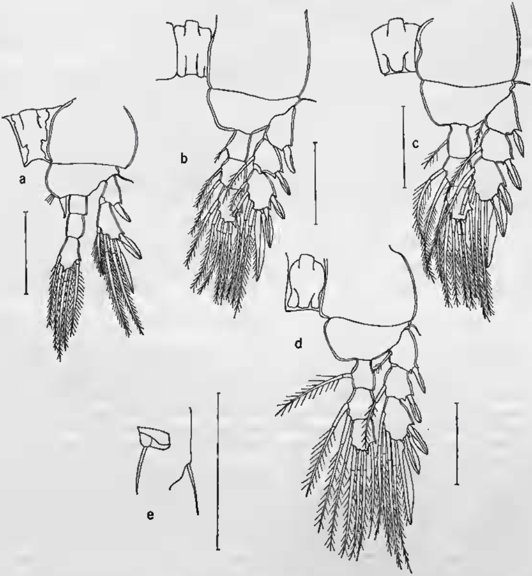

FIG. 36. — *Enterocola fertilis*, new species, allotypic male : a, first leg ; b, second leg ; c, third leg ; d, fourth leg ; e, fifth leg. Scales = 0.1 mm.

The pediform projection (figs. 33, o ; 34, 1) is a curved plate with subcircular margin. Set distally on the margin are 2 separated minute setules. The caudal rami (figs. 33, d ; 34, b) are conical and apparently form a definite articulation with the urosome. The ovisac (fig. 33, p) has a rather strong curvature.

The female in this species is very close to *E. petiti* and *E. brementi*, but differs from the former by the form of the antenna, the external seta of the maxillule and outlines of the endopodites of the legs. From the latter it differs by the form of the outlines of the endopodites of the legs.

Male, from *Amaroucium* (*Parascidia*) *areolata* (figs. 35, 36) : The overall length measures 0.93 mm from the tip of the cephalosome to the end of the caudal rami, excluding the caudal setae. The body (fig. 35, a) is divided into 3 regions. The cephalosome doubtless incorporates the body regions corresponding to the appendages through the maxillipeds, but the latter and the mandibles are lacking. There are 4 free thoracic segments bearing the swimming legs. The urosome (fig. 35, b) is 6-segmented. The first 2 segments bears the fifth and sixth legs. The second segment contains the bilaterally arranged spermatophoral sacs. There is an unaccountable single mid-ventral slit-like aperture. The remaining segments of the urosome are somewhat narrower than the first 2.

The rostrum (figs. 35, c, d) is elongate, tapering, and bifid terminally. The head appendages are shown in an *en face* view (fig. 35, c). The antennule (fig 35, c, d) is elongate, 7-segmented. The basal segment is approximately a third wider than the remaining segments which show little taper. The basal segment has a line on one surface but it is not subdivided by a real articulation. The setation of the segments is as follows : I — 13 setae ; II — 2 setae ; III — 2 setae ; IV — 1 seta ; V — 1 seta ; VI — 1 seta ; VII — 8 setae, 1 aesthete.

The antenna (fig. 35, e) is trimerous, the articles having the proportional lengths of 1.5 : 1 : 1. The basal article has a long seta at the distal inner corner. The second article is unarmed. The terminal article bears an articulated hook and 4 short setae.

The labrum (fig. 35, f) is obviously degenerated and consists of a crumpled lobe, without setae or palps.

The maxillule (fig. 35, g) is uniramous, and obscurely bimerous. The base has lost the medial projections of earlier copepodids and the terminal portion is fan-shaped, with 6 long, plumose setae uniformly spaced on the distal margin. The setae are not clearly articulated with the appendage but extend directly.

The maxilla (fig. 35, h) is uniramous and unimerous. It terminates in a long, unarticulated, plumose seta, which lacks a clear articulation.

The first leg (fig. 36, a) is biramous, with bimerous protopodite, trimerous endopodite and bimerous exopodite. There is a trapezoidal intercoxal lamella. The coxopodite lacks armature or ornamentation. The basipodite bears a short seta on the lateral margin and a distal medial spine, which reaches slightly beyond the distal margin of the first article of the endopodite. A cluster of hairs is found just medial to the spine. The 2 basal articles of the endopodite are unarmed. The terminal article bears 2 lateral setae, 2 terminal setae, and a medial seta. The basal article of the exopodite bears a distal lateral spine. The second article has a distal lateral spine, a terminal spine, a terminal seta and 2 medial setae.

The second leg (fig. 36, b) is biramous with bimerous protopodite, trimerous rami. The coxopodites are joined by a subrectangular intercoxal lamella. The basipodite bears a seta on the lateral margin. The basal article of the endopodite bears a short seta at the distal medial third. The second articles has 2 medial setae. The terminal article bears a lateral seta, 3 terminal setae, and 2 medial setae. The basal article of the exopodite bears a distal lateral spine. The second article bears a distal lateral spine, a medial seta. The terminal article bears 2 lateral spine, a terminal spine, a terminal seta, and 3 medial setae.

The third leg (fig. 36, c) is much like the second except that the basal segment of the exopodite bears a short medial seta and the terminal segment bears 5 setae rather than 4.

The fourth leg (fig. 36, d) is similar to the 2 preceding except that there are only 5 seta on the terminal article of the endopodite rather then 6, and the exopodite is as in the third leg.

The fifth leg (fig. 36, e) consists of a bimerous setiferous plate-like lobe on the lateral ventral surface of the first urosomal segment. It is not readily possible to determine if the plate is proximally articulated because it is so strongly outlined. There is an additional setiferous projection far laterally on the segment which perhaps represents a basal portion of the usual fifth leg.

The caudal ramus (fig. 35, b) is broad and flat, slightly longer than the anal somite. There are 4 setae on the truncate terminal margin, a short dorsal seta at the distal fifth, and a short seta set in an emargination at the middle of the lateral margin.

We find a very good correspondence of our specimen with the account of CANU for the male of *E. fulgens*, which is described in general terms. Since we have not had access to a specimen of the latter for detailed anatomical comparison we are not able to provide a specific discrimination at this point.

ENTEROCOLA LATICEPS, new species
(Figure 37)

Types :

Holotypic female, (type locality, San Juan Islands, Washington, in *Styela gibbsii* (Stimpson)); paratypes, all specimens listed below.

Specimens examined :

From Washington :
From *Styela gibbsii* (Stimpson) (all specimens less than 7 mm in diameter) :
Mixed collection, Harney Channel 48°34.7′ N, 122°53.1′ W, 30-40-15 fathoms, P. L. DUDLEY, June 20, 1964, 2 females.
Blakely Island West, 122°50.1 W, 48°33.3′ N, 16-18 fathoms, P. L. DUDLEY, June 20, 1964, 4 females.
Blakely Island West, 16-18 fathoms, J. NOLFI, August 15, 1966, 1 female.
From British Columbia, Canada :
From *Styela gibbsii* (Stimpson) :
Nanoose Bay, shallow dredge, R. CAMPBELL, August 9, 1964, 1 female third copepodid.

Description :

Female (fig. 37) :

Body (fig. 37) 3.1 mm, 2.8 mm, 2.5 mm, 2.0 mm and 1.5 mm, total length from 5 available specimens measured from the anterior margin to the end of the caudal rami. The body is very heavily sclerotized overall, with strong demarcation into cephalosome and metasomal and urosomal segments. The cephalosome is broad and rather flat and there is no rostrum. The major body articulation lies between the fourth and fifth leg-bearing segments, so the metasome is composed of 4 well delimited segments. The urosome (fig. 37, b) is very distinctive in configuration, 5-segmented. The first urosomal segment expands laterally as conspicuous, larged curved lamellae, which are unarticulated but which probably include the fifth legs. On the same segment at the ventral midline is a conspicuous lobed sclerotization associated with insemination pore. From this diverging tubes lead to lateral seminal receptacles at the oviducal apertures. The remaining urosomal segments bear no appendages; the caudal rami are well developed and bear a characteristic armature. The urosome is generally covered ventrally with broken rows of spinules.

The head appendages are described from an *en face* preparation (fig. 37, c) so the terms of orientation refer to this and not to the basic anatomical relations on the body.

The antennule (fig. 33, d) is unimerous, but the pattern of sclerotization indicates 4 ingredient segments. The portion representing a basal article bears 1 seta and 2 setules distally on the anterior margin. The short second component has 2 anterior setae; third 2 setae; the terminal component bears 9 setae around the apical and posterior margins.

The antenna (fig. 37, e) is clearly bimerous, heavily sclerotized and with distinctive sclerotized pataches on the basal article. The basal article is longer than the terminal article and lacks armature. The terminal article bears apically 5 setae, 1 much longer than the others.

The labrum (fig. 37, f) is heavily sclerotized and bilobed. It bears 2 spinulose, extremely heavy setae laterally and dorsally inserted. The general ventral surface has rows of denticles. There is a complicated postoral apparatus on the body surface (fig. 37, c).

The maxillule (fig. 37, g) is bilobed with the articulation on the head very complicated. The basal portion is heavily sclerotized and considerably modified. It is produced medially to terminate in heavy lobes and there is a lateral subterminal thumb-like process, which has rows of heavy spinules. At the base of this process there is inserted a stout seta ornamented with long spinules. The palp is flattened and bilobed, 1 lobe with 2 spinulose seta, the other with 3 terminal setae, 2 of these stout

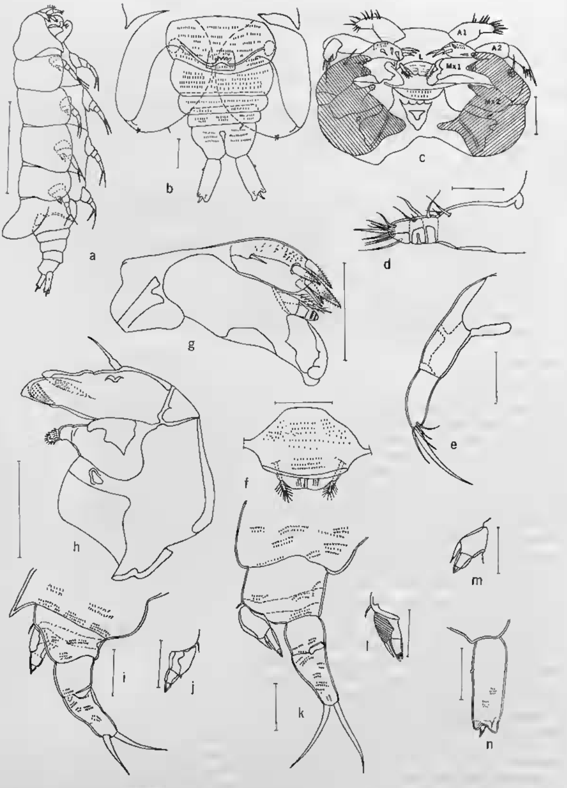

Fig. 37. — *Enterocola laticeps*, new species, paratypic female : a, habitus, lateral ; b, urosome and pediform projections, ventral ; c, *en face* view of cephalosome : A1 = antennule, A2 = antenna, L = labrum, Mx1 = maxillule unshaded, Mx2 = maxilla, shaded ; d, antennule ; e, antenna ; f, labrum ; g, maxillule ; h, maxilla ; i, first leg ; j, exopodite of second leg ; k, third leg ; l, exopodite of third leg ; m, exopodite of fourth leg ; n, caudal ramus. Scale for a = 1.0 mm ; other scales = 0.1 mm.

and covered with heavy spinules, the third unornamented. There is an additional short seta at the proximal fourth of the ventral margin. The lateral face is heavily sclerotized and is ornamented with rows of heavy spinules.

The maxilla (fig. 37, h) is bimerous and heavily sclerotized. The basal segment bears an endite with a spinulose thumb-like process. The articulation of the component articles is very complicated. The distal article ends medially in 2 pointed spinulose, heavily sclerotized processes. There is a single seta, with a much expanded base on the anterior margin.

The first leg (fig. 37, i) is biramous and its articulation with the body is rather weakly delimited. The entire appendage is very heavily sclerotized. The coxopodite has a pointed protrusion at the distal lateral corner. Rows of spinules form the ornamentation of the anterior surface. The basipodite tapers somewhat and bears a seta at the middle of the lateral margin. The anterior surface bears rows of spinules. The endopodite is bimerous. The basal article lacks armature but has 2 rows of spinules on the anterior surface. The distal article is slightly tapered to an apex bearing 2 setae, one about one-fourth longer than the other. Short lines of spinules ornament; the anterior surface. The exopodite is obscurely bimerous and very small in proportion to the endopodite, equalling about half its length. The ramus tapers and bears on the truncate apex a broad, flattened spine. The basal article has no armature or ornamentation.

In most specimens examined the second leg is just like the first. In one case the exopodite is definitely bimerous and there is a small spinule at the distal lateral corner of the basal article (fig. 37, j).

The third leg (fig. 37, k) is much like the first and second with the following exceptions. The basipodite is subrectangular rather than trapezoidal and the rami are both borne on the terminal margin. The exopodite is strongly bimerous and there is a heavy spine-like element at the distal lateral corner of the basal article. The features of this leg are in strong contrast to the structure in most species of *Enterocola,* where the third leg differs in a characteristic way from the others.

The fourth leg is in most cases like the third. In 1 case 1 exopodite (fig. 37, l) has 2 flattened terminal spines, contrasting with its partner (fig. 37, m).

The pediform projection of the sixth thoracic segment (fig. 37, b) is a very large curved flap which reaches almost to the end of the urosome. There are 3 minute setae spaced along the posterior margin, possibly indicating involvement of the fifth leg.

The caudal ramus (fig. 37, n) is flattened, almost rectangular and slightly longer than the anal somite. It has 3 terminal lobes and an apical flattened, short seta, 1 subterminal dorsomedial setule and a minute knob-like element on the lateral margin at the proximal third. Rows of fine spinules ornament the dorsal surface.

The animal is eyeless. It is usually a glistening white, but may acquire a brownish tinge from gastric secretions of the host. There may also be orange streaks on the dorsal surface. All specimens were taken from the stomachs or proximal intestine of specimens of *Styela gibbsii* less than one centimeter in diameter.

No males have been found so far.

This species has been dealt with in an extended description because of its many differences from the species of *Enterocola* associated with compound ascidians. In its habitus it definitely approaches the other species, with the body cruciform ; the head well demarcated, flat and broad ; in the presence of expansive pediform projections on the sixth thoracic somite ; and with the urosome much shorter than the anterior body. The elongate legs and the well-developed caudal rami are perhaps fairly obvious differences. In more detailed characters, the distinction becomes considerable. The antennule has indications of 4 segments and it bears more setae than does any previously known species of *Enterocola.* The antenna, although bimerous as in most species, has the basal article much longer than the terminal and there are only 5 setae on the latter, as opposed to the consistent appearance in other species of 6 or 7 setae. The most distinctive differences are in the characters of the legs, and these also differ from those of *Lequerrea* and *Enterocolides.* Although the 4 thoracic legs are extremely large in proportion to the body, the ventral lamelliform or mammiform processes characteristically associated with the legs of many other species do not occur here. Further, the notably differentiated third leg is not encountered in the present form.

The lateral seta on the basipodite on each leg is not found at all in other species nor does any other have the endopodites clearly bimerous throughout. The exopodites are clearly related to the basic plan of legs 1, 2, and 4 of *Enterocola* species, but differ by elaboration of an auxiliary process of the basal article on the third and fourth exopodites. The exopodites of the third and fourth legs of *Lequerrea* show great similarity to these, but in *Lequerrea* the processes of the basal articles have no articulations. The endopodites of *Lequerrea* are quite dissimilar, being unimerous and without armature, as again are those of *Enterocolides*. The pediform projections of the sixth thoracic segment bear 3 setae, and none other of the enterocolins has more than 2 here ; in many species of *Enterocola* there are none. None of the other enterocolins have comparably developed caudal rami and all lack armature on the ramus ; in this species there are at least 2 setae represented, although these are modified. It is probably considerably significant that our species is symbiotic in a solitary ascidian. All species of *Enterocola* for which the host is known come from aplousobranch compound ascidians, mostly from the family Polyclinidae, with 2 species from Didemnidae and 1 from Clavelinidae. *Lequerrea*, which also reaches large size, is known only from species of the simple ascidian *Polycarpa*. We are somewhat inclined to suspect that the so far poorly understood species, *E. bilamellata* Sars and *E. setifera* Hansen, although they were found free in bottom trawls, may turn out to have solitary ascidians as hosts.

INDETERMINABLE SPECIES

Biocryptus flavus Hesse, 1865, p. 244-247, pl. 6, figs. 1c-6c (no locality, in compound tunicate attached to *Cystoseira fibrosa*). — *Enterocola flavus*, Gerstaecker, 1870-71, p. 801. — Hartmeyer, 1911.

Biocryptus roseus Hesse, 1865, p. 242-244, pl. 6, fig. 1B-10B (no locality, in social tunicate attached to frond of *Zostera*). — *Enterocola roseus*, Gerstaecker, 1870-71, p. 774, 801. — Hartmeyer, 1911, p. 1736.

Biocryptus calthaeus sp. n. Hesse, 1872, p. 29-30 (unidentified tunicate, no locality). — Hartmeyer, 1911, p. 1736.

SUBFAMILY ENTEROPSINAE AURIVILLIUS 1885

Enteropsidae Aurivillius, 1885a, p. 236-237. — 1885b, p. 282. — Shimkevich', 1889, p. 76.

Enteropsidés Canu, 1892, p. 30, 107.

Ascidicolidae Gerstaecker, 1870-1871, p. 719 (part). — Canu, 1891, p. 472, 474, 475 (part) ; 1892, p. 30, 107, 186 (part). — T. Scott, 1901b, p. 241-245 (part). — Calman, 1908, p. 177, 182 (part). — Chatton & Brément, 1909b, p. 196 (part).

Ascidicolinae Schellenberg, 1922, p. 219-220 (part).

Aplostomiens Canu, 1886a, p. 373-374 (part).

Enterocolidae Sars, 1921, p. 73-74 (part). — Gray, 1933, p. 523 (part). — Gotto, 1953, p. 659 (part) ; 1954, p. 659. — Bresciani & Lützen, 1962, p. 376 (part). — Monniot, 1965, p. 160 (part). — Dudley, 1966, p. 155, 160 (part). — Gotto, 1966a, p. 193 (part). — Stock, 1967a, p. 9 (part).

When Aurivillius (1885a) described the genus *Enteropsis*, he proposed a family for it also ; he was struck by the distinctive features of the copepod. In the relatively few publications concerning members of the genus there has been very little consideration for the familial position. The very broad treatment of Canu (1892) and Schellenberg (1922) included the genus in the Ascidicolidae and Ascidicolinae, respectively. Sars (1921) placed it in the Enterocolidae, with *Mycophilus* (his spelling). Chatton & Harant, (1922, p. 163) recognized the family but termed it the Enteropsidés and assigned the much better known *Mychophilus* also to the family. The latter often has been confused with *Enteropsis* and indeed CHATTON & BRÉMENT (1909c, p. 239-240) point out that the genera probably should be combined, We are following their precedent in conserving the genus *Mychophilus* (see p. 103) but it is obvious that the differences between *Mychophilus* and the series of *Enteropis* species now known are not profound ones. Accordingly, the subfamilial diagnosis is a relatively cohesive one. We have stated (p. 15) that we consider it necessary to place *Enteropsis pilosus* Canu as a *species incerta sedis* in the family Ascidicolidae, so do not account for its characters in our diagnosis of the subfamily Enteropsinae. CANU has many garbles in the description of *E. pilosus*. We strongly suspect he had a species of *Enteropsis* before him but that he mixed in some details deriving from a haplostomin.

In the female the body is cruciform to fusiform, inflated, with segmentation usually not obvious, tending to indication only by indentations and the positions of the legs ; without pterostegites and without pediform projections of the sixth thoracic segment (that is, without any indication of fifth legs). The demarcations of the 2 posterior regions of the body tend to be obscure. The habitus and posture may be highly distinctive. The size ranges from minute in *Mychophilus* to very large dimensions in species of *Enteropsis* (length up to 8 mm).

The cephalosome does not form a distinct articulation with the body but is typically rather well set off, by a constriction or by a sharp inflection, and may be strongly indicated laterally by pleural folds. The appendages are the antennules, antennae, maxillules, maxillae. Practically all the literature is erroneous in reference to these ; the maxillules are usually referred to as mandibles, and in many cases the maxillae are termed maxillipeds.

The metasome effectively consists of the segments of the 4 major thoracic legs, and the demarcation from the urosome is obscure. In the absence of fifth legs or of the corresponding pediform projections, it is not possible to determine whether the corresponding segment is metasomal or urosomal. The metasome is the widest and longest body region. The legs protrude from it conspicuously, without any distinct articulation.

Although the urosome may appear annulated, the segmentation is usually obsolescent. The anterior portion is marked by the presence of the genital apparatus. There is usually a midventral insemination pore which may be seen to connect with diverging internal tubes which loop anteriorly then laterally toward the oviducal apertures. The latter are usually marked by various sclerotizations and sometimes by setules. The caudal rami are always reduced and vaguely articulated on the body and vary in the presence or absence of a feeble setation.

The antennule varies from unsegmented to obscurely trimerous. The setation is always somewhat reduced, or may be absent. There are at most 10 setules and setae, mostly borne on the terminal article.

The antennae are modified appendage, always much tapered and varying in segmentation. Up to 4 articles may be indicated ; most forms have the appendage bimerous. There may be actual setae on the appendage, but usually it tends to prolongation in 1 or 2 setiform processes. It is very characteristic that circular patches of spinules occur, sometimes on actual lobes on the surface of the appendage.

The labrum is rather central on the head and typically conspicuous. The subterminal margin may be unornamented, but in many species is set with a row of spinulose setiform elements, ranging in number from 2 to 9 in various species of *Enteropsis*. There is no mandible in the adult.

The maxillule is a complex structure of obscure anatomical derivation in which articulations may be suppressed. There are always 2 prominent lobes, one usually articulated. The armature is various, ranging from fully articulated setae to setiform processes, or to obsolescence with vestiges as lobe-like projections. There is a tendency for the basal medial process rather consistently to have 2 elements of armature. The palp-like lobes are more various and may have 2 or 3 elements of armature.

The maxilla is a massive appendage, the greatest bulk representing a basal article. In *Mychophilus* there is a small subapical spine ; in *Enteropsis* there is a terminal article forming a complicated articulation on the basal article.

There is no maxilliped, but there are many published references to such an appendage due to misconceptions as to the head appendages.

The 4 pairs of thoracic legs are all uniramous and bimerous. The basal article is vaguely articulated with the body and strongly articulated terminally. There is no armature on this article. The terminal article has a characteristic apical hooded hook with an opposed process.

Schellenberg interpreted in *Enteropsis onychophorus* 2 feeble lateral prominences at the posterior margin of the metasome as fifth legs. No other form in the subfamily has fifth legs and we consider Schellenberg's interpretation as dubious.

There are complicated structures associated with the oviducal aperatures on the sides of the urosome, which may include sclerotizations and, in a few cases, setules. The adult male is not known in the subfamily, but see below (p. 105) our discussions of male fifth copepodids in *Enteropsis* and *Mychophilus*. It is expected that males for this subfamily will be readily diagnosable on the basis of the mouthparts, which probably will correspond well in basic structure with those of the females.

The subfamily shows close affinity with the Enterocolinae, sharing with the latter many of the most distinctive anatomical adaptations. Many astute observers (e. g. Sars, Gotto, Monniot, Stock) have referred one or both of the enteropsin genera to the " Enterocolidae ".

Many published misconception as to the head appendages in *Enteropsis* stem from misapprehensions of Canu with regard to his *Enteropsis pilosus*. All of his conclusions as to structures in this animal seem to have derived from purely anatomical observations on the adult Futhermore, as stated above, his original description would seem to present features derived from an undoubted *Enteropsis* plus some others from some other ascidicolid. Curious, Canu presented several times subsequent to the original description exactly the same figured representation and seems never to have made fresh observations. The ambiguities in his presentation have been obvious to all subsequent students and it is very strange that they escaped his keenly observant eye.

Using purely anatomical criteria he termed the mouthparts of *Enteropsis* the mandibles and the second maxillae. As to the mandible he was definitely mistaken, a most curious circumstance because his demonstration, on the basis of observations on a series of developmental stages that the exactly equivalent appendages in *Enterocola* are the maxillules was an outstanding *tour de force*. These appendages in the two genera are by no means identical but they are much alike and both differ so substantially from any mandible known among ascidicoles that it is most surprising that he was not struck by the discrepancy.

As to the " second maxillae " he was right, but for wrong reasons. His terminology would have as equivalent to this appendage in *Enteropsis* a similar prehensile appendage in *Enterocola*, and the strongly prehensile mouthpart of *Haplostoma*, calling them all " simple second maxillae ". This terminology stemmed from his misconception, derived curiously enough, from his very perspicacious observations on development, that the second maxillae of copepods develop in bipartite fashion, the endopodite and exopodite respectively evolving as separate lobes from the general body surface. He never used the term " maxilliped ", nor considered that such an appendage belonged to the complement of copepod appendages. In modern terminology his " external second maxilla " is the true maxilla, his " internal second maxilla " is the maxilliped, and they indeed develop as the separate lobes he observed.

In the case of *Enterocola* he saw a single lobe develop behind the maxillule so termed it a " simple second maxilla ". This was a fortunate term because the appendage thus designated conforms to current terminology. His choice was less fortunate in the case of *Haplostoma* where again he found a single lobe and termed it a " simple second maxilla " ; In this instance current information identifies this appendage as the maxilliped.

In his description of adult anatomy of *Enteropsis pilosus* he compared the structures to those of " *Aplostoma* ". He was correct in terming the first mouthpart of *Haplostoma* the mandible, but wrong in the case of *Enteropsis*. He then compared the second mouthparts in the two and considered them as counterparts. They are not, but here it was his erroneous terminology in calling them both " second maxillae " which had the result of applying the right term to *Enteropsis* for the wrong reason.

KEY TO FEMALES OF GENERA OF *ENTEROPSINAE*

1. Anus displaced dorsally to just posterior to thorax at anterior end of urosome ; maxilla a massive unarticulated lobe with articulated subapical spine.................... *Mychophilus*

1'. Anus terminal on urosome ; maxilla distinctly bimerous, with massive base and well developed distal article directed medially.. *Enteropsis*

Mychophilus Hesse, 1865

Mychophilus Hesse, 1865, p. 233-236, 255 (no type species designated ; type species, *Mychophilus roseus*, by reference to its synonym *M. curvatus* Chatton & Brément, improperly designated as type by Chatton & Brément, 1909). — Gerstaecker, 1870-1871, p. 719. — Chatton & Brément, 1909d, p. 235-236, 238 ; 1910, p. 91-92. — Hartmeyer, 1911, p. 1736. — Chatton & Harant, 1922b, p. 163 ; 1922c, p. 249. — Schellenberg, 1922, p. 292, 294. — Harant, 1931, p. 372. — Wilson, 1932, p. 602. — Neave, 1939, p. 234. — Sewell, 1949, p. 183, 189. — Stock, 1967a, p. 9.

Mychephilus, Canu, 1892, p. 216.

Mycophilus Sars, 1921, p. 78-79. — Gray, 1933, p. 525-527. — Lang, 1948, p. 16-17, 22. — Gotto, 1952, p. 674 ; 1954, p. 659 ; 1960, p. 216 ; 1961, p. 151. — Bresciani & Lützen, 1962, p. 376. — Gotto, 1966a, p. 193.

Michophilus Chatton & Harant, 1922b, p. 163.

Enteropsis, T. Scott, 1901b, p. 241-242 (part) ; 1907, p. 369 (part).

Adranesius, Chatton & Brément, 1909a, p. 202 (part).

Chatton & Brément, 1909d, pronounced the genus of Hesse recognizable, but claimed the 2 species he described were indeterminable. They then designated as type of the genus the species they described from their own material, *Mychopilus curvatus* Chatton & Brément, 1909. This designation is contrary to the International Code of Zoological Nomenclature (1961). In any case the specific name is a synonym of Hesse's species *M. roseus*.

This genus has been studied by us through bibliographic sources and from some specimens collected at Plymouth, England and Banyuls-sur-Mer, France. Because all of the appendages of *M. roseus* have never been completely described, we have had to obtain anatomical details to compare with the species of *Enteropsis* in order to determine the taxonomy of the subfamily Enteropsinae. There remain many problems involving the biology, the life history, the morphological variation, and perhaps genetic differentiation within this genus, as pointed out especially by Lang (1948) and Gotto (1954).

Although several specific names have been proposed in the genus, all referred to *M. roseus* until 1967, when Stock described a second species.

The characteristics of the genus are essentially those of the subfamily Enteropsinae, discussed above, with the salient additional distinctive features utilized above in the key to the genera.

The body form of *Mychophilus* is highly distinctive, with the displacement of the anus and the elongation of the urosome proportional to the metasome. In *M. roseus* there is a tendency to extreme lateral displacement of the first legs. In most of the characters of the appendages the differences from forms of *Enteropsis* seems to be only at about the specific level. In the maxillae, however, there is a definite distinction. The males of *Enteropsis* and *Mychophilus* would seem to approach each other even more than the females but the separation can undoubtedly be made at the specific level, even on the fifth copepodid males now available.

KEY TO SPECIES OF *MYCHOPHILUS*, BASED ON FEMALES

1. Antenna distinctly not prehensile ; urosome and cephalosome-metasome roughly subequal.... *roseus* Hesse, 1865

1′. Antenna prehensile ; urosome much exceeding the cephalosome-metasome.. *fallax* Stock, 1967

Mychophilus roseus Hesse, 1865
(Figures 38, 39)

Mychophilus roseus Hesse, 1865, p. 232-235, pl. VI, figs. 1-8 (type locality, coast of Finistère, France, from compound tunicate attached to *Zostera marina*). — Gerstaecker, 1870-1871, p. 774, 801. — Hartmeyer, 1911, p. 1736. — Chatton & Brément, 1909d, p. 234, 238 (indeterminable species). — Stock, 1967, p. 9.

Mycophilus roseus Sars, 1921, p. 79-80, pl. 36, fig. 2. — Lang, 1948, p. 3, 17-22, fig. 7-14, 15-17. — Sewell, 1949, p. 189. — Gotto, 1952, p. 674 ; 1954, p. 659-665, fig. 105 ; 1960, p. 216 ; 1961, p. 151. — Bresciani & Lützen, 1962, p. 376. — Gotto ,1966a, p. 193.

Mychophilus pachygaster Hesse, 1865, p. 235-236 (type locality, coast of Finistère, France, from compound ascidian). — Gerstaecker, 1870-1871, p. 774, 801. — Chatton & Brément, 1909d, p. 238 (indeterminable species). — Hartmeyer, 1911, p. 1736. — Stock, 1967a, p. 9.

Mycophilus pachy gaster, Sewell, 1949, p. 189.

Mychophilus curvatus Chatton & Brément, 1909d, p. 236-238, fig. 1 (type locality, Banyuls-sur-Mer, Golfe du Lion, France, from *Polycyclus renieri*). — Schellenberg, 1922, p. 292, 295. — Harant, 1931, p. 371. — Stock, 1967a, p. 9.

Mycophilus curvatus, Sewell, 1949, p. 183, 189.

Mycophilus rosovula Gray, 1933, p. 523-528, figs. 1-2 (type locality, Millport, Scotland, from *Botrylloides leachii* Savigny). — Stock, 1967a, p. 9.

Enteropsis vararensis, T. Scott, 1901b, p. 241-242, pl. XVII, figs. 28-34 (type locality, Moray Firth, Scotland, from *Botryllus* sp.) ; 1907, p. 369.

Adranesius vararensis, Chatton & Brément, 1909b, p. 202. — *Mychophilus vararensis*, Chatton & Brément, 1909d, p. 239. — Stock, 1967a, p. 9.

Distribution :

European west coast ; British Isles ; Mediterranean.

Hosts :

Botryllus schlosseri (Pallas) *B. smaragdi*, *B. violaceus* ; *Polycyclus renieri* Lamarck ; *Botrylloides leachi* (Savigny).

Specimens examined :

From *Botryllus schlosseri* (Pallas) :
Off Cap Béar, Anse de Paulilles, near Banyuls-sur-Mer, France, 50-20 m, May 28, 1958, immature male.
Nord et nord-est Port-Vendres, near Banyuls-sur-Mer, France, mixed trawl, 70 m and 30-60 m, May 6, 1958, 2 females.
From *Botrylloides leachi* (Savigny) :
Gaiola, Bay of Naples, Italy, 35 m, February 20, 1958, 1 female.

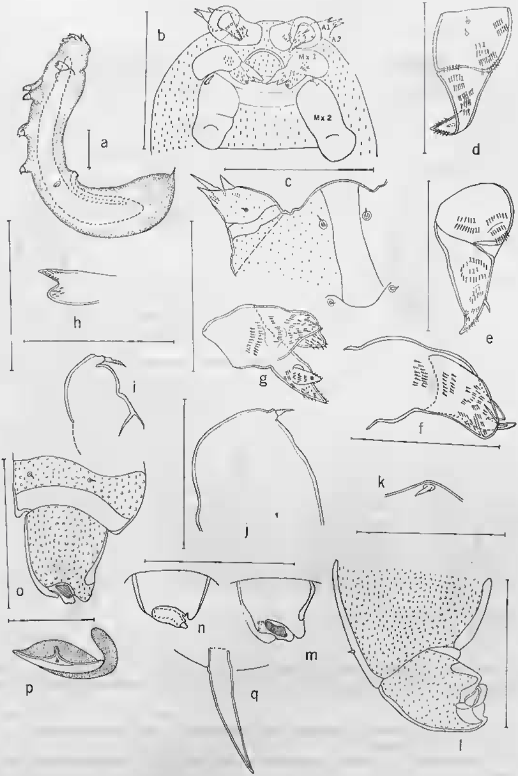

FIG. 38. — *Mychophilus roseus* Hesse, female : a, habitus, lateral ; b, *en face* view of cephalosome : A1 = antennule, A2 = antenna, Mx1 = maxillule, Mx2 = maxilla ; c, sclerotized area on dorsal cephalosome and antennule, d, antenna, ventral ; e, antenna, dorsolateral ; f, maxillule ; g, maxillule ; h, palp of maxillule ; i, maxilla ; j, maxilla ; k, apex of maxilla ; l, first leg, medial ; m, distal article of second leg ; n, distal article of third leg ; o, fourth leg, anterior ; p. genital aperture and ornament ; q, caudal ramus. Scale for a = 0.2 mm ; for b = 0.1 mm ; other scales = 0.05 mm.

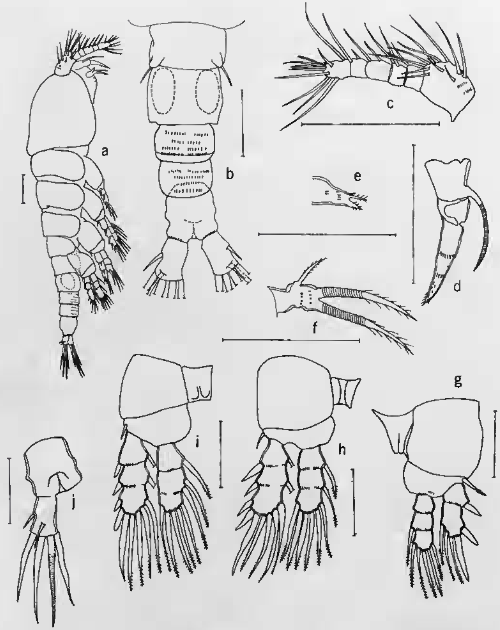

FIG. 39. — *Mychophilus roseus* Hesse, male fifth copepodid ; a, habitus, lateral ; b, urosome, ventral ; c, antennule ; d, antenna ; e, maxillule, basal portion ; f, maxillule, palp ; g, first leg ; h, second leg ; i, fourth leg ; j, anal somite and caudal ramus. Scales = 0.1 mm.

Duke Rock, near Plymouth, England, 6 m, September 8, 1958, many females.

From *Polycyclus renieri* Lamarck :

Near Banyuls-sur-Mer, France, September 26, 1910, CHATTON number 212, 60 females.

From *Polycyclus* sp. :

Near Banyuls-sur-Mer, France, October 24, 1910, CHATTON number 136, 1 female.

Description :

Adult Female :

The overall lengths of 2 specimens from anterior ends to ends to ends of urosome were 1.49 mm and 1.40 mm.

The body (fig. 38, a) has been described and figured many times. It is notable for the curved posture, the elongate cylindrical form and the unique recurvature of the intestine, with consequent displacement of the anus dorsally to the anterior end of the urosome. The lateral displacement of the first legs, reffered to particularly by LANG (1948) and by GOTTO (1954) is notable.

The head appendages are described below from the orientation on an *en face* preparation (fig. 38, b) so the terms of orientation used are pertinent only to this preparation and not necessarily to the general anatomy of the body.

There is no rostrum, but on the dorsal anterior part of the cephalosome there is a strongly sclerotized area (fig. 38, c) and 4 setules emerge from pits in the surrounding unsclerotized cuticle, at the corners.

The antennule (fig. 38, c) is obscurely articulated with the cephalosome, it is unimerous, flattened and has a slight taper. Heavy sclerotizations form a distinctive pattern on the surface. Terminally there are 4 large, flattened, spiniform projections. Two setules, 1 on the dorsal face, 1 on the ventral face, emerge from pits. There is a general covering of small protuberances.

The antenna (figs. 38, d, e) is bimerous, with a strongly sclerotized fold separating the articles both dorsally and ventrally. The basal article has 2 setules emerging from pits on the ventral proximal surface. Several patches of spinules also ornament this surface. The distal article is essentially conical, but the pointed tip actually probably represents a fused apical seta. There is a short articulated spiniform process on the posterior margin just proximal to the apical projection.

The labrum is an unornamented hemispherical lobe.

The maxillule (figs. 38, f-h) is bilobed, with a medial basal prolongation and fused setiferous lobe representing the palp. The entire appendage is relatively heavily sclerotized. There are 2 rows of spinules on the ventral face of the base. The palp portion is stout and somewhat flattened. On the ventral surface there is an apical depression, supported to either side by sclerotizations, so that in views from some aspects the tip appears bilobed (fig. 38, g) in others appears entire (fig. 38, f). The entire ventral surface is covered with spinulose stout pointed projections. In some specimens (fig. 38, h) this apex appears as 1 such projection and rounded spinulose lobe. On our specimens there is no large seta basal to the palp, as was described and figured hy CHATTON & BRÉMENT (1909d).

The maxilla (figs. 38, i, j, k) is unimerous, indistinctly articulated on the body and consists of a lobe with a single apical medially directed, articulated spine. There is no other ornamentation or armature.

The 4 pairs of legs are much alike (figs. 38, l-o). Each leg is bimerous and uniramous. The whole appendage is covered with generally distributed fine protuberances. Sclerotizations form a distinct ve pattern on the articles. The basal article has 2 setules emerging from pits in the sclerotization on the ventral survace. The distal article bas a complicated apical structure. There is a medial lobe, opposing an articulated spine, which is invested, when retracted, by a cuticular covering. On tbe second leg, there is a setule at the base of the spine, which is lacking in the other legs (fig. 38, m).

There seem to be no fifth legs.

At approximately the level of the anus, on the sides of the urosome, complicated structures perhaps involving the sixth legs are situated at the oviducal apertures (fig. 38, p). Eacb consists of 2 sclerotized pieces. The more anterior of these is bilobed and it is somewhat exceeded anteriorly and dorsally by the more posterior piece. A membrane between the pieces is pierced by the oviducal aperture and anterior to this on the membrane, a small setule is inserted.

The caudal rami, exceedingly small, are at the apex of tbe urosome. Eacb (fig. 38, q) is a cone with no ornamentation or element of armature. It is a remarkable feature of tbe genus that the anus is displaced completely away from the bases of the rami.

The many females, taken near Plymouth, in *Botrylloides leachi*, were all found in the branchial baskets of the hosts.

The literature provides a number of statements as to localization within the hosts of the copepod. Chatton & Brément reported they found specimens at Banyuls in the matrix of colonies of the ascidian hosts. Scott found his form in branchial cavities of a species of *Botryllus*. Schellenberg added a finding in the cloacal cavity of a compound ascidian. Gray stated his specimens occupied canal systems in the matrix of *Botrylloides leachi*. Gotto, 1954, p. 665, provided the summary statement that " The precise relationship of *Mycophilus* (sic) to its host remains problematical ".

Male fifth copepodid (figs. 39, a-j) :

The body form (fig. 39, a) is cyclopoid, with the qualification that the habitus is distinctly copepodid (immature) and the exact configuration of the adult cannot directly be inferred. The overall length, measured from the apex of the head to the end of a caudal ramus is 0.92 mm. The segmentation is well defined ; the cephalosome includes the appendages through the maxilla. The mandible and maxilliped are absent, but the corresponding body regions are incorporated into the cephalosome. There are 4 free thoracic segments. The urosome (fig. 39, b) is 5-segmented. The first segment bears the minute fifth legs, and developing spermatophoral sacs are visible in the second segment. The third and fourth segments bear rows of spinules on the ventral surface.

We did not observe whether there was a rostrum, before dissecting the specimen.

The antennule (fig. 39, c) is 6-segmented ; the basal article is about 2 times as long and 2 times as wide as any other article. The terminal 5 articles are all of approximately the same width, but vary in length. The setation is as follows : Article I — 11 setae ; II — 2 ; III — 2 ; IV — 2 ; V — 2 ; VI — 8 setae, 1 setule, 1 aesthete. Two rows of spinules ornament the anterior surface of the basal article.

The antenna (fig. 39, d) is obscurely trimerous. The basal article bears an elongate seta which reaches to the distal fourth of the appendage. The second article is unarmed and unornamented. The terminal article tapers to a point and is longer than the other 2 articles combined. It is ornamented with rows of spinules and a row of spinules lies on the apex.

We did not make observation on the labrum.

The maxillule is bilobed. The palp (fig. 39, f) is a lamella bearing a short seta on the margin and terminates in 2 apical setiform processes, these approximately one and a half times longer than the palp proper. The surface of the appendage are ornamented with rows of spinules. The basal portion of the appendage extends medially to form a tapered lamella, terminating in 2 setiform processes, these much shorter than the lamella (fig. 39, e).

The maxilla was not observed, because of difficulties in dissection.

The first leg (fig. 39, g) is biramous, with bimerous protopodite, trimerous endopodite, bimerous exopodite. There is a bilobed triangular intercoxal lamella. The coxopodite is elongate, approximately equalling in length the remainder of the appendage. The basipodite lacks the distal medial spine characteristic of most notodelphyids and occurring in some ascidicolids. The usual lateral seta is present. The endopodite is about one-fourth longer than the exopodite. The basal segment of the endopodite has no setae, the second segment bears a distal medial seta, the terminal segment bears a lateral, 2 terminal, 2 distal medial setae. The basal segment of the exopodite bears a distal lateral spine ; the terminal segment, which is about 2 times longer than the basal segment, bears a distal lateral spine, a terminal spine, a terminal seta, 2 medial setae. The setae of the appendage are not much longer than their respective rami. Spinules ornament the distal margins of all the leg segments except the coxopodite and the terminal endopodite article.

The second (fig. 39, h) and the third legs have bimerous protopodites and obscurely trimerous rami. There is a subquadrangular intercoxal lamella. The coxopodite has no armature ; the basipodite bears a short seta on the lateral margin. The endopodites are slightly shorter than the exopodites. The basal and second segments of the endopodites each bear a seta at the distal medial corner. The terminal segment bears a lateral, 2 terminal, 3 medial setae. The basal and second segments of the exopodite each bear a lateral spine, 1 medial seta. The terminal segment bears 2 lateral spines, 1 terminal spine, 1 terminal seta, 3 medial setae. Spinules ornament the distal margins of the basal and second segments of the rami.

The fourth leg (fig. 39, i) has the protopodite and exopodite the same as the second and third legs ; the endopodite differs by bearing on the second segment 2 (rather than 1) setae and on the terminal segment 5 (rather than 6) setae.

The fifth leg (fig. 39, b) consists of a simple lobe at the distal margin of the first urosomal segment, bearing a terminal seta. The is no indication of sixth legs on the second urosomal segment.

The caudal ramus (fig. 39, j) is articulated on the urosome so as to diverge from the other ; the shape is rather characteristic and may reflect the immature state. There is a stout lateral seta at about the middle of the lateral margin, in the emargination. There is a seta at the distal third of the dorsal surface and there are 4 subequal stout terminal setae.

A single specimen was available to us for examination, and the details we made out are only partial. LANG (1948) and GOTTO (1954) have documented the great rarity of occurrence of the males of this copepod. From their publications, we judge that the male described by LANG must be the fifth copepodid, because of the correspondence to our specimen. Our impression as to the stage of our specimen derives from a certain juvenility of the habitus and some of the appendages, as compared with other ascidicoles, and the 5-segmented urosome. We concur with GOTTO that the male described by him was probably subadult ; we would estimate it as the fourth copepodid. Some possible discrepancies in our description and the tabulations of the other authors, as to the setation of the legs, cannot be dealt with now because of the scarcity of material and the general juvenile facies of all the specimens so far studied.

From these studies we feel that we can infer for this species a male which will conform very satisfactorily with the general features of an ascidicolid male, as discussed above in our characterization of the family.

The many correspondences of *Mychophilus* to *Enteropsis* have been pointed out before (i. e,. CHATTON & BRÉMENT, 1909c) but we feel that there is considerable desirability in retaining the generic separation at present, particularly with the recent reënforcing contribution of the addition of a second species in *Mychophilus* (STOCK, 1967a).

MYCHOPHILUS FALLAX Stock, 1967

Mychophilus fallax Stock, 1967a, p. 9-11, fig. 1a-1i, (type locality Dahlak Archipelago, Red Sea, from *Botrylloides nigrum* Herdman).

Distribution :

Red Sea.

Host :

Botrylloides nigrum Herdman.

ENTEROPSIS Aurivillius, 1885

Enteropsis Aurivillius, 1885a, p. 237-239, (types species, by monotypy, *Enteropsis sphinx* Aurivilius, 1885) ; 1885b, p. 282. — Canu, 1886a, p. 370-372 ; 1890, p. 759 ; 1891, p. 469, 475. — Shimkevich', 1889, p. 76. — Schimkewitsch, 1896, p. 345, 350, 352. — Canu, 1892, p. 25, 29, 30, 52, 58, 66, 108, 117, 132, 133, 218, 220, 221, 222 (part). — T. Scott, 1901b, p. 241-242 (part) ; 1907, p. 369 (part). — Calman, 1908, p. 182. — Chatton & Brément, 1909b, p. 196-198 ; 1909 d, p. 239 ; 1910, p. 91-92. — Hartmeyer, 1911, p. 1734, 1735. — Chatton & Harant, 1922b, p. 157-162 ; 1922c, p. 249, 250. — Schellenberg, 1922, p. 290-292. — Harant, 1931, p. 371. — Wilson, 1932, p. 599, 600, 602. — Neave, 1939, p. 241. — Sewell, 1949, p. 192. — Gotto, 1960, p. 226. — Monniot, 1961, p. 98. — Gotto, 1961, p. 151. — Monniot, 1965, p. 160. — Dudley, 1966, p. 155, 157, 158, 159, 160.

Haligryps Aurivillius, 1885a, p. 242-243 (type species, first listed, *Haligryps aculeatus* Aurivillius, 1885) ; 1885b, p. 282. — Neave, 1939, p. 552.

Synthetys Canu, 1886a, p. 371 (lapsus).

This genus is very cohesive, once *Enteropsis pilosus* Canu 1886, is removed ; we have assigned the latter form as Ascidicolidae *species incerta sedis* (p. 132). The body of the female of an *Enteropsis* species is characteristic in form, basically cruciform, elongate, with indistinct segmentation. There is usually a general covering over the cuticle, typically of very fine hairs. The anus is terminal. The cephalosome is somewhat set off from the metasome, may have pleural folds developed and bears, 4 pairs of appendages. The mandibles and maxillipeds are always lacking.

The metasome is the longest and widest portion of the body and bears 4 pairs of equispaced uniramous legs. The sixth thoracic segment may possibly be involved in the metasome, but if so, the participation is not expressed in the form of fifth legs or pediform projections.

The urosome may be demarcated by a groove and the anterior portion carries the genital apparatus. There is a midventral insemination pore ; internal diverging canals ; and at the lateral oviducal apertures there may be sclerotizations and setules. The caudal rami may be present or absent, but are always reduced.

The antennule, antenna, labrum, maxillule and legs conform to the subfamilial diagnosis.

The maxilla is generically diagnostic and usually not distinctive in the species. It is a bimerous appendage, with a massive basal article, forming a complicated articulation with a medially directed terminal article. There is a prominence on the medial distal corner of the basal article opposing the terminal article. The latter is drawn out as a slightly falcate, sclerotized process. It bears a seta on the distal margin near the articulation.

No species in the genus is really well known. The majority are very rare and almost all are described from very few specimens. Some of the descriptions are confusing and incomplete. The original descriptions of Aurivillius and those of various forms in his collection have been variously interpreted in subsequent revisions. We propose to continue the usage of most authors (Canu, 1892, Schellenberg, 1922) and recognize the various forms described by Aurivillius from the single host *Molgula ampulloides* (*Enteropsis sphinx* ; *Haligryps teres* ; *Haligryps aculeatus*) as forms and stages of a single species, *E. sphinx* Aurivillius. We propose to recognize Schellenberg's form from the Antarctic, *E. sphinx* var. *georgianus* as a nominate species *E. georgianus* Schellenberg (1922).

After careful study we cannot accept the arguments of Chatton & Harant, (1922b, p. 158-162) as to the probable bispecific composition of Aurivillius' material. We feel that in the absence of new information from actual specimens that the best interpretation of the 1885 material is to treat all as the same species. We acknowledge there are discrepancies among various of Aurivillius' statements, but the correspondences, when allowances are made for the fact that the 2 sexes and individuals of various sizes and ages were treated, are truly remarkable and, in our opinion, substantiate identification.

The specimen from *Tethyum papillosum* from Port-Vendres, identified as *E. sphinx* by Chatton & Harant (1924b, p. 158-159, figs. 1-3) and figured in part, below, we consider to represent a different species, which has been subsequently described as *Enteropsis chattoni* Monniot, 1961. As a result of this reconsideration we relegate *Enteropsis teres* (Aurivillius) *sensu* Chatton & Harant (1922b, p. 162) to the synonym of *Enteropsis sphinx* Aurivillius.

In chronological order, the species of *Enteropsis* we are recognizing here are : *E. sphinx* Aurivillius, 1885 ; *E. roscoffensis* Chatton & Brément, 1909 ; *E. georgianus* Schellenberg, 1922 ; *E. onychophorus* Schellenberg, 1922 ; *E. chattoni* Monniot, 1961 ; and we are proposing the following new species : *E. capitulatus* ; *E. minor* ; *E. superbus*, and *E. abbotti*.

ENTEROPSIS FIFTH MALE COPEPODID

So far there has never been an adult male of a species of *Enteropsis* available for study. The only information which could apply at all to males derives from Aurivillius' descriptions (1885) of *Haligryps teres* and *H. aculeatus* (1885a, p. 243-246). Canu (1891, p. 469; 1892, p. 218-22) proposed that the *Haligryps* species of Aurivillius were the adult and immature males of *Enteropsis sphinx* Aurivillius. This scheme has received subsequent concurrence (Schellenberg, 1922); and Chatton & Harant (1922b, p. 161), correctly, in our opinion, revised the attribution of *H. aculeatus* to the antepenultimate stage (fourth copepodid) (note below that we do not agree with the complete synonymy of Chatton & Harant in connection with the *Haligryps* forms). We would make a further revision of considering *H. teres* the male fifth copepodid. Even though the seminal vesicles are illustrated by Aurivillius, they are not necessarily at the definitive stage of spermatophore formation. Further, such development of the seminal vesicles, well up in the thoracic region, as depicted by Aurivillius, is diagnostic of male late fifth copepodids in the Notodelphyidae. The urosome is 5-segmented, a consistent feature of fifth copepodids.

There is a considerable correspondence of the *Enteropsis* male fifth copepodid, as can be deduced from Aurivillius' presentation, and the male copepodid of *Mychophilus*, as described and discussed above (p. 102). We present our inferences below, but must emphasize that the characters of the definitive male could very well be further modified.

The body form is essentially cyclopiform, with the cephalosome including the appendages though the maxilla, and probably also the segment corresponding to the maxilliped, although this appendage is absent. The metasome has 4 free leg-bearing segments. The urosome, including the segment of the fifth legs, is 5-segmented.

The antennule is 6 or 7-segmented, and presents a rather general ascidicolid habitus.

The antenna is much like that of the female *Enteropsis sphinx* Aurivillius. In both cases this author described and depicted 4 segments in the appendage, but we feel that he may have misinterpreted some surface details and the appendage is perhaps 2-segmented, as it is throughout most of the species of the genus. The terminal armature consists of 2 unequal setae.

The labrum is a distinct lobe, and the author did not describe ornamenting setae.

The maxillule is much like that of the female, bilobed. One lobe bears 3 setae ; the other bears 2 setae.

The maxilla corresponds well to that of the female. It consists of a massive basal lobe, with a terminal hooked precess. There seems to be a pad on the basal part, opposable to the distal hook. The correspondence here of male with female appears to be much greater than is the case in *Mychophilus*.

The legs are all biramous and some of the details of armature can be inferred. In the first and fourth legs the coxopodites have no armature, and the basipodite bears a lateral seta. In the first legs the endopodites are trimerous, the basal segment bears no armature, the second segment bears a medial seta, the third segment has 1 medial, 2 terminal, 3 lateral setae. The exopodite is bimerous ; the basal segment bears 1 lateral spine ; the terminal segment bears 1 lateral spine, 1 terminal sea, 2 medial setae.

The endopodite of the fourth leg is trimerous. The first segment bears 1 medial seta, the second segment bears 2 medial setae ; the terminal segment bears 1 medial, 2 terminal, 2 lateral setae. The exopodite is trimerous. The basal and second segments each bear 1 lateral spine and 1 medial seta. The terminal segment bears 2 lateral spines, 1 terminal spine, 1 terminal seta, 3 medial setae.

A single seta is depicted as representing the fifth leg, and there is no indication of sixth legs.

The caudal rami diverge ; each bears 1 lateral seta, 1 dorsal setae, 4 terminal setae.

We are struck with the correspondence of the characters of this male copepodid with those of the female *Enteropsis sphinx*, particularly in the mouthparts. Even in the fifth stage, the male of

Mychophilus seems to show a somewhat greater dimorphism in the mouthparts, although the male retains the basic pattern of the female appendages. In features of the antennules, the swimming legs, the fifth legs, the caudal rami and the general habitus, the male fifth copepodids of *Enteropsis*, and *Mychophilus* show striking similarity. Probably in this subfamily it could be said the males will be readily diagnosable by the characters of the females, but the mouthparts will have longer setae. This would seem to indicate a different trend of dimorphism from that found in the genus *Botryllophilus* and in the haplostomins, where the mouthparts of the male tend to reduce greatly beyond the condition found in the female. There is also some contrast with the enterocolins where the trend is also toward reduction of masticatory elements, with other modifications, such as elongation of more distal setae.

KEY TO SPECIES OF *ENTEROPSIS*, BASED ON FEMALES

1\. Labrum without setiform processes ; antenna with 2 apical processes 2

1'. Labrum with setiform processes ; antenna with 1 or 2 apical processes 3

2\. Palp portion of maxillule with 2 setiform processes .... *chattoni* Monniot, p. 106

2'. Palp portion of maxillule with 3 more or less setiform processes .. *superbus*, new species, p. 108

3\. Antenna with 1 apical process 4

3'. Antenna with 2 apical processes 7

4\. Prominent seta-like structure at each lateral corner of labrum 5

4'. Row of seta-like structures on margin of labrum 6

5\. Maxillule complex basally, prominent medial extension terminating in 2 subequal setiform acute projections .... *minor*, new species, p. 111

5'. Maxillule complex basally, prominent medial extension bifid terminally, one element acute, setiform, 1 forming a narrow lobe with spatulate apex .... *abbotti*, new species, p. 128

6\. Antennule unimerous, short ; antenna bimerous .... *roscoffensis* Chatton & Brément, p. 114

6'. Antennule longer, indistinctly bimerous ; antenna unimerous ....
onychophorus Schellenberg, p. 131

7\. With 8 or 9 setiform processes on labrum .... *sphinx* Aurivillius, p. 120

7'. With 5 or 6 minute setiform processes on labrum 8

8\. One apical process of antenna twice the length of second ; caudal ramus very short, terminating in tiny point, placed far laterally to anus .... *capitulatus*, new species, p. 123

8'. Apical processes of antenna subequal ; caudal ramus subterminal, terminating in setiform process.
georgianus Schellenberg. p. 126

ENTEROPSIS CHATTONI Monniot, 1961
(Figure 40)

Enteropsis sphinx (non Aurivillius) Chatton & Harant, 1922b, p. 156-162, fig. 1 (from Port-Vendres, Golfe du Lion, France, in *Halocynthia papillosa* [L.]). — Gotto, 1960, p. 225 ; 1961, p. 151-152.

Enteropsis sp. Monniot, 1961a, p. 98.

Enteropsis chattoni Monniot, 1961b, p. 113-116, fig. 1 (type locality, Banyuls-sur-Mer, Golfe du Lion, France, in *Microcosmus vulgaris* Heller) ; 1965, p. 160.

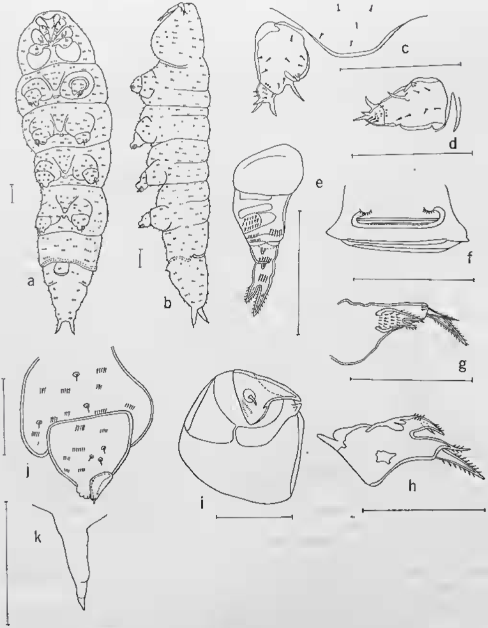

Fig. 40. — *Enteropsis chattoni* Monniot, female : a, habitus, ventral ; b, habitus, lateral ; c, antennule and anterior end of cephalosome ; d, antennule ; e, antenna ; f, labrum ; g, maxillule ; h, maxillule ; i, maxilla ; j, second leg ; k, caudal ramus. Scales = 0.1 mm.

Distribution :

French and Italian Mediterranean coasts ; British Isles.

Hosts :

Microcosmus vulgaris Heller, *Halocynthia papillosa* (L.), *Diazona violacea* Savigny.

Specimens examined :

From *Microcosmus vulgaris* Heller :

Pozzuoli, Bay of Naples, Italy, 40 m, January 16, 1958, 1 female.

We offer what we consider to be pertinent supplementary information to the descriptions of Monniot and of Chatton & Harant, and figure our specimen to compare it with other specimens and other species in the genus. The specimen, an adult female, measured 3.48 mm, overall length (cf. Monniot : " environs 4 mm "). The proportions of our specimen, cephalosome : metasome : urosome, are about 1.5 : 5 : 3.

The habitus (figs. 40, a, b) agrees well with that figured by Monniot. Chatton & Harant did not present a figure of the habitus. We figure the oviducal aperture and the insemination pore (figs. 40, a, b), not previously illustrated. Monniot refers to a movable rostrum, but we have not so far found any such in all the species of *Enteropsis* we have studied ; there is a pronounced ventral bulge of the anterior portion of the cephalosome, and it may carry some ornamentation. The antennule (figs. 40, c, d) agrees essentially with the earlier description in ornamentation and setation, but the terminal article is shorter than that illustrated by Monniot and by Chatton & Harant. The antenna (fig. 40, e) appears as it was illustrated and described by Monniot. The figure and illustration of Chatton & Harant would seem to depart strongly, because they consider as a terminal segment what we are convinced is the swollen basal portion of the larger distal setiform process of the appendage. These processes, doubtless homologous with setae, do not actually form the strong articulations which previous illustrations would tend to indicate. The labrum (fig. 40, f) is not prominent and there are no labral setiform ornamentations ; this concurs with the findings of the previous authors. The maxillule, termed mandible by the French authors, agrees in essential characters (fig. 40, g, h), but one of the terminal setae of the medial extension of the basal lobe is somewhat longer in our material than was illustrated by Monniot. There are no actual articulations, on the appendage although the representations of strong outlines in the previous publications would seem to indicate joints. The maxilla (fig. 40, i) agrees with the published accounts and figures. The four thoracic legs (fig. 40, j) are all essentially similar in structure. We feel, on the basis of extended studies on several species in the genus, that there is a misinterpretation of the structure of these legs in the original description of *E. chattoni*. They are stated to bear " deux stylets égaux, parallèle, l'un dorsal, l'autre ventral ". Referring to this character, Monniot pointed out a difference from the description of Chatton & Harant He accordingly accepted their designation of their material as *E. sphinx*. We have discussed our findings on the legs 1 to 4 in *Enteropsis* and our conviction is that there is a remarkable uniformity throughout the genus. We would suggest that the appearance of 2 stylets could readily be derived from some views of the terminal articulated spine in its sheath. Our specimen from Naples, conforming throughout otherwise to the description of *E. chattoni*, has the structure of the legs as we have found them in other species. We illustrate the caudal ramus (fig. 40, k).

Our record extends the known distribution to the Bay of Naples. Gotto provides (1961, p. 152) interesting data on the form he observed from *Diazona violacea*. All the young and non-ovigerous stages were found in the stomach of the host. Adult females and egg-strings were found in the pharynx. Gotto suggests that the female migrates through the long, slender esophagus just prior to the extrusion of the egg-strings and he offers a brief discussion of possible factors involved in the adaptive significance of this behavor. The occurrence in the branchial basket is a relatively rare feature for a species of *Enteropsis*. Most of the living ovigerous females we observed were obtained from the atrial cavity of the host.

ENTEROPSIS SUPERBUS new species

(Figure 41)

Types :

Holotypic female, San Juan Islands, Washington, August 1, 1966, in *Pyura haustor* (Stimpson), 1 female, 7.7 mm. Paratypes listed below.

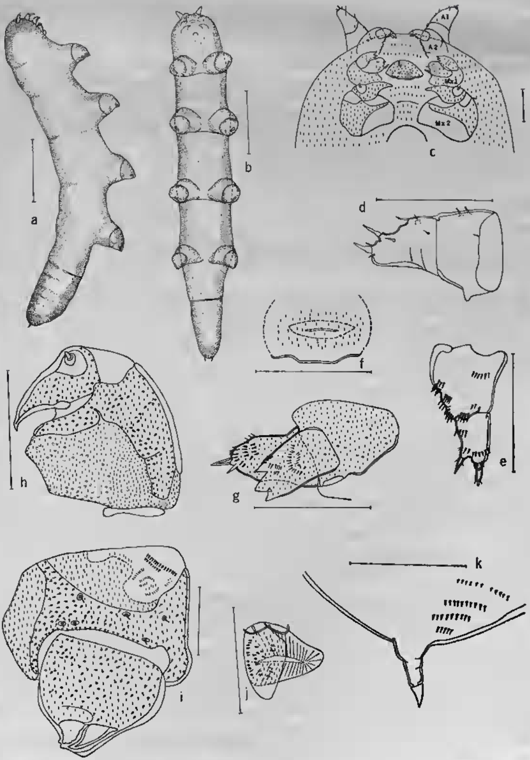

Fig. 41. — *Enteropsis superbus*, new species, paratypic female : a, habitus, lateral ; b, habitus, ventral ; c, *en face* view of cephalosome : A1 = antennule, A2 = antenna, L = labrum, Mx1 = maxillule, Mx2 = maxilla ; d, antennule, ventral ; e, antenna, ventral ; f, labrum ; g, maxillule, ventral ; h, maxilla, ventral ; i, first leg, anterior ; j, genital aperture ; k, caudal ramus. Scales for a, b, c = 1.0 mm ; other scales = 0.1 mm.

Specimens examined :

From *Pyura haustor* (Stimpson) :

Upright Channel, San Juan Islands, Washington, 1 female, 5.3 mm.
Lopez Pass, San Juan Island, Washington, 15 July, 1950, 1 immature female, 7.2 mm.
Parker Reef, Orcas Island, Washington, 8 July, 1950, 1 immature female, 1.54 mm.
" Potato Patch ", San Juan Islands, Washington, July, 1952, 1 female, 8.2 mm.
West Sound, Orcas Island, Washington, 3 fourth copepodids, 3 fifth copepodids, 2 adult females, 1 5.3 mm long — from many hosts examined.
San Juan Islands, Washington, August, 1966, 1 female, 7.5 mm.

Description :

Female :

The overall body length from the anterior end of the cephalosome to the posterior end of the caudal rami ranges from 1.54 mm to 8.2 mm in available specimens, with an average of 6.9 mm in mature adults.

The body (figs. 41, a, b) is almost uniformly cylindrical, rounded at the extremes and with the well spaced legs markedly salient. The cephalosome is not set off notably from the body. The metasome is only slightly indented as an indication of the component segments. The urosome is not distinctively articulated or otherwise set off from the metasome and exhibits only a slight taper. The minute caudal rami are terminal on the rather truncate posterior surface of the urosome, set somewhat ventrally. In the overall impression of the body the urosome is prominent. The proportions of the lengths of the three major body regions in the specimens seen so far are about 1 : 5 : 2.5, cephalosome : metasome : urosome. The thickness (that is, the depth at midpoint in lateral view) of the body is about 1/7 the overall length. The body is generally covered with very fine hairs. The illustrations wil depict these variously or omit them, depending on the degree of magnification applied.

The head appendages are described from an *en face* preparation, so the terms of orientation refer to this (fig. 41, c), not necessarily to the basic anatomical relations on the body.

The antennule (fig. 41, d) is obscurely bimerous but distinctly articulated on the head. There is a strong articulative line on the ventral surface but no interruptions of the dorsal cuticle. There are no ornamenting spinules or hairs. The basal article has 2 setules on the anterior margin at about its middle. The terminal article is tapering and truncate. There are a stout seta and 2 setules apically, a stout seta on the anterior margin at the proximal third. There are 2 setules near the base, 1 each on the dorsal and ventral surface, and an additional setule on the ventral surface at the base of the second anterior seta.

The antenna (fig. 41, e) is clearly bimerous, heavily sclerotized uniformly overall, distinctly flattened, and the outline is tapering. The basal article has 3 rounded lobes along the posterior margin and a similar lobe on the distal margin on the ventral surface. These lobes are set with patches of elongate heavy spinules and there are additional curved rows of shorter spinules proximally and distally on the ventral surface. The dorsal surface is unornamented. The distal article has one terminal, articulated seta and a subapical articulated, subequal spine on a prominence at the distal fourth. There are rows of spinules on the ventral face, 1 row at the base of the distal spine, 1 row across the face of the segment just proximal to the subapical spine base and a short row at the proximal fourth. The dorsal surface has patches of finer spinules.

The labrum (fig. 41, f) is a rather simple lobe with sclerotized distal margin and lacking marginal " setae ". The ventral surface is finely spinulose.

The maxillule (fig. 41, g) is bilobed with the lobes well articulated on the unsegmented base. The appendage is only weakly sclerotized but the surfaces are roughened by a general covering of small protuberances. The basal lobe has no armature. The lateral lobe is flattened and subrectangular in outline, the distal margin formed by 3 unarticulated flattened processes, triangular in outline and equivalent to the setae of the palp and base of other species. Two of the processes are apical, the other is just subapical and the 3 are subequal. A curving row of spinules crosses the ventral surface at about the middle and a patch of hairs lies proximal to these. Some rows of finer spinules lie at the basal region of the subapical process. The articulated spine is accompanied by a subterminal spiniform setule, about two-thirds as long as the spine. Three rows of spinules curve across the ventral surface beyond the middle.

The maxilla (fig. 41, h) is distinctly bimerous and distinctly articulated on the body. Heavy sclerotizations form a distinctive pattern. The surface of the sclerotized areas are uniformly pitted and each pit surrounds a small hair. The unsclerotized surfaces are roughened by a general covering of small protuberances. The appendage is probably representative of the basic structure throughout the genus, and distinctive proportions would only be significant as such information became available from the previously described species. The basal article has no armature. The articulation of the 2 component articles is most complicated but the terminal article can be doubtless move only in a restricted fashion. It is directed medially as a result of the arrangement. The distal article is tapering in outline, and curves slightly at the tip. The heavy sclerotization contributes to its development as a stout, somewhat flattened claw. Set in a subcircular unsclerotized space on the ventral face, there is a modified seta, encircled at the base by a sclerotized ring. The seta, about twice as long as thick, is peg-like with a smoothly curved apex.

The 4 pairs of legs are much alike (first leg, fig. 41, i); each leg is bimerous and with the apex directed somewhat medially. The articulation of the leg with the body is obscure because the cuticle is essentially uninterrupted. The leg has generally distributed fine hairs over the whole surface. The proximal article has heavy sclerotizations, probably in a distinctive pattern. On the anterior surface there are about 6 short setules, emerging from pits in the sclerotization. The distal article is sclerotized overall and the apex is complicated in structure. There is an apical medial tuberculated lobe beside a socket which receives the opposable articulated terminal spine, which is heavily sclerotized. The terminal spine is probably retractile into the terminal article.

There is no fifth leg.

A complicated structure, perhaps involving the sixth leg (fig. 41, j) is proximal to the posterior margin of the sixth thoracic segment near the middle of the lateral surface. This structure is a bilobed sclerotized ridge, with a minute setule on each lobe. Underlying this structure there is an ovoid lobe of cuticle with surface spinulations. Under this is a slit, the oviducal opening, surrounded by a peculiarly striated cuticle.

The caudal rami (fig. 41, k) are minute and very inconspicuous on the rounded posterior end of the body. Each is a conical process, unarticulated at the junction with the body, but with a clearly articulated tip.

This rare copepod occurred in the atrium or distal intestine of the host. The animal is very handsomely colored. There is an overall bright yellowish-orange coloration, with a conspicuous bright, light-red eye. The ova in the oviducts, which form conspicuous, paired, extensive tubes along the sides of the body, are scarlet-purple. The movements are as described for *E. roscoffensis* below, with the addition that antennae and maxillae show strong striking movements when the animal is turned on its back.

ENTEROPSIS MINOR new species
(Figure 42)

Types :

Holotypic female : Peavine Pass between Blakely Island and Obstruction Island, Washington, July 13, 1956, 1 female, 1.6 mm, from *Metandrocarpa taylori* Huntsman ; paratypes, listed below.

Specimens examined :

From *Metandrocarpa taylori* Huntsman : Peavine Pass between Blakely Island and Obstruction Island, Washington, August 15, 1966, 3 females, 1.4 mm, 1.6 mm, and 1.6 mm.

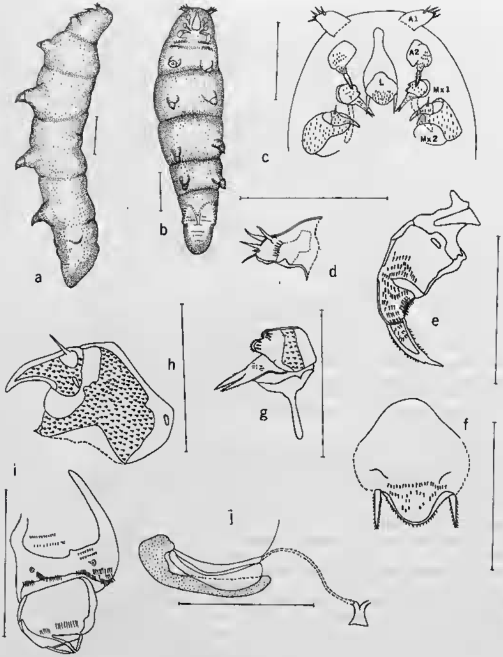

FIG. 42. — *Enteropsis minor*, new species, paratypic female : a, habitus, lateral ; b, habitus, ventral ; c, *en face* view of cephalosome : A1 = antennule, A2 = antenna, L = labrum, Mx1 = maxillule, Mx2 = maxilla ; d, antennule ; e, antenna ; f, labrum ; g, maxillule, attached to head sclerotization ; h, maxilla ; i, first leg ; j, oviducal aperture and ornament. Scales for a and b = 0.2 mm ; other scales = 0.1 mm.

Description :

Female :

The overall body length from the anterior end of the cephalosome to the posterior end of the urosome ranges from 1.4 to 1.7 mm in the available specimens of mature females.

The body (figs. 42, a, b) has only a slight anterior taper, is more pronouncedly tapering posteriorly.

The cephalosome is not set off markedly from the metasome. The metasome consists of 4 leg-bearing segments, these clearly delimited by cuticular lines dorsally and ventrally. Laterally, the segments are not defined except by indentations. The slightly tapered urosome, with 2 ingredient segments marked by indentations only, is rounded posteriorly and no caudal rami are seen. The proportions of lengths of the 3 major body regions in the specimens seen are about 1 : 4.5 : 2, cephalosome : metasome : urosome. The depth of the body at midpoint in lateral view is about 1/5 the overall length. No ornamentation could be discerned on the general body surface. This species differs greatly from other local species by its small size.

The head appendages are described below from the orientation of an *en face* view (fig. 42, c) so the terms of orientation refer to this and not necessarily to the basic anatomical relations on the body.

The antennule (fig. 42, d) is unimerous and articulated very indistinctly on the head. There is a small sclerotized patch on the dorsal surface and also a row of spinules just distal to this. The ventral surface has no ornamentation. The elements of armature are inserted apically and subapically on the anterior margin. There are 3 stout setae, 1 filiform seta, and 1 setule.

The antenna (fig. 42, e) is incompletely bimerous, because on the ventral surface the articulation reaches only part way across the appendage. The terminal spine is so stout and the jointing of the articles is so strongly indicated that casual observation might well lead to interpretation of this as a trimerous appendage. The basal " article " bears no setae or spines but is ornamented with rows of spinules near the distal margin on the ventral face. The second " article " tapers and the apex is occupied by the articulation of the very strong terminal spine which is longer than the article. The whole ventral surface of the article and the entire basal third and both margins of the spine are ornamented with spinules.

The labrum (fig. 42, f) is a simple lobe with strongly convex sclerotized posterior margin. Directed posteriorly from the lateral bases of the lobe are 2 strong, plumose setae. The ventral surface of the labrum is covered with fine hairs.

The maxillule (fig. 42, g) appears to be uniramous and the distal lobed portion has no articulation with the base. The entire appendage is relatively heavily sclerotized and there are ventral sclerotized areas on the basal portion. The sclerotizations bear pits through which fine hairs emerge. At the base of the appendage, on the head surface, there is a sclerotization of distinctive outline. The basal portion is expanded as 2 heavily sclerotized lobes thickly covered with rows of spinules. Our series of local species, in the genus *Enteropsis* offers sufficient graduation of structure in maxillules that we are convinced that these lobes represent a vestige of the palp, indeed of its apical setae. The medial process of the basal portion is long, tapered, and the distal margin is formed, without articulation, by 2 stout, ciliated setae, one of which is about three-fourths as long as the other.

The maxilla (fig. 42, h) is bimerous and distinctly articulated on the body. Heavy sclerotizations form a distinctive pattern on both articles. The surface of the sclerotized areas is pitted with a fine hair emerging from each pit. In addition, there are a few heavy spinules on the ventral sclerotized surfaces of the appendage. In general, the appendage conforms to generic characteristics. The distal article is complexly articulated and tapers in outline. It curves slightly at the tip to form a long, stout, flattened claw. Set in a subcircular unsclerotized space on the ventral side there is a relatively long, simple seta.

The 4 pairs of legs (first leg, fig. 42, i) are much alike, all bimerous and uniramous, but obscurely articulated with the body. The proximal article has heavy sclerotizations distinctly arranged. On the anterior surface of the sclerotization are 2 pits, from each of which a spinule emerges. Just proximal to the more medial pit there are 2 rows of spinules. Two rows of spinules also ornament the unsclerotized portion of the anterior surface. Curved rows of fine, long spinules ornament the distal margin. The distal article is sclerotized overall and has a complicated apex. There is a medial lobe, composed of a medial, heavy, sclerotized rod in the cuticle supporting anterior and posterior unsclerotized cuticular extensions with lobulated lateral margins. A triangular sclerotized base piece subtends this structure. Apposing the lobe is an articulated spine. There is a sclerotization around the posterior surface of the spine which may provide a hooded covering.

At the posterolateral boundaries of the first urosomal segment are sclerotized plates and flaps associated with the oviducal aperture (fig. 42, j). Part of the complex may represent a sixth leg. From an insemination pore found mid-ventrally at the posterior margin of the first urosomal segment, elongate, looping seminal tubes diverge toward the oviducal apertures.

There are no caudal rami. Broken rows of spinules ornament the ventral surface of the urosome.

The coloration of the female is an overall dull orange, with a large conspicuous red eye. The ova in the oviducts are purplish red, embryos in egg sacs are cerise red. In several hundred specimens of *Metandrocarpa*, only 3 females were found. In 4 other specimens of *Metandrocarpa*, free in the atrium, egg sacs containing embryos of *Enteropsis minor* were found, but there were no females. In 2 of these cases, 2 egg sacs were found, these containing embryos of different ages. These observations lead to the speculation that females may move from individual to individual of the social tunicate. This species appears to be much more active than any of the other local species observed. When the female is placed ventral surface down on a substratum, she can progress slowly in a coordinated manner by moving the legs metachronically. When the female is placed on her back, she is unable to turn over, but when she is in this position, the antennae are moved with violent striking movements, the maxillae strike medially and the legs move like those of *Enteropsis roscoffensis*, with first a full extension and then a posteriorly directed flexion during which the apical spine is retracted and then the distal article telescopes into the basal. Flexion of the leg consists of a distinctively clawind action. The body can generally elongate and contract, or curve in a bow-like fashion, and the urosome can swing actively. Because the host is so minute and extraction of the large copepod is extremely difficult we have been unable to determine the actual site of occurrence within the body of the ascidian.

ENTEROPSIS ROSCOFFENSIS Chatton & Brément
(Figures 43, 44, 45, 46)

Enteropsis roscoffensis Chatton & Brément, 1909b, p. 198-200, fig. 1-5 (type locality, near Roscoff, France, from *Styelopsis grossularia* van Beneden). — Schellenberg, 1922, p. 291. — Chatton & Harant, 1922b, p. 159-160. — Harant, 1931, p. 371. — Sewell, 1949, p. 189. — Gotto, 1960, p. 226.

Distribution :

Atlantic and Mediterranean coasts of France.

Hosts :

Dendrodoa grossularia (van Beneden), *Pyura microcosmus* (Savigny), *Tethyum savignyi.*

Specimens examined :

From *D. grossularia* (van Beneden) :

Plymouth, England, exact locality of collection unrecorded, from laboratory specimens, September 5, 1958, 1 female.
Roscoff, France, August, 1909, CHATTON number 27, type lot, 5 females.
Coast of France, June, 1911, CHATTON number 51, 3 females.

From *Phallusia mammillata* (Cuvier) :

No collection record, CHATTON number 249, 1 female.

From *Styela gibbsii* (Stimpson) :

Off Upright Head, Lopez Island, Washington, 1 ovigerous female, approximately 3 mm.
Friday Harbor Labs, Washington, August 21, 1953, 8 females ; 4 specimens measured were 5.1 mm, 3.9 mm, 3.5 mm, 3.8 mm.

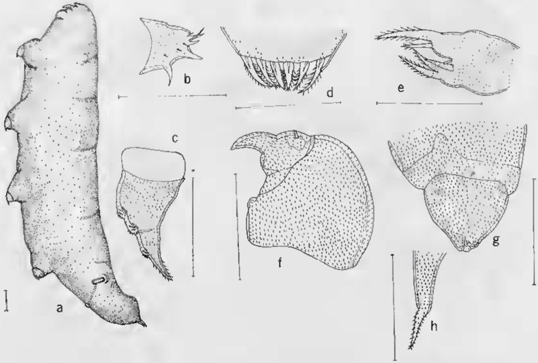

FIG. 43. — *Enteropsis roscoffensis* Chatton & Brément, female from *Dendrodoa* : a, habitus, lateral ; b, antennule ; c, antenna ; d, labrum ; e, maxillule ; f, maxilla ; g, first leg ; h, caudal ramus. Scale for a = 0.2 mm ; other scales = 0.1 mm.

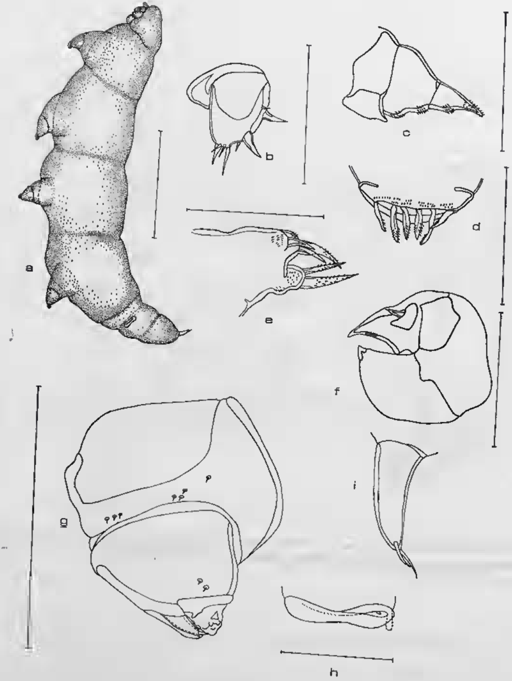

FIG. 44. — *Enteropsis roscoffensis* Chatton & Brément, female from *Dendrodoa*, Plymouth ; a, habitus, lateral ; b, antennule ; c, antenna ; d, labrum ; e, maxillule ; f, maxilla ; g, fourth leg ; h, oviducal aperture ; i, caudal ramus. Scales for a, h = 1.0 mm ; other scales = 0.1 mm.

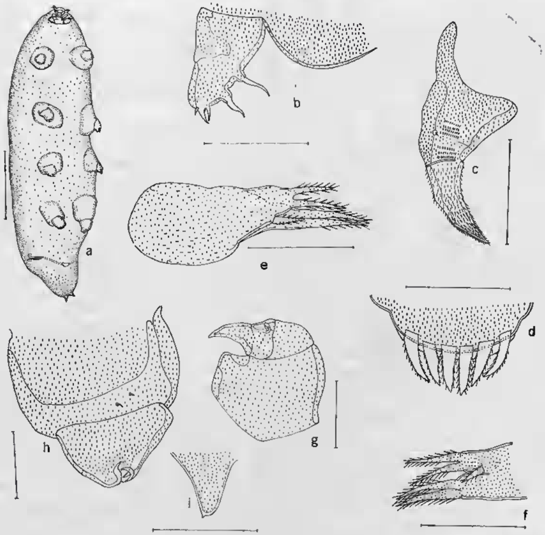

Fig. 45. — *Enteropsis roscoffensis* Chatton & Brément, female from *Phallusia* : a, habitus ; b, antennule and anterior end of cephalosome ; c, antenna ; d, labrum ; e, maxillule ; f, maxillule ; g, maxilla ; h, second leg ; i, caudal ramus. Scale for a = 1.0 mm ; other scales = 0.1 mm.

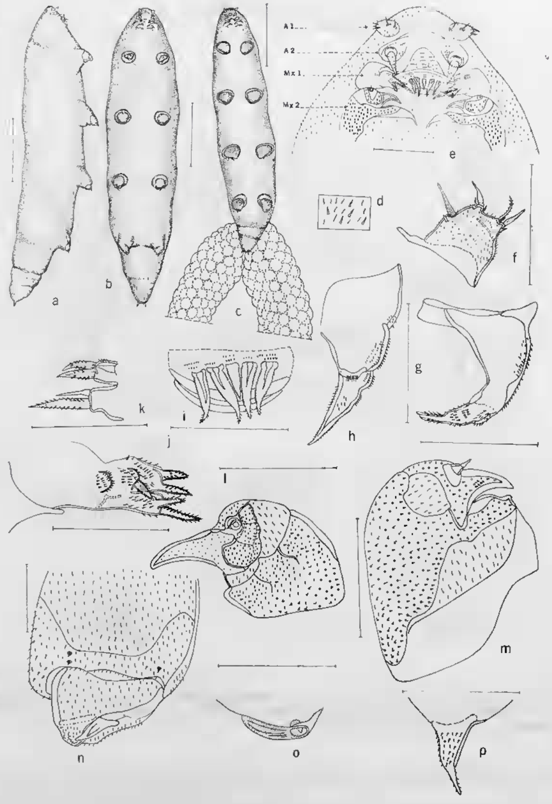

Fig. 46. — *Enteropsis roscoffensis* Chatton & Brément, female from *Styela gibbsii* : a, habitus, lateral ; b, habitus, ventral ; c, habitus, ventral, showing egg sacs ; d, detail of general body ornamentation ; e, *en face* view of cephalosome : A1 = antennule, A2 = antenna, L = labrum, Mx1 = maxillule ; Mx2 = maxilla ; f, antennule, ventral ; g, antenna, dorsal ; h, antenna, ventral ; i, labrum ; j, maxillule, ventral ; k, apex of maxillule, ventral ; l, maxilla, ventral ; m, maxilla, ventral ; n, first leg, anterior ; o, oviducal aperture ; p, caudal ramus. Scales for a, b, c = 1.0 mm ; other scales = 0.1 mm.

Off Lopez Island, Washington, June 26, 1954, 5 females, 5.0 mm, 4.3 mm, 4.1 mm, 3.7 mm, 3.3 mm.
Upright Head, Lopez Island, Washington, August 23, 1954, 1 ovigerous female, 3.1 mm.
Upright Head, Lopez Island, Washington, August 6, 1954, 1 female, 4.0 mm.
Friday Harbor Laboratory, Washington, August, 1966, 3 females, only 2 measured : 3.6 mm, and 2.8 mm.
Reef Island, Washington, 10-17 fathoms, August 26, 1966, 2 females : 3.1 mm and 3.7 mm.

We offer what we consider to be pertinent supplementary information to the original description and figure one specimen from the type host, *Dendrodoa grossularia*, from the type collection, one collected by us from *D. grossularia*, from Plymouth, England, one specimen from *Phallusia mammillate*, from the Chatton collection, but not identified by him and a representative specimen from a considerable series we have accumulated from *Styela gibbsii* from Washington. As in many species of *Enteropsis* the cuticle over the body has a general covering of fine hairs. This has not been depicted in some of our figres.

Specimens from *D. grossularia* (figs. 43, 44) : overall measurements, 3.5 mm and 3.77 mm, lying about in the middle of the range of size for the species as reported by Chatton & Brément. The proportions of our specimens, cephalosome : metasome : urosome, were 1 : 9 : 3 or 4. The corresponding formula given by Chatton & Brément (p. 198) read 1 : 14 : 13. which we must consider a misprint. Examination of their figures suggests the actual reading should have been 1 : 14 : 5.

The habitus (figs. 43, a ; 44, a) is in agreement with the earlier figure and description, except the formula for the proportions. The oviducal aperture on the urosome we saw just as was represented in the original figure and we present an enlargment (fig. 44, h). The antennules (figs. 43, b ; 44, c) agree essentially with the earlier figure and description ; we saw a few more setae. The antenna (figs. 43, c ; 44, d) appears as it was figured in the original description ; we interpret the appendage as obscurely trimerous, since the terminal portion has a strong articulative line on one face. The basal articulation is strong and complete. We agree with the authors' interpretation of the labrum and present figures (figs. 43, d ; 44, e). The bilobed maxillule, termed mandible by Chatton & Brément, (figs. 43, e ; 44, f) is just as figured earlier. In furnishing supplementary information on the species, Chatton & Harant (1922b, p. 159) evidently confused the positions of the parts, since they stated that the spinulose seta of the basal portion inserts at the base of the endopodite. This seta is actually at the base of the lateral lobe, this possibily representing an entire palp. The maxilla agrees with the authors' statements and we present figures (figs. 43, f ; 44, g). In the legs we see the details somewhat differently from the authors' description and figure of the first leg. We agree that all the legs are alike and from our specimens figure the first legs (figs. 43, g ; 44, h). As they state, the leg is uniramous and the base is massive. They describe the terminal article as bearing a triangular, lamellose crotchet, not protruding prominently. As in all other species we find a hooded triangular articulated spine, opposing an unarticulated, tuberculated lobe. The caudal ramus of the specimen from France is as described originally (fig. 43, h), but in the specimen from Plymouth (fig. 44, i) we find 2 small setae at the apex rather than 1. We consider this condition definitely anomalous and not significant in the taxonomy. The record from Plymouth adds the species to the British faunal list.

Specimen from *Phallusia mammillata* (fig. 45) : In the Chatton collection there was found a vial labelled simply " *Enteropsis* des *Phallusia mammillata* ", with no other data available. Aside from minor differences, we can identify the specimen as *E. roscoffensis*, and herewith offer figures. The overall length measures 4.5 mm. The proportions, cephalosome : metasome : urosome, are 1 : 10 : 3. The habitus (fig. 45, a) corresponds very well to the original. The antennule (figs. 45, e, f), maxilla (fig. 45, g), second leg (fig. 45, h) correspond. The caudal ramus (fig. 45, i) is somewhat smaller than in the original form and bears a tiny apical point rather than an elongate setiform process.

Specimen from *Styela gibbsii* (fig. 46) : The overall body length is 4.82 mm ; additional specimens measured ranged in length from 2.8 to 5.1 mm, with an average of 3.7 mm. The body (figs. 46, a, b, c) is somewhat plumper than in the European material, with the proportion, cephalosome : metasome : urosome, about 1 : 6 : 2. As in all the other specimens the cuticle of the general body surface is covered with moderately fine hairs interspersed with spinules (fig. 46, d). The head appendages are described from the orientation of an *en face* preparation (fig. 46, e). The antennule corresponds well to the original description (fig. 46, f). The segmentation of the antenna (figs. 46, g, h) is apparently suppressed, with a single strong articulation evident, and only on the dorsal surface, but with indications of trimery. The outline of the appendage is just like that in the other material. The labrum (fig. 46, i) bears only 5 setiform ornamenting elements, rather than 6 as in the original description and in all the European specimens we have studied. The maxillule (figs. 46, j, k) is bilobed, but with neither lobe set off by a clear articulation. The basal portion extends without interruption into the lobes but at the basal divergence of these, on one side there is a small prominence set with numerous spinules, which forms the base for an articulated spinulose seta. Just proximal to this on the ventral surface is a second spinulose, prominence. At this level there is an internal sclerotization furnishing the insertion for a major muscle. The armature of the lobes is as described previously. The maxilla (figs. 46, l, m) and the leg (fig. 46, n), oviducal aperture (fig. 56, o), and the caudal ramus (fig. 46, p) agree with the original description.

The coloration of this female is an overall soft light orange, with the red eye conspicuous. The ova in the oviducts are purplish-light red. The egg string is lively bright red, the transparency increasing as development progresses. Observations on living specimens give some information about movements of the body and some of the appendages. The body can elongate and contract, and it flexes in a curved, bow-like fashion. The major flexure is usually between the second and third legs. Secondary flexures are at the junctures of cephalosome and metasome, metasome and urosome, and also between the other pairs of legs. The urosome beyond its juncture is immobile and the caudal rami are inert. The legs move powerfully, mainly in the parasagittal planes. At full extension the leg is directed slightly laterally and the apical spine extends almost fully free of the tip of the leg. The first legs point anteriorly at full extension, the other legs reach about a right angle with the body axis. In flexion the leg moves posteriorly and medially. First the spine is retracted, then the distal article telescopes into the basal. The latter does not intrude into the body. The result of these components of flexion is a distinctly clawing action of the leg.

None of the specimens was collected from the branchial baskets of the hosts. The usual site of detection was the atrium, but at least some specimens were taken from the digestive tract proper. Freshly collected examples may be difficult to observe because they are coated with sticky detritus-like material, probably the feces of the host.

We adopt an illustrious precedent, set by Chatton and his colleagues, in assigning a perhaps somewhat improbable identification to our specimens from Washington. The general anatomical conformity between our specimens from the Pacific and the Atlantic is so thorough that we feel the best solution is to conform to a purely morphological diagnosis.

Enteropsis sphinx Aurivillius, 1887
(Figure 47)

Enteropsis sphinx Aurivillius, 1887, p. 238-242, pl. 8, fig. 12-28 (type localities, Stations 28, 66, 76, Vega Expedition : Station 28, W. of Taimurlandet, 76º99′ N latitude, 92º20′ E longitude ; Sta 76 — no data, from *Molgula ampulloides* van Beneden). — Shimkevich', 1889, p. 75, 78, 79. — Canu, 1890, p. 759 ; 1891a, p. 469 ; 1892, p. 30, 53, 54, 220. — Chatton & Brément, 1909b, p. 200, 201. — Hartmeyer, 1911, p. 1734. — Schellenberg, 1922, p. 290. — Harant, 1931, p. 371.

non Enteropsis sphinx, Chatton & Harant, 1922b, p. 158-159, 160 (Port-Vendres, Golfe du Lion, France, from *Tethyum* [= Cynthia] *papillosum*) (synonym of *Enteropsis chattoni* Monniot, 1961).

Haligryps aculeatus Aurivillius, 1887, p. 244-246, pl. 9, fig. 11-20 (type localities, Stations 28, 29, Vega Expedition : W. Taimurlandet, 76º88′ N latitude, 92º20′ E longitude : Station 28 ; Taimurlandet 76º18′ N latitude, 95º30′ E longitude : Station 29, from *Molgula ampulloides*).

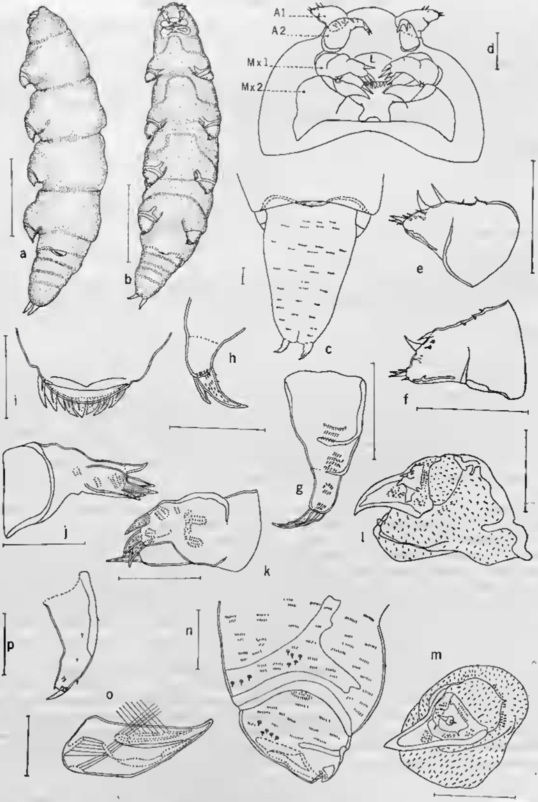

FIG. 47. — *Enteropsis sphinx* Aurivillius, female : a, habitus, lateral ; b, habitus, ventral ; c, urosome ; d, cephalosome, ventral ; A1 = antennule, A2 = antenna, L = labrum, Mx1 = maxillule, Mx2 = maxilla ; e, antennule ; f, antennule ; g, antenna ; h, apex of antenna ; i, labrum ; j, maxillule ; k, maxillule ; l, maxilla ; m, maxilla ; n, first leg, anterior surface; o, oviducal aperture ; p, caudal ramus. Scale for a, b = 1.0 mm ; other scales = 0.1 mm.

Haligryps teres Aurivillius 1887, p. 243 244, pl. 9, fig. 1-10 (type localities Stations 28, 76, Vega expedition, from *Molgula ampulloides*).

Synthetys sphinx, Canu, 1886a, p. 371 (*lapsus*).

Enteropsis teres Chatton & Harant, 1922b, p. 161-162 (for specimens of Aurivillius' collections including the adult and ovigerous females and the male adults and antepenultimates : the *Haligryps teres* and *aculeatus* specimens). — Harant, 1931, p. 371.

Distribution :

Siberian Arctic coast.

Hosts :

Molgula manhattensis (DeKay).

Specimen examined :

From *D. grossularia* (van Beneden) : Off Alaskan Coast, Lat. 67°43.3′ N, Long. 164°55′ W, 90 feet, Station 57, SS Hugh Smith, taken by diving, 1 female.

Description :

Female (fig. 47) :

Overall body length, from anterior end of cephalosome to posterior end of caudal rami measures 3.95 mm. The body (figs. 47, a, b) is eruciform, with tapering anterior and posterior ends. The segments of the body are not articulated, but are indicated by the legs and by indentations at appropriate positions. The body is not particularly contracted and there are no obvious ventral projections between the thoracic legs. The proportions of cephalosome : metasome : urosome, are 1 : 6 : 2. The urosome (fig. 47, c) is not distinctly articulated or otherwise set off from the metasome. The minute caudal rami are inserted somewhat laterally. The body is generally covered with short rows of very fine hairs.

The head appendages are described from an *en face* preparation so the terms of orientation refer to this (fig. 47, d) and not to basic anatomical relations on the body.

The antennule (figs. 47, e, f) is obscurely bimerous and obscurely articulated on the head. There is a strong articulative line on the ventral surface but none on the dorsal surface. The portion of the appendage corresponding to the usual basal segment has only 3 small spinules on the anterior margin. The tapering terminal portion has 4 setae on the anterior margin and apex, accompanied by 5 setules.

The antenna (figs. 47, g, h) is obscurely bimerous. The distal portion bears 2 articulated marginal setae, one twice the length of the other. There is a basal cuticular emargination and the larger of the 2 apical setae has a swollen base, thus suggesting a 4-segmented composition upon superficial observation. Patches of spinules lie on the ventral surface.

The labrum (fig. 47, i) is a hemispherical lobe, with 8 setiform ornamentations on the dorsal surface, near the posterior margin.

The maxillule (figs. 47, j, k) is bilobed, the unsegmented projections continuing from the base without definite articulations. The palp portion bears 3 unarticulated setiform processes, 2 borne apically, 1 on the anterior margin. The medial extension of the base is subrectangular in outline, the distal margin formed of 2 setiform processes, one about twice as long as the other. Patches of spinules ornament dorsal and ventral surfaces of the appendage.

The maxilla (figs. 47, l, m) is distinctly bimerous. Heavy sclerotizations form a distinctive surface pattern. The surfaces have a general covering of relatively heavy hairs and patches of spinules. The basal article has no armature. The distal article continues into a curved claw. Set in a subcircular ventral space there are 2 stout, short modified setae.

The 4 pairs of legs are alike (first leg, fig. 47, n). Each leg is bimerous, with the apex directed somewhat medially. The articulations of the legs on the body are indistinct but cuticular specializations outline medial areas which seem to unite the legs of each pair. The proximal article has a heavy sclerotized plate, doubtless serving for the insertion of major muscles. On the anterior surface of the article there are groups of short setules, emerging from pits. The distal article has a complicated apex. There is a medial tuberculated lobe, beside a sheath which encloses the opposable articulated terminal spine. This spine is retractile into the sheath. There is no fifth leg.

A complicated subtriangular structure possibly involving the sixth leg (fig. 47, o) is located laterally on the area of the urosome corresponding to the corresponding thoracic segment. In this species this lobe is salient. It consists of heavy sclerotized ridges and among these the oviducal aperture is located centrally. Muscles attach to the sclerotized ridges and presumably function in the control of the aperture.

The caudal ramus (fig. 47, p) is proportionately long, conical, with a terminal articulated spiniform seta. The ramus is obscurely articulated with the body.

This specimen was found in the stomach of the host, the mouth of the copepod was at the opening of the esophagus into the stomach. Ovisacs, containing embryos, wholly separated from the copepod, were found lying in the atrium, apparently anchored at their proximal ends to the outer wall of the pharynz. The question of the identity of this specimen is a vexed one, for several important reasons. The original description offers definite discrepancies from several anatomical features subsequently established for the genus. The segmentation of the cephalic appendages very likely was described on the basis of superficial observations of *in toto* preparations. We can draw on analogous information from two other copepods described from the same collections by Aurivillius, namely *Doropygus demissus* and *Schizoproctus inflatus*. The author tended to represent the general features of habitus with great accuracy. In features of the appendages, particularly in segmentation and numbers of elements of ornamentation, he tended to offer numbers of units which differ from those typical for the taxa involved. We strongly suspect his estimates for this species were excessive for the numbers of segments in the antennule, the antenna, and the maxillule. In general outline the appendages of our specimen correspond fairly well with his presentation. His largest specimen is bigger than ours, but he shows equal development of the specific characteristics on a much smaller representative as well. We are sure he represented graphically his observations on the contracted state of the bodies and the resultant protrusions and groovings of the surfaces However, we are equally sure that the basis for much of these features was response to fixation procedures and they are not a reliable basis for taxonomic treatment. The ventral protrusions of the thoracic segments are a case in point. They very likely are artifacts, but subsequent authors have relied on them very strongly in the differentiation of other taxa from *E. sphinx*. *Enteropsis dubius* Shimkevich' would be one example ; *E. sphinx georgianus* Schellenberg is another. We feel this character must be disregarded. Drawing on full published information we have concluded that there is a strong possibility that *E. dubius* is conspecific ; that *E. sphinx georgianus* most likely is not ; and that *E. sphinx* Chatton & Harant definitely is not (see our treatments of *E. chattoni*, p. 104, and *E. georgianus*, p. 126).

The question of the host specificity of *E. sphinx* is a very interesting one. There seems little doubt of the reliability of the original determination of the host as a species of *Molgula*. The finding of our specimen in *Dendrodoa grossularia* is somewhat counter to the generality of our experience in the occurrence of *Enteropsis* species, where there seems to be some taxonomic conformity of hosts. However, we have good evidence that a considerable degree of polytopy may occur, as in *E. chattoni*. There are good geographical grounds for our identification of our specimen. It occurs in the same marine basin as the original collection, the Chuckchi Sea, and we have found host diversity in the Arctic ascidicole copepods to be almost a general rule. Furthermore we find the truly Arctic assemblage of ascidicoles to be a very sparse one. The total number of species cannot be very great.

ENTEROPSIS CAPITULATUS new species
(Figure 48)

Enteropsis sp., Dudley, 1966, p. 157, 158, 159, 160.

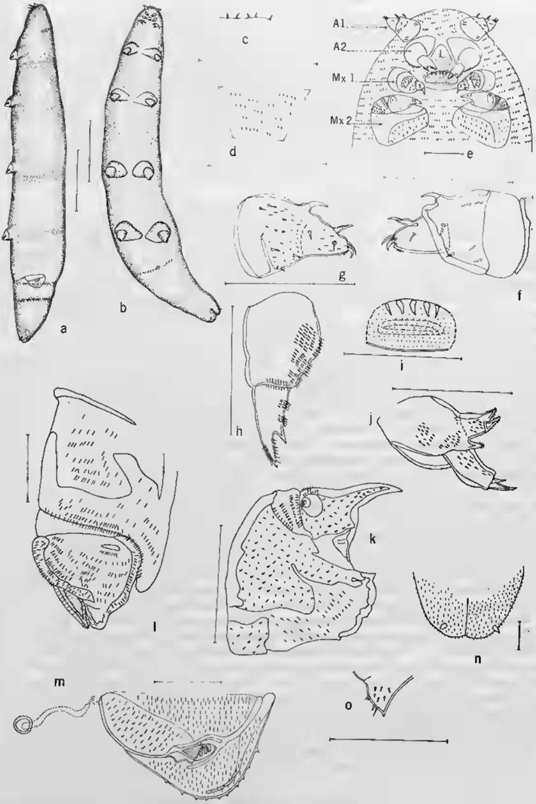

Fig. 48. — *Enteropsis capitulatus*, new species, paratypic female : a, habitus, lateral ; b, habitus, ventral ; c, detail of general body ornamentation, marginal ; d, detail of general body ornamentation, surface view ; e, *en face* view of cephalosome : A1 = entennule, A2 = antenna, L = labrum, Mx1 = maxillule, Mx2 = maxilla ; f, antennule, ventral ; g, antennule, dorsal ; h, antenna, ventral ; i, labrum ; j, maxillule, ventral ; k, maxilla, ventral ; l, first leg, anterior ; m, insemination pore, seminal tube, oviducal aperture ; n, posterior end of body showing position of caudal rami ; o, caudal ramus. Scales for a, b = 1.0 mm ; other scales = 0.1 mm.

Types :

Holotypic female, West Sound, Orcas Island, Washington, November 26, 1955, 2 females, 3.5 mm and 4.0 mm (type locality, San Juan Islands, Washington, in *Boltenia villosa* (Stimpson)) : paratypes, specimens listed below.

Specimens examined :

From *Boltenia villosa* (Stimpson) :

Blake Island, Washington, May 27, 1956, 1 female, 4.0 mm.
West Sound, Orcas Island, Washington, July, 1956, 1 female, 5.5. mm.
West Sound, Orcas Island, Washington, August, 1956, 1 female, 3.3 mm.

Description :

Female (fig. 48) :

The overall body length from the anterior end of the cephalosome to the posterior end of the caudal rami ranges from 3.3 mm to 5.5. mm, with an average of 4.1 mm in 5 available specimes of mature females.

The body (figs. 48, a, b) is strongly tapered anteriorly with the notably small head set off by a neck-like constriction or indication. The posterior taper is not strong, and the overall aspect is somewhat fusiform. The legs are relatively inconspicuous. The metasome is rather elongate, with the legs widely spaced. There are very slight indications of the component segmentation of the metasome. The urosome is most inconspicuously set off from the metasome. The caudal rami are minute and set far laterally. The proportions of lengths of the 3 major body regions are about 1 : 8 : 4, cephalosome ; metasome : urosome. The body is generally covered with broken rows of spinules, these somewhat more closely spaced on the ventral surface of the urosome (figs. 48, c, d).

The head appendages are described below from the orientation of an *en face* preparation (fig, 48, e), so the terms of orientation used are pertinent only to this preparation and not necessarily to the general anatomy of the body.

The antennule (figs. 48, f, g) might be termed obscurely bimerous, since there is no articulation of the dorsal surface, but there is a strong, well developed sclerotization, serving for insertion of the major muscles, extending across the entire ventral face, and clearly demarcating 2 ingredient articles of the appendage. The basal article has a stout, curved seta, articulated on a prominence, subterminally on the anterior margin. There are 5 short setules, 5 heavy spinules and a general covering of small spinules on the dorsal surface ; there is no additional ornamentation on the ventral surface. The distal article is truncate and somewhat tapered. At about the middle of the anterior margin, and somewhat on the ventral side, there is an unarticulated heavy seta. At its base there is on each surface a setule. Terminally there are a hooked seta, a filiform seta and a setule. Additional elements of ornamentation include proximal setules on the dorsal surface, several small spinules and some short hairs on the distal fifth of the posterior margin. The entire appendage is relatively heavily sclerotized.

The antenna (fig. 48, h) is derived from 2 basic articles, but the articulation is represented only by a weak fold on the dorsal surface, although ventrally there is a strongly sclerotized fold. The appendage is generally heavily sclerotized. The basal article has no spines or setae but is ornamented with numerous spinules arranged in patches over 3 lobes along the posterior margin. Two rows of spinules are set on the distal margin on the ventral side. The distal article is essentially conical but the pointed tip actually represents the fused apical seta. A subapical sharply pointed process doubtless represents a posterior seta. Two small lobes, set with spinules, protrude on the posterior margin, one just basal to the posterior process, one more proximal to this. The apical process has rows of heavy spinules, the posterior process is unornamented.

The labrum (fig. 48, i) is a semicircular lobe with an unornamented entire posterior margin, well sclerotized. The ventral surface is covered with rows of fine protuberances. Directed posterior from the anterior margin of the labrum there is a row of 5 to 6 stout, somewhat curved, non-plumose setae.

The maxillule (fig. 48, j) is bilobed, with the palp set off by a faint articulative line on the dorsal surface only. The entire appendage is relatively heavily sclerotized. Distally on a lobe drawn out as base for the palp there is set a stout pointed process, doubtless representing a fused seta of the base. There are 2 patches of spinules on the ventral surface of the base. The palp is short, flattened, subrectangular and the distal margin is formed by 2 equal, stout, sharply pointed processes, these thus triangular in outline and doubtless equivalent to setae of other species. The ventral surface is covered with spinules. The medial lobe of the basal portion is about twice as long as the palp, truncate terminally, bearing on the distal margin a stout, articulated, curved, spinform seta accompanied by a shorter seta which is unarticulated. The ventral surface is covered with spinules.

The maxilla (fig. 48, k) is bimerous and distinctly articulated on the body. Heavy sclerotizations form a distinctive pattern on both articles. The surface of the sclerotized areas is uniformly pitted and each pit surrounds a small hair. The unsclerotized surfaces are ornamented by rows of spinules. The appendage in general conforms to the generic characteristics. The basal article has no setae or spines but is produced at the distal medial corner as a short conical process which probably opposes the movable terminal hook. The distal article, complexly jointed, is tapering in outline and curved slightly at the tip, forming a stout, flattened hook. Set in a subcircular, unsclerotized space on the ventral side there is a short seta, surrounded at its base by a sclerotized ring. There are several (about 4) heavy spinules distally, on the ventral face of the hooked tip. There are several rows of spinules just distal to the seta.

The 4 pairs of legs (first leg, fig. 48, e) are much alike, all bimerous and uniramous. The whole appendage is covered with generally distributed fine hairs. The proximal article has no setae or spines but has heavy sclerotizations, probably distinctively arranged. The distal article is sclerotized overall, with a complicated apical structure. There is a medial tuberculated lobe opposing an articulated spine, which is invested except at the tip, when retracted, by a cuticular covering.

There is no fifth leg.

A complicated structure, perhaps involving the sixth leg (fig. 48, m) is proximal to the posterior margin of the first urosomal segment near the middle of the lateral surface. This consists of 2 lobes, containing sclerotized zones, which on each side surround a sclerotized flap, which covers the genital aperture. There is a mid-ventral insemination pore at the posterior margin of the first urosomal segment from which diverging seminal tubes lead to the area of the lateral oviducal apertures.

The caudal rami (figs. 48, n, o) are minute and set somewhat ventrolaterally on the rounded posterior end of the body. Each is a heavily sclerotized flattened lobe covered with heavy spinules.

The coloration is an overall orange, with a bright red eye. The embryos in the egg strings are bright purplish-pink. Two specimens, one mature but non-ovigerous, one with egg strings, were taken from the intestines of the host tunicates. The intestinal wall encased the copepod very firmly in each case, and even in living material had to be picked away. The ova in the oviducts of these individuals were garnet red.

ENTEROPSIS GEORGIANUS Schellenberg, 1922
(Figure 49)

Enteropsis sphinx Aurivillius var. *georgianus* Schellenberg, 1922, p. 291, 295 (type locality, South Georgia, from *Polyzoa pictonis* var. *georgiana* (Michaelsen).

Distribution :

South Georgia and Patagonia.

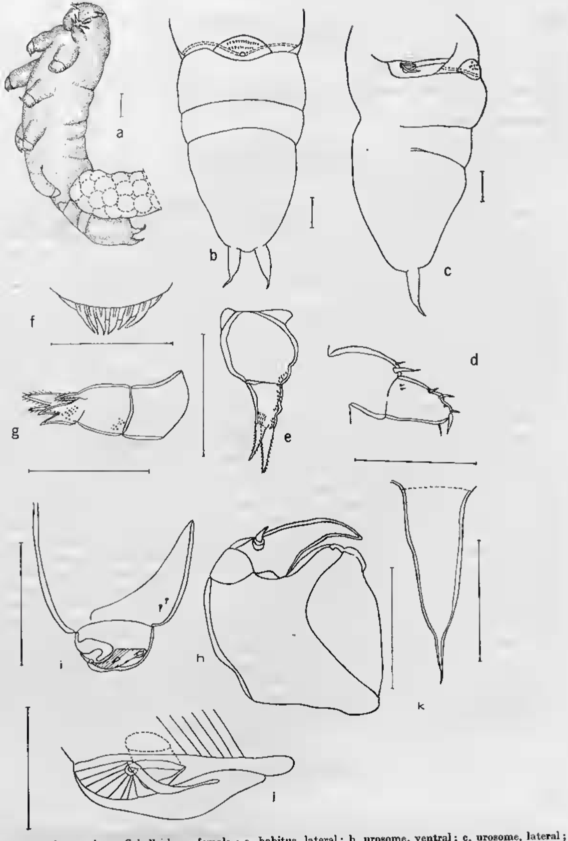

FIG. 49. — *Enteropsis georgianus* Schellenberg, female : a, habitus, lateral ; b, urosome, ventral ; c, urosome, lateral ; d, antennule ; e, antenna ; f, labrum ; g, maxillule ; h, maxilla ; i, first leg ; j, oviducal aperture ; k, caudal ramus. Scale for a = 0.2 mm ; other scales = 0.1 mm.

Host :

Polyzoa opuntia Lesson, subspecies ? (= *Polyzoa pictonis*).

Specimens examined :

From *Polyzoa opuntia* Lesson : San Julian, Patagonia, Argentina :

USNM No. 10565, Accession Number 97902, Station 123, May 6, 1927, collector W. L. Schmitt, id. W. G. Name, 1 female.

We offer below what we consider to be pertinent supplementary information to the description of Schellenberg and present our figures for comparison. Our specimen, an adult female, measures 2.5 mm in overall length, as compared to Schellenberg's 4 specimens, which ranged from 2.7 to 3.2 mm. The proportions, cephalosome : metasome : urosome, are 1 : 4 : 2, as compared to Screllenberg's 2 : 9 : 7. We present a figure of the habitus for the first time (fig. 45, a). The urosome (figs. 45, b, c) has a midventral insemination pore set on a raised area ; diverging seminal tubes pass laterally toward the oviducal apertures. The antennule indicated by the author as being bimerous or trimerous, with a seta on the basal segment and several on the outer margin of the tip, is definitely bimerous in our specimen (fig. 49, d). The terminal segment is approximately as long as the basal segment but only two-thirds as wide, but the appendages agree in other details. The antenna (fig. 49, e) is bimerous and has 2 subequal spinulose terminal setiform processes. Schelleneerg stated that the appendage had 4 segments and that the terminal elements were unequal. Although this would seem to be a distinct difference between our specimens, we feel the matter of interpretation of segmentation of the head appendages has not been resolved satisfactorily. We are sure there are many instances of accepting superficial grooves and folds and partial articulative lines as expressions of full segmentation. We have tried to take a consistent position of describing segment numbers based only on definite interruptions in the cuticle. The labrum (fig. 49, f) bears 6 setiform ornamentations, concurring with Schellenberg's indications. The maxillule, termed mandible by Schellenberg, is bilobed (fig. 49, g). We find his terminology of the " rami " more or less the reverse of our own. In the *en face* view, the most ventral lobe is the palp, thus lateral (he called it endopodite). In our specimen it terminates in 2 equal unornamented setiform processes. At the base of this lobe, not the " endopodite ", there is a stout hairy setiform process, born on a lobe which is strongly set off. The medial extension of the base terminates in a broad flattened hairy setiform process, which is accompanied by an articulated narrower and shorter hairy seta. The appendage has a strongly set off basal article. Patches of spinules ornament the surfaces of the base and the palp. The maxilla, termed maxilliped by Schellenberg, concurs essentially with his description (fig. 49, h). The legs (first leg, fig. 49, i) have elongate basal segments, measuring about 3 times as long as the terminal segments, and about twice as wide. The apex of the terminal segment bears the usual characteristic hooded spine. The caudal ramus (fig. 49, k) is elongate, conical, ending in an abruptly constricted flexible setiform tip. The oviducal apertures (fig. 49, j) are found laterally on the urosome. They occur on subtriangular lobes. Complex sclerotization to which muscles attach surround the apertures.

As we pointed out above we find no great difficulty in reconciling our specimen with Screllenberg's indications. Our study of several species within the genus furnishes us the background for the opinion that the differentiation from *E. sphinx* is essentially at the specific level.

Enteropsis abbotti new species

(Figures 50, 51)

Type :

Holotypic female, from Academy Bay, Santa Cruz Island, Galapagos Islands, from stomach or anterior intestine of *Styela* sp., collected under intertidal rock, by D. P. Abbott and J. L. Barnard, 8 February, 1964.

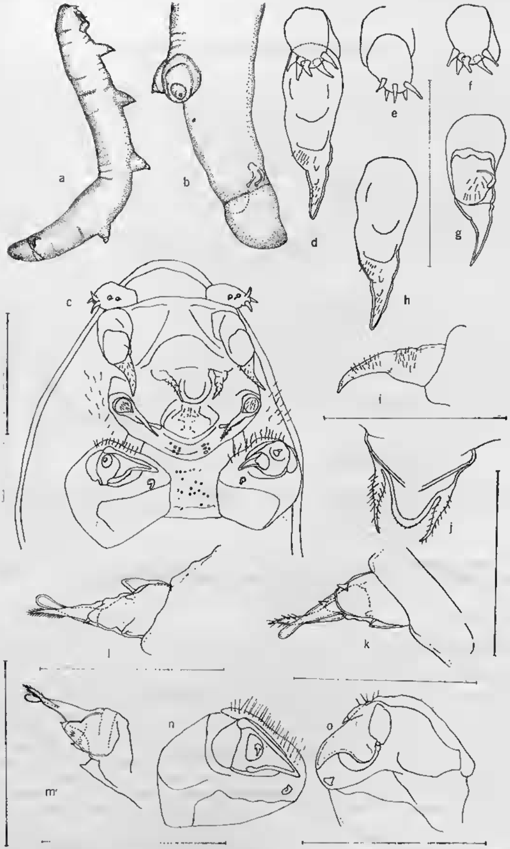

Fig. 50. — *Enteropsis abbotti*, new species, holotypic female : a, habitus, lateral ; b, posterior end of body, lateral ; c, head, ventral ; d, antennule and antenna ; e, antennule ; f, antennule from other side ; g, antenna ; h, antenna, another view ; i, antenna, apical portion ; j, labrum ; k, maxillule, dorsal ; l, maxillule, ventral ; m, maxillule of other side, ventral ; n, maxilla ; o, maxilla, another view. Scales = 0.1 mm.

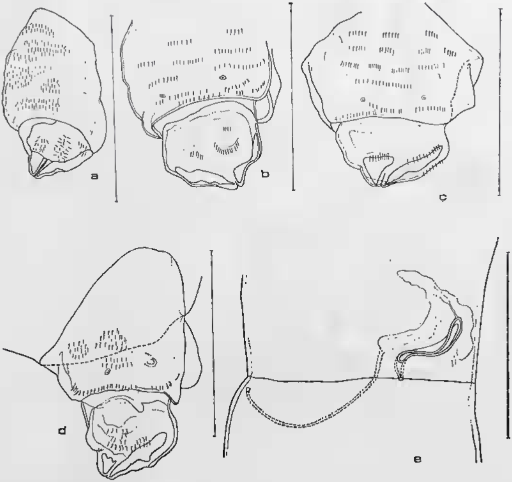

FIG. 51. — ***Enteropsis abbotti***, new species, holotypic female : a, first leg ; b, second leg ; c, third leg ; d, fourth leg ; e, insemination pore, seminal tube and oviducal aperturle, lateral. Scales = 0.1 mm.

Specimen examined :

Holotype, unique specimen.

Female (figs. 50, 51) :

The overall body length from the anterior end of the cephalosome to the posterior end of the urosome is 3.0 mm. The body (fig. 50, a) is almost uniformly cylindrical, with gently curved apices, and held in a gently curved posture in our specimen. The egg sacs were lacking. There are some slight indentations of the cuticle but they do not seem to indicate directly the component segments of the body. The cephalosome is very slightly set off dorsally by indentations. The boundary of the metasome and the urosome is not at all clearly indicated and the major evidence of the composition of the latter is the pair of prominent pair of oviducal apertures (figs, 50, b, e). There are no caudal rami. By rough estimates the body regions measure in the ratio cephalosome : metasome : urosome about 1 : 7 : 2.

The appendages correspond well to the generalizations given in the diagnosis of *Enteropsis* with the following specific features : The antennules (figs. 50, d, e, f) are simplified in outline, unsegmented, ornamented with 5 about equal setae arranged around the apex ; there are no other antennules just like these in the species we have studied. The antennae (figs. 50, d, g, h) show no apparent segmentation, although there is a strong line across one face (fig. 50, g). The sclerotized apex is produced in a strong pointed process. The labrum (fig. 50, c) shows distinctive characters in consisting of a rounded lobe, with strong seta-like processes inserted at the proximal corners, and without marginal setiform teeth, so that the only species to which it bears any resemblance in this regard is *E. minor*. The maxillules (figs. 50, k, l, m) are unique although the basic composition is of the general type for the genus. There is a basal portion with indications of 2 component articles. These bear marginal spiniform projections and the more distal article is also much produced about midway on the margin. There are 2 differentiated apical processes, not completely articulated on the more distal article, one of these setiform, broad basally and with plumose margin. The other is very distinctive with a somewhat spoon-like outline of the terminal portion, and with sclerotized margins. One of the two usual major lobes is very little developed. Probably the process representing the palp in other species here is reduced to a pointed process on the basal portion of the appendage.

The maxillipeds (figs. 50, n, o) are not especially distinctive. The basal portion bears rather long hair-like ornaments on one margin.

The first to fourth legs (figs. 51, a, b, c, d respectively) do not show specifically distinctive characteristics. As is true of much of the general surface of the body these appendages bear lines of fine hair-like ornaments.

The insemination apparatus and the complications of the cuticle at the apertures of the oviducts (fig. 51, e) do not show markedly distinctive features. The absence of the caudal rami is unusual for the genus.

We dedicate this interesting species to Dr. D. P. Abbott, who sent it to us, in acknowledgment of this and many other favors we owe him.

Enteropsis onychophorus Schellenberg, 1922

Enteropsis onychophorus Schellenberg, 1922, p. 291-292, 295 (type locality Tauranga, New Zealand, From *Alloeocarpa thilenii* Michaelsen).

Distribution :

New Zealand.

Host :

Alloeocarpa thilenii Michaelsen.

There have been no subsequent reports of this species. We feel the description of the fifth legs for the species is misleading. From observations on other species of *Enteropsis* we are sure that Schellenberg observed structures connected with the oviducal apertures and termed them fifth legs. We are convinced that the latter appendages are lacking throughout the genus.

INDETERMINABLE SPECIES

Enteropsis dubius Shimkevich', 1889

Enteropsis dubius Shimkevich', 1889, p. 75-92, pl. 3, fig. 1-17, pl. 4, fig. 19-27, 34, pl. 5, fig. 53-58 (type locality, White Sea, from *Molgula groenlandica*). — Canu, 1892, p. 53, 91, 92, 215, 220. — Schimkewitch, 1896, p. 342, 345, 352, pl. XV, fig. 36-38. — Chatton & Brément, 1909b, p. 201-202. — Chatton & Harant, 1922b, p. 161. — Schellenberg, 1922, p. 290, 295. — Sewell, 1949, p. 192.

EXCLUDED SPECIES

ENTEROPSIS PILOSUS Canu, 1886

Enteropsis pilosus Canu, 1886a, p. 365-374, pl. III, fig. 1-5 (type locality, vicinity of Iles Glenans, Concarneau, France, from *Diazona hebridica* [Forbes]) ; 1892, p. 52-53, 67, 143, 219, 220, fig. 4, 17. — Chatton & Brément, 1909b, p. 197, 201. — Hartmeyer, 1911, p. 1735. — Schellenberg, 1922, p. 290, 295. — Chatton & Harant, 1922b, p. 160-161. — Harant, 1931, p. 371. — Sewell, 1949, p. 184, 188. — Gotto, 1960, p. 226 ; 1961, p. 151, 152.

GOTTO, 1961, called attention to difficulties he encountered in trying to deal with *E. pilosus*. Our study of the literature and comparison with specimens of other species leads us to conclude that this species cannot be classified in the genus *Enteropsis*. The head appendages correspond excellently to the generic characters. However, the thoracic legs, particularly the description of fifth legs, definitely give grounds for exclusion. It is tempting to speculate that there was some confusion of specimens involved in CANU's original description. It gives every evidence of hasty assembly and there is some distinctly garbled information presented. In two different parts of the paper he compares the thoracic appendages to those of *Aplostoma* (sic) and explicitly states he finds the fifth legs to correspond with those of " Aplostoma ".

ENTEROPSIS VARARENSIS T. Scott, 1901

Enteropsis vararensis, T. Scott, 1901b, p. 241-242, pl. XVII, fig. 28-34 (type locality, Moray Firth, Scotland, from branchial chambers of *Botryllus* sp.). This species was correctly assigned to *Mychophilus* by CHATTON & BRÉMENT, 1909c, p. 239, and to the synonymy of *M. roseus* by SARS, 1921, p. 79.

SUBFAMILY HAPLOSTOMINAE Chatton & Harant, 1924

This subfamily, proposed by E. CHATTON & H. HARANT (1922-1924) for a small group of closely allied genera, was reviewed by OOISHI & ILLG (1977) in connection with description of a series of new species. Essential to the preparation of these descriptions were extensive developmental studies on species of the general *Haplostoma*, *Haplostomides*, *Haplostomella*. The results of these, to be published in a paper now in preparation following a lead established by DUDLEY (1958, 1966), and the findings included in the present paper have been crucial to our morphological and taxonomic conclusions in treating our diverse collection of species as a phyletic assemblage.

We repeat here, for completeness, selected strategic references from our synonymies of the subfamily and genera and keys to the genera and species. We refer the interested reader to the full treatment in the paper cited.

Ascidicolidae (part). — Canu, 1891, p. 475 ; 1892, p. 186. — Gotto, in Anderson & Rossiter, 1969, p. 464.

Ascidicolidés (part), Brément, 1909, p. 61-62, 86-87.

Ascidicolinae (part), Chatton & Brément, 1915, p. 143, 144. — Schellenberg, 1922, p. 220, 277-281.

Enterocolidae (part), Sars, 1921, p. 73-74. — Blake, 1929, p. 6 ; 1933, p. 226. — Lang, 1948, p. 25-27. — Monniot, 1962, p. 570. — Dudley, 1966, p. 155. — Gotto, 1966, p. 193.

Notodelphyidae (part), Sewell, 1949, p. 174.

Aplostomiens Canu, 1886, p. 373-374.

Haplostomiens, Chatton & Harant, 1922c, p. 250-252 ; 1924d, p. 406-407.

Haplostominae, Chatton & Harant, 1924e, p. 415, 416-421. — Gotto, 1959, p. 9-10. — Ooishi & Illg, 1974, p. 365 ; 1977, p. 12-15.

KEY TO GENERA OF THE SUBFAMILY HAPLOSTOMINAE

1. Exopod of legs 1 to terminating in a single lobe, ornamented with 1 or 2 thorn-like spines apically 2
1′. Exopod of legs 1 to 4 terminating in 2 lobules, one of them setiferous apically .... *Haplostomella*, p. 135
2. All mouthparts present 3
2′. One or more pairs of mouthparts lacking .... *Haplostoma*, p. 133
3. At least some of the cephalic mouthparts partially setiferous .... *Haplostomides*, p. 134
3′. Mandible, maxillule and maxilla reduced lobes without normal setae ...... *Haplosaccus*, p. 135

HAPLOSTOMA (Canu, 1886)

Enterocola (part), Norman, 1869, p. 300.

Aplostoma Canu, 1886a, p. 313-320 (types species, by monotypy, *A. brevicauda* Canu, 1886) (not *Aplostoma* Mouquin-Tandon, 1856) ; Canu, 1886b, p. 1025-1027 ; 1891, p. 471, 474, 475 ; 1892, p. 220-223. — T. Scott, 1906, p. 363-364 ; 1907, p. 361, 369-370. — Brément, 1909, p. 78-87. — Chatton & Brément, 1909b, p. 228 ; 1910, p. 80-81, 88-92. — Schellenberg, 1922, p. 288-289. — Salfi, 1926, p. 1-2. — Neave, 1939, p. 256. — Dudley, 1966, p. 155, 157, 158, 160.

Cryptopodus Hesse, 1865, p. 237-241, 255 (unidentifiable genus for 2 unidentifiable species ; no type designated). — Canu, 1892, p. 222 ; unidentifiable genus. — Sars, 1921, p. 74-75 (part). — Blake, 1929, p. 6 ; 1933, p. 226. — Lang, 1948, p. 3.

Tranestoma Wilson, 1924, p. 14, for *Aplostoma* Canu, preoccupied (type species, by monotypy, *Aplostoma brevicauda* Canu, 1886) ; 1932, p. 601 (in key).

Haplostoma Chatton & Brément, 1915, p. 144, 145, 153. — Chatton & Harant, 1922c, p. 249-252 ; 1924b, p. 363 ; 1924c, p. 399, 405 ; 1924d, p. 407 ; 1924e, p. 413, 418-419. — Harant, 1931, p. 371. — Wilson, 1932, p. 598, 600 (in key). — Neave, 1939, p. 570. — Gotto, 1952, p. 674 ; 1954, p. 665 ; 1959, p. 9, 10 ; 1960, p. 216 (in key) ; 1966, p. 193 ; 1970, p. 272. — Monniot, 1962, p. 573. — Ooishi & Illg, 1974, p. 365 ; 1977, p. 15-21.

KEY TO SPECIES OF *HAPLOSTOMA*, BASED ON FEMALES

1. One pair of mouthparts (maxillules) lacking .... *elegans* Ooishi & Illg, 1977
1′. Two (maxillules and maxillae) or 3 (mandibles, maxillules and maxillae) pairs of mouthparts lacking 2

2. Armature of terminal segment of antenna including 3 spines.......................... 3
2′. Armature of terminal segment of antenna including 4 spines.......................... 4
3. Mandible with 1 small seta.............................. *setiferum* Ooishi & Illg, 1977
3′. Mandible with 2 small setae.............................. *gibberum* (Schellenberg, 1922)
4. Posterior margin of labrum with processes.. 5
4′. Posterior margin of labrum without processes.. 9
5. Posterior margin of labrum with 8 distinct processes........ *dentatum* Ooishi & Illg, 1977
5′. Posterior margin of labrum with 4 to 6 processes...................................... 6
6. Exopod of legs 3 to 4 with 4 spines.. 7
6′. Exopod of legs 3 to 4 with 2 spines.. 8
7. Posterior margin of labrum with 4 indistinct processes...... *ambiguum* Ooishi & Illg, 1977
7′. Posterior margin of labrum with 6 distinct processes........ *banyulensis* (Brément, 1909)
8. Posterior margin of labrum with 6 distinct processes ; body length beyond 2 mm..........
eruca (Norman, 1869)
8′. Posterior margin of labrum with 6 indistinct processes ; body length less than 1.5 mm......
minutum Ooishi & Illg, 1977
9. Exopod of legs 3 to 4 with 2 spines...................... *albicatum* Ooishi & Illg, 1977
9′. Exopod of legs 3 to 4 with 3 or 4 spines.. 10
10. Legs 1 to 4 without distinct endopod lobe................ *canui* Chatton & Harant, 1924
10′. Legs 1 to 4 with endopod represented by subconical lobe........................... 11
11. Fifth leg with 2 apical setules.............................. *brevicauda* (Canu, 1886)
11′. Fifth leg with 3 apical setules.............................. *mizoulei* Monniot, 1962

Haplostomides Chatton & Harant, 1924

Enterocola (part), T. & A. Scott, 1895, p. 359-360.

Aplostoma (part), Brément, 1909, p. 84, 85. — Chatton & Brément, 1909b, p. 228 ; 1910, p. 84-86. — Schellenberg, 1922, p. 228, 289.

Haplostoma (part), Chatton & Harant, 1924b, p. 363. — Gotto, 1959, p. 10.

Cryptopodus (part), Blake, 1929, p. 6 ; 1933, p. 226.

Haplostomides, Chatton & Harant, 1924d, p. 406-412 (type species, by original designation, *H. scotti* Chatton & Harant, 1924) ; 1924e, p. 418. — Harant, 1931, p. 371. — Wilson, 1932, p. 600 (in key). — Neave, 1939, p. 570. — Gotto, 1952, p. 674 ; 1954, p. 665, 666 ; 1960, p. 213, 216 ; 1966, p. 193 ; 1970, p. 271. — Ooishi & Illg, 1974, p. 365 ; 1977, p. 77-78.

KEY TO SPECIES OF *HAPLOSTOMIDES*, BASED ON FEMALES

1. Armature of terminal segment of antenna consisting of 2 spines..........................
hibernicus (T. & A. Scott, 1895)
1′. Armature of terminal segment of antenna consisting of 4 spines.......................... 2
2. Maxilla with 4 setae.. *luteolus* Ooishi & Illg, 1977

2'. Maxilla with 2 or 3 elements of armature.. 3
3. Maxilla with 2 setae 4
3'. Maxilla with 3 variously developed elements of armature.. 5
4. Mandible with 3 apical setae............................ *scotti* Chatton & Harant, 1924
4'. Mandible with 2 apical setae......................... *brementi* Chatton & Harant, 1924
5. Mandible with 3 apical setae................................. *amarouci* (Blake, 1929)
5'. Mandible with 2 apical setae............................. *bellus* Ooishi & Illg, 1977

Haplosaccus Chatton & Harant 1924

Aplostoma (part), Chatton & Brément, 1910, p. 86-92. — Schellenberg, 1922, p. 289. — Salfi, 1926, p. 1.

Haplostoma (part), Chatton & Harant, 1922c, p. 249, 251, 252.

Haplosaccus, Chatton & Harant, 1924e, p. 413, 415, 419 (type species by original designation, *Aplostoma sacculus* Chatton & Brément, 1910). — Harant, 1931, p. 371. — Wilson, 1932, p. 600 (in key). — Neave, 1939, p. 569. — Gotto, 1960, p. 227 ; 1970, p. 271. — Ooishi & Illg, 1974, p. 365 ; 1977, p. 88-90.

KEY TO SPECIES OF *HAPLOSACCUS*, BASED ON FEMALES

1. Antenna with 1 terminal spine ; exopod of legs 1 to 4 with 1 simple claw-like element........ *sacculus* (Chatton & Brément, 1910)
1'. Antenna with 1 terminal and 1 subterminal spine ; exopod of legs 1 to 4 with 1 deeply and equally bifurcated claw-like element (2 spines).................... *elongatus* Ooishi & Illg 1977

Haplostomella Chatton & Harant 1924

Aplostoma (part), Chatton & Brément, 1910, p. 82-84, 89-91. — Schellenberg, 1922, p. 289. — Salfi, 1926, p. 1-4. — Sewell, 1949, p. 174.

Haplostomella, Chatton & Harant, 1924c, p. 398-406 (types species, by original designation, *H. malacocera* Chatton & Harant, 1924) ; 1924e, p. 413, 417, 419-421. — Wilson, 1932, p. 601 (in key). — Neave, 1939, p. 570. — Gotto, 1969 (in Anderson & Rossiter), p. 464 ; 1970, p. 267-272. — Ooishi & Illg, 1974, p. 365-374 ; 1977, p. 96-99.

Rhabdomarpha, Fukui, 1965, p. 61-63 (type species, by monotypy *R. halocynthiae* Fukui, 1965).

KEY TO SPECIES OF *HAPLOSTOMELLA*, BASED ON FEMALES

1. Posterolateral protrusion for fifth leg distinct ; mandible developed as lobe................ 2
1'. Posterolateral protrusion for fifth leg indistinct ; mandible reduced into spiniform projection or absent.. 3
2. Mandible unimerous with 1 terminal seta ; exopod of legs 2 to 4 with 1 terminal seta.......... *tuberculata* Chatton & Harant, 1924

2′. Mandible partially bimerous each with 1 seta ; exopod of legs 2 to 4 with 2 terminal setae.... *dubia* Ooishi & Illg, 1977

3. Antennule cylindrical with rounded end ; body lacking indentations or folds to suggest body regions or segments.................................... *reducta* Ooishi & Illg, 1977

3′. Antennule conical ; body with or without indentations or folds to suggest body regions or segments. 4

4. Urosome relatively short, comprising about 1/7-1/10 body length.......................... 5

4′. Urosome relatively long, comprising about 1/3 body length............................. 8

5. Caudal ramus lacking setae.................................. *sycozoae* (Salfi, 1926)

5′. Caudal ramus with setae.. 6

6. Antennule 4-segmented ; caudal ramus with 1 terminal seta.............................. *magellanica* (Chatton & Brément, 1910)

6′. Antennule unsegmented ; caudal ramus with 5 setae................................. 7

7. Maxilla with 1 seta ; fifth leg with 2 seta and 1 spine.. *malacocera* Chatton & Harant, 1924

7′. Maxilla with 2 setae ; fifth leg with 2 setae.................. *oceanica* Ooishi & Illg, 1977

8. Each metasomal segment with well-developed dorsolateral plates of suboval outline........ 9

8′ Each metasomal segment with weakly-developed dorsolateral plates of subtriangular outline *distincta* Ooishi & Illg, 1977

9. Urosome 4-segmented... *australiensis* Gotto, 1970

9′. Urosome unsegmented....................................... *halocynthiae* (Fukui, 1965)

SUBFAMILY BOTRYLLOPHILINAE *NOMEN CONSERVANDUM*

Kossmectridi Della Valle, 1883, p. 252 (new family).

Ascidicolidae, Gerstaecker, 1870-1871, p. 719 (part). — Canu, *in* Giard, 1888, p. 505 (part). — Canu, 1891a, p. 472, 475 (part) ; 1892, p. 107, 186 (part). — T. Scott, 1901a, p. 351-352 (part) ; 1901b, p. 241-245 (part). — Thompson & Scott, 1903, p. 255, 273 (part).

Ascidicolidés Brément, 1909, p. LXXXVI (part).

Schizoproctidae Aurivillius 1885a, p. 246-247 ; 1885b, p. 282.

Notodelphyidae, Norman & Scott, 1906, p. 201, 203 (part). — Schellenberg, 1922, p. 219-220. — Barnard, 1955, p. 237 (part).

Botryllophilidae Sars, 1921, p. 66-67. — Wilson, 1932, p. 391. — Leigh-Sharpe, 1934, p. 216 (part). — Pesta, 1934, p. 8. — Lang, 1948, p. 23, 25. — Sewell, 1949, p. 20, 145, 156-158. — Rose & Vaissière, 1953, p. 90. — Bresciani & Lützen, 1962, p. 374. — Dudley, 1966, p. 155, 160. — Gotto, 1966a, p. 193. — Lützen, 1968, p. 101. — Stock, 1970, p. 1, 16-17.

Botryllophidae, Rose & Vaissière, 1953, p. 90.

Ascidicolinae, Schellenberg, 1922, 219-220 (part). — Brehm, 1927, p. 490 (part). — Barnard, 1955, p. 237 (part).

Doropygidae, Sewell, 1949, p. 169-170.

The concept of a family Botryllophilidae would seem to be a fairly incisive one but there are some complications in the history and a series of equivocations in assigning the genus *Botryllophilus* to a higher category. Much of the difficulty stems from the fact that the genus was described by Hesse (1864) and there are the usual problems of reconciling his statements and figures with any actual species. The identity of the principal host, *Botryllus* sp., is reasonably firm, and the indications he gave were descriptive enough that few authors have hesitated to recognize his genus, although he described a whole series of species which cannot be evaluated with any degree of reliability. For the majority he attributed as host " un botrylle " and, moreover, he did not fix a type. This was done in the same year as the first description by Bate (1864), who selected *B. ruber* Hesse, 1864. There has never been a full-scale description nor complete set of figures presented for this species based on unequivocally identified material and so comparisons and additions within the genus have rested upon a very uneasy base. Moreover, there are some most peculiar variabilities in the morphology of most species. Indeed, Lang (1948) was so impressed by the variability of a series of material he collected in Sweden that he decided to synonymize all the species described, except for a couple of notably distinctive forms, within the original species. There seem to be well validated cases of essentially the same morphological type occurring either in compound or simple ascidians.

Della Valle (1883) described a species of *Botryllophilus*, *B. notopus*, but either did not know of Hesse's work or, as did many reputable taxonomists, chose to ignore it. He proposed a genus, *Kossmechthrus*, for his species, and was sufficiently impressed with the distinctiveness of its characters that he also stated the genus should be assigned to a family of its own, termed by him Kossmectridi. No author followed this usage. In 1885, Aurivillius, in describing the striking genus *Schizoproctus*, also erected a family for, it, namely the Schizoproctidae. This genus, highly distinctive, clearly finds it closest affinities among the species of *Botryllophilus* and the 2 genera should be referred to the same subfamily. Most workers active just after this time either overlooked these familial terms or simply assigned *Botryllophilus* and/or *Schizoproctus* to the Ascidicolidae or Ascidicolinae (Canu, 1892 ; Scott, 1901 ; Schellenberg, 1922, etc.).

Sars (1921, p. 66) used Botryllophilidae for *Botryllophilus*, *Schizoproctus*, and a new genus *Pteropygus*, without any diagnosis or discussion of the family. Most authors after Sars have used the family name in his sense and attributed the concept to him. There are a dozen or so such citations, and although the group is not such a conspicuous one that the matter is of any great consequence, it would appear most practical to continue this usage. We accept it here with the modification of assigning the taxon subfamilial level within the Ascidicolidae.

As well as the somewhat clouded nomenclatural history, certain zoological considerations complicate the status of the taxon. The latter are the more interesting. Although few valid instances are known, some of the males of *Botryllophilus* species are uncannily similar to males of species of *Haplostoma*. If no other taxa were known, there would seem to be very good grounds to include the two genera in a single subfamily. But the two seem to stand at an interesting taxonomic divergence. In the first place there are two types of males in *Haplostoma* (Ooishi & Illg, 1977) and the more modified type is readily distinguished from *Botryllophilus*. Moreover, we are informed by Dr. J. Stock (in correspondence) that there is a dimorphism of males within *Botryllophilus*. We have seen no pertinent material among our collections. More substantially, there is little doubt of the close relationship of *Haplostoma* and *Haplostomella* and in the latter the males have taken on a much modified anatomy (Ooishi & Illg, 1977), removing them considerably from the condition in *Haplostoma-Botryllophilus*. In another direction, the male of *Schizoproctus*, depicted by Sars (1921), is very different from the male of *Botryllophilus*, tending to show a closer correspondence to the features of the female.

Diagnosis :

Female :

The body in the adult is inflated, with varying degrees of expression of ingredient segmentation. The cephalosome bears the head appendages and the maxillipeds ; usually there is a very substantial demarcation behind these appendages. The metasome usually consists of evident (sometimes quite clearly demarcated) thoracic segments bearing the so-called swimming legs (thoracic segments 2-5). The segment of the fourth legs is coalesced to a substantial degree with that of the fifth legs. Basically the urosome consists of the seventh thoracic segment, the abdominal segments and the terminal anal somite bearing the caudal rami. Commonly there are substantial modifications because of the coalescence of 2 or more segments at the metasome-urosome boundary. The segment of the fourth legs is coalesced to a substantial degree with that of the fifth legs. In some forms the segment bearing the genital apertures (thoracic segment 7) fuses essentially completely with the next anterior segment. As a result the usual demarcation between metasome and urosome may be obscure with no true major body articulation at this level. The urosome then consists of the true abdominal segments, the number varying according to species. Frequently additional annular cuticular constrictions lead to an appearance of multiplication of the number of urosomal segments. The end piece of the urosome, here called the anal somite, which bears the caudal rami, is doubtless some sort of a complex rather than a simple telson (Dudley, 1966, p. 10) and thus surely also not a regular segment. The caudal ramus bears 4 (typically) subequal, strong, clawed setae, and usually 1 or more additional setae.

The rostrum may or may not be conspicuously developed but there is usually some sort of prominence between the base of the antennules.

The antennules are short, usually massive basally, with a short, slender terminal lash-like component composed of rather few free or fused segments. All the segments bear setae, and these are so abundant as to suggest that the appendage derives morphologically from one of a much higher degree of segmentation. It is very characteristic that some of the setae, particularly of the basal segments, are borne singly or in groups on protuberances of the segments proper.

The antenna is conspicuous, relatively elongate and slender, with a strong articulation at the middle, indicating a considerable freedom of action of the terminal portion relative to the base. At this articulation there is often a considerable complication of the configuration of the cuticular pieces. At one extreme the appendage is clearly 2-segmented. At the other, a separate article appears to be delimited between the basal and terminal segments. Evidence is not available as to whether this is a real segment or an articulating ring somehow related functionally to activities of the appendage. However, the development is often so pronounced that the best descriptive designation is as a 3-segmented appendage. Ornamentation is restricted to the terminal article. There are some spines inserted at intervals, sometimes in shallow emarginations, on the medial margin, and a group of several around the truncate apex. Probably these elements are derived from setae, but there is a graduation of modification resulting in a series of elements varying from substantially setiform character to well-developed spines. Most species have 7 or 8 of these elements. There is typically some additional ornamentation of spinules, near the bases of the spines or on the general surface in some sort of pattern. These appendages usually show the asymmetry characteristic of many of the appendages in the genus ; the differentiations tend to be in configuration of the segments and in the aspect of the ornamenting elements.

There is usually no elaboration or complication of the structure of the labrum, which simply consists of the superior margin of the mouth opening.

The mandibles are symmetrical, always bearing basally a coxal masticatory lamella. The segmental composition of the appendage distal to the coxopodite is obscure. Essentially there is a substantial setiferous palp. Laterally on this at about mid-margin there are 3 setae, often on an unarticulated lobe, or in some cases a lobe with 2 setae and a third at its base, these apparently representing the exopodite. About 5 setae around the more distal portion probably correspond, in part at least, to elements of an endopodite.

The maxillules are symmetrical and show again a coalescence of elements. A medial lobe, probably an endite of the coxopodite, bears a row of graduated setae, up to 7, often fewer, in number. The distal portion of the appendage forms a palp with some lobes and setae which are probably indicative of the basic composition. Medially and subterminally 2 setae probably correspond to the armature derived from the endopodite ; this usually extends laterally. Some lateral lobes and setae may represent the exopodite and epipodite. One of these setae is distinctive in protruding proximally from a lateral protuberance.

The symmetrical maxillae are reduced but are less modiefid than the other mouthparts. The outline is triangular and several setae are set along the medial margin and at the apex. There are several segments represented, 3 or 4 clearly seen in some species. The larger medial setae are borne singly or in pairs on protrusions, usually without clear articulations of the setae on the bases. Smaller setae insert singly on these bases. There is a characteristic apical pattern of a medially directed long seta, with a very wide base and no articulation, this base serving for support of a much smaller distally directed apical seta, this in turn accompanied by a laterally directed small subapical seta.

The symmetrical maxillipeds are characterized by massive bases, and terminal articulated claws. The exact number of segments has not so far been determined. Two well-marked large segments form the massive base. The much tapered articulation for the terminal claw involves an articulating ring, sometimes rather complex, and whether all this represents a single segment and whether the claw is a segment or alternatively a much transformed element of ornamentation, remain to be determined. There may be a very few reduced setules or spinules furnishing additional ornament on the appendage, and in some cases there are patches or rows of spines, spinules, tubercles, or some similar element.

The first to fourth legs, the so-called swimming legs, vary from symmetrical to asymmetrical, the latter in the majority of species, perhaps all the species of the genus *Botryllophilus*. The patterns of symmetry are specifically variable. This is also the case with the segmentation of the rami. However, in all cases the rami represent only one or at most 2 segments. These are typically set with ornamenting elements, with a great tendency for these to have the aspects of spines. In some species there are surely some individual variations in the number of segments of the rami and also in the number of ornamenting elements.

The appendages of the sixth thoracic segment, the so-called fifth legs vary in the species and their exact anatomy is not clearly understood as yet. They are always displaced very considerably dorsally, and take a broad origin on the body segments without a definite articulation. It becomes very difficult to say whether these pediform projections represent only the fifth legs or also involve an extension into a protruding process of a portion of the body segment. The presence of a basal seta very commonly would seem to indicate there is a basal segment, but this is completely coalesced with the body proximally and with the remainder of the appendage distally. Terminally there tend to be 3, sometimes fewer ornamenting elements, these usually short and slender, varying from spiniform to setiform. In the considerable gamut of aspects of these pediform projections there are alternatively the aspect of a slender process, with the terminal ornaments rather prominent,on the one band, and at the other extreme the enlargement of the process into a subcircular voluminous lamella, with the ornaments small or lacking.

The genital segment shows consistent structural features The insemination pore is midventral, with diverging internal tubes leading laterally to seminal receptacles near the oviducal apertures. The latter usually involve a cuticular flap, in each, which may have some minor features of ornamentation. There are characteristically 2 egg sacs, each firmly fastened to the apparatus at the gonopore and therefore taking a dorsolateral position. The fifth legs do not usually seem to form a firm attachment to the sacs, although in the case of pediform processes, they closely subtend them, and in the case of lamelliform processes they may completely envelop the egg sacs.

Male :

It is difficult to characterize the male at the subfamily level because so little is known. We do have information on a male of *Botryllophilus*, astonishingly like that of *Haplostoma*, and a rather typically cyclopoid swimming form. Sars illustrates very convincingly for *Schizoproctus inflatus* (1921, pl. XXXIV) an associated pair with the male represented as very much smaller than the female but resembling her in general habitus, therefore hardly a typically cyclopoid form. We have seen some material from late developmental stages in species of this genus which lead us to believe Sars correctly depicted the male for *S. inflatus*. We are further informed by Dr. J. Stock, by letter, that he has found a dimorphism among males of *Botryllophilus*. It is therefore premature to offer an extended diagnosis of males for the subfamily.

In the material we have seen of males in *Botryllophilus* (fig. 52) there are some important considerations in addition to the general form of the habitus. The antennules are furnished profusely with aesthetascs, contributing to our impression of similarity between these males and those of some species of *Haplostoma*. The mouthparts are much modified (fig. 52 b) with the masticatory lamella

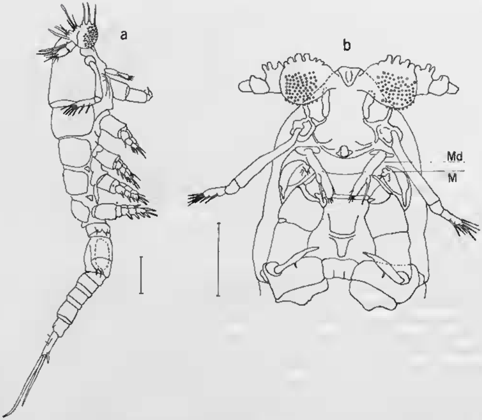

Fig. 52. — *Botryllophilus* sp., Washington, male : a, habitus, lateral ; b, *en face* view of anterior cephalosome : Md = mandible, M = mouthpart prominence, including possible rudiments of maxillule and maxilla. Scales = 0.1 mm. Circles on antennules indicate insertions of aesthetascs.

of the mandible lacking and the maxillule and maxilla reduced to minute vestiges. The first legs show a modification of the endopodites, this tending to vary at the specific level. With this highly developed dimorphism, there seems to be a conservatism in the antenna and a correspondence of the number of ornaments in the 2 sexes. The latter feature has furnished us the only reliable guide so far for differentiating the male we studied from the swimming males of *Haplostoma* species. None of the latter has more than 4 elements of armature on the distal antennal segment ; the male of *Botryllophilus* has 7. In the males of Sars' *Schizoproctus* type there seems to be fair correspondence in the structure and ornamentation of the first to fourth legs, which also are symmetrical. We have found no asymmetry in the males we have studied.

KEY TO GENERA, BASED ON FEMALES

1. Fifth leg displaced distinctly laterally and dorsally, of various shapes, always separated by both wide ventral and wide dorsal spaces, not forming a distinct enclosure for the ovisac or ovisacs. . *Botryllophilus*

1.' Fifth leg a lamella, the pair taking origin close together so their dorsal medial margins are closely adjacent, forming an enclosure or paired enclosures for the ovisac or ovisacs.... *Schizoproctus*

BOTRYLLOPHILUS Hesse, 1864

Botryllophilus Hesse, 1864, p. 345-348 (type species, *B. ruber* Hesse, by subsequent designation). — Bate, 1864, p. 308. — Hesse, 1865, p. 224 ; 1866, p. 85 ; 1869, p. 345-358. — Gerstaecker, 1870-1871, p. 719, 774. — Aurivillius, 1886, p. 44-46. — Canu, 1891a, p. 473 ; 1892, p. 29, 33, 35, 66, 108, 203-209 (part). — T. Scott, 1900, p. 388-389 ; 1901a, p. 242-245. — Thompson & A. Scott, 1903, p. 255. — T. Scott, 1907, p. 367-368. — Brément, 1909, p. LXIX-LXX. — Hartmeyer, 1911, p. 1734 (part). — Chatton & Brément, 1915, p. 145. — Sars, 1921, p. 67-68. — Schellenberg, 1921, p. 9 ; 1922, p. 280, 281-287 (part). — Hansen, 1923, p. 25. — Harant, 1931, p. 370. — Wilson, 1932, p. 392, 600, 602. — Neave, 1939, p. 460. — Lang, 1948, p. 8 (part). — Sewell, 1949, p. 145-146, 170. — Rose & Vaissière, 1953, p. 90. — Barnard, 1955, p. 240. — Gotto, 1960, p. 225. — Bresciani & Lützen, 1962, p. 374. — Dudley, 1966, p. 155, 157, 160. — Gotto, 1960a, p. 193. — Stock, 1970, p. 16-17.

Kossmechthrus Della Valle, 1883, p. 248-252 (types species by monotypy, *K. notopus* Della Valle, 1883). — Canu, *in* Giard, 1888, p. 505.

Kosemcthrus Canu, 1886a, p. 311 ; 1886b, p. 1025. — Neave, 1939, p. 835.

Blakeanus Wilson, 1921, p. 10-11 (type species, by original designation, *B. corniger* Wilson, 1921). — Hansen, 1923, p. 24-25. — Wilson, 1932, p. 391, 601. — Préfontaine, 1936, p. 76. — Neave, 1939, p. 436. — Sewell, 1949, p. 000.

non Ceratrichodes Hesse, Schellenberg, 1922 (synonym of *Botryllophilus*), p. 281, (cf. LANG, 1948,.p. 8)

Female :

The body in the adult is inflated, with varying degrees of expression of the ingredient segmentation. The cephalosome bears appendages through the maxillipeds and is usually well demarcated. The metasomal segments bear the 5 pairs of legs and exhibit the most inflation. There is basically a clear-cut articulation between the segment of the fifth legs and the first urosomal segment, which is demonstrated as being thoracic by the presence midventrally of a considerably developed apparatus surrounding the insemination pore and the lateral or dorsolateral apertures of the oviduct, usually also with auxilliary cuticular structures. Rarely the genital segment fuses with the forebody and there is no well-developed major body articulation. There seems to be a basic number of 4 true abdominal segments between the segment of the genital apertures and the well developed article bearing the caudal rami, here termed the anal somite and not considered as a true segment but some kind of complex including the telson. In many forms abdominal annulation involving distinct inflections of the cuticule present the aspect of a multisegmented urosome, up to 8 such elements being present among species examined. The evidence from internal anatomy, particularly with regard to the musculature, is so far lacking to make an exact interpretation of this phenomenon. The caudal ramus usually is set on a complication of the end of the anal somite. The ramus bears terminally 4 stout curved claw-like elements and 1 or more additional setae.

The rostrum may or may not be conspicuously developed but is typically present.

The antennule is typical for the whole genus, of few, usually 4, segments, the basal portion massive and the terminal much reduced in diameter. All segments bear setae. On the basal segment there is a row of protuberances furnishing support for the major setae and such protuberances also exist on the more distal segments.

The antenna varies from 2-segmented, to the appearance of having 3 segments, because of an articulating region between the basal and terminal segments. The ornamentation, restricted to the distal article, consists of marginal spines or seta, inserted at intervals, often in emarginations, and a terminal row of elements. No form has so far been found with less than 7 of such elements. Many of the species we have studied have exhibited an asymmetry in the appendages, this characterizing the antennae and the swimming legs 1 to 4. In the antennae the asymmetry is not marked. There may be subtle differences in the contour of the segments, particularly the distalmost. More apparent is a different degree of development of the elements of the armature of the distal segment. On one side the elements may tend more to a spiniform appearance, on the other they would then be more setiform. We do not know of a case of different numbers on the 2 sides. This asymmetry is not expressed in the other head appendages in the material we have observed.

The labrum is usually not distinctive. The mandible, maxillules, maxillae and maxillipeds are not usually specifically distinctive and in general conform to the characteristics described for the subfamily.

The first to fourth legs, the so-called swimming legs, are asymmetrical in most members carefully examined. However, the pattern of segmentation of the rami, ranging from 1- to 2-segmented, often is in a different pattern in the various members of the leg series. This variability can evidently be very great, even within a rather local population of a single species, as was demonstrated by Lang (1949), but unfortunately his statements and illustrations are not sufficiently detailed for a clear understanding of the situation without a re-examination of material from his sources. We agree with Stock (1970, p. 16) that the variability in these appendages is quite distinctly bound to certain limitations. We also reject the sweeping synonmyization of practically all previously described species that was applied by Lang on the basis of his observations on the asymmetry.

The fith legs are of uniform basic construction throughout the genus, with a degree of development of specifically distinctive patterns of proportion and ornamentation. They have so far been found to be symmetrical. There are some specifically distinctive patterns of posture and configuration, these extending to groups of species in some cases.

The genital segment of the female shows the insemination pore midventral, with diverging internal tubes leading laterally to seminal receptacles near the oviducal apertures. The latter bear a cuticular flap in each, with minor features of ornamentation. There are sometimes patterns of sclerotization in the cuticle of the flaps or in the area around the oviducal apertures.

Males :

The male has been known for a fairly long time, but there are some confusions involved in the identifications. The first decriptions and figures attributed to a male of the genus were those of Hesse (1866). Even so rigorous a critic as Schellenberg found Hesse's information recognizable and considered he accounted for the male of *Botryllophilus ruber*. Canu (1892, Pl. 20) figured a male he ascribed to *Aplostoma brevicauda*; this, as Schellenberg pointed out, is the male of a *Botryllophilus*. Furthermore, Canu presented a figure (1892, pl. 16) which he identified as a male of *B. macropus*. Bresciani & Lützen (1962, p. 374, fig. 2, j) show this to be a young female, and they chose to assign it to *B. ruber*. Scott (1901, p. 242, pl. XVII) presented a male identified as *B. ?ruber* and the observations were corroborated by Bresciani & Lützen (1962, p. 374-376, figs. 2, a-i) to the extent that one can at least accept Scott's generic designation. The dimorphism, as shown by this male, is very striking. Some statements of Stock (1970, p. 16-17) indicate there are still other patterns to be described for the males within the genus.

On the basis of the males so far described and what we have found the body is distinctly cyclopiform, with substantial modifications. The antennule emphasizes a sensory function, bearing a great number of aesthetascs arranged in a characteristic pattern. The mouthparts are modified, tending to great reduction, with the masticatory lamella of the mandible lacking and the maxillule and maxilla scarcely distinguishable as appendages. The first legs show a modification of the endopods, this tending to vary at the specific level. The first 4 legs otherwise seem adequately developed natatory appendages. A very significant point is that there seems to be a conservatism in the antenna and the number, at least of the elements of ornamentation, appears to show a close correspondence in the two sexes, although the shapes and proportions of the segments themselves may vary somewhat. The males we studied were not asymmetrical.

Because of the variations it is expected that discovery of males of additional species will bring forth it is not fruitful to proceed further to try to formulate a generalized example for the male of the genus.

SPECIES OF *BOTRYLLOPHILUS*

Unfortunately *Botryllophilus ruber* Hesse, the type species of the genus, has not been fully described or illustrated from unequivocally determined material. In his original description, Hesse presented figures, but of these only his Pl. 12, fig. 1 and 2, which approximately depict the general habitus of the female, may be said to convey any information. There are no precise facts on the anatomy of the appendages to be gained from his descriptions or from any of the figures he included. Canu pointed out that the fifth leg of Hesse's form was very long, and this can be inferred from the figure accompanying the original description.

T. Scott, 1901b, figures a copepod he called *Botryllophilus ruber* Hesse. Sars, 1921, p. 68, chose to differentiate the animal represented by Scott as differing from *B. ruber*, and referred to it as *B.* sp. Some features were well presented, including some of the appendages of the male. Lang, 1949, presented some figures he attributed to *B. ruber*, but since he synonymized practically all described species under the one name, it is difficult to use his presentation. Probably what he figures, as *B. ruber, sensu* Lang, was the animal described by Sars as *B. brevipes*, which very possibly differs from the true *B. ruber*, in the light of Stock's remarks (1970, see below). Lang's material was from the same region as Sars' and from Sars' typical host, *Botrylloides leachi*. Ambiguity is compounded by the fact that Hesse specified *Botryllus* sp. as the typical host of *B. ruber*. Many accounts subsequent to that of Hesse used the designation *B. ruber*, derived from a wide array of different hosts. To return to Lang's treatment, his figures are of little practical value, but his statements indeed bear out his claim that he found anatomical facts which essentially invalidated many previously presented morphological discriminations.

Bresciani & Lützen, 1962, fig. 2, figured a male and young female of *Botryllophilus ruber sensu* Lang, again from the Swedish West Coast, and the host *Botrylloides leachi*. They pointed out some minor disagreement with Scott's presentation of the male, and indicated they were accepting the conspecificity with their material. This then leaves open to question whether they actually were dealing with *B. ruber sensu* Hesse.

Stock, 1970, p. 15-16, stated he had access to topotypic material of *B. ruber*, and he compared various details with his descriptions of specimens from the West Indies. From his statements one can infer certain of the anatomical details characterizing *B. ruber sensu* Hesse, but not sufficiently to gain a thorough appreciation of the species. Dr. Stock informed us in correspondence, some time ago, that he is in process of revisionary studies on European species of *Botryllophilus*. Until topotypes of several species have been fully described and figured there remains a substantal sector in the genus which cannot be definitely treated.

Central to the problem of the disposition of the previously described species is the fact that the genus *Botryllophilus* is marked almost throughout, in the females, by a peculiar asymmetry of certain appendages. It is particularly striking in legs 1 to 4, so much so as to imply strongly some sort of differentiation of function. This condition is typically accompanied by an asymmetry in the antennae, much less striking, and not very obviously suggestive of a functional diversification.

In the legs the asymmetry is expressed at several levels. It may refer to all or only some pairs. It tends to involve both rami, but not necessarily. In the endopodites the expression tends to be in the degree of coalescence of the ingredient segments, and, somewhat less commonly, in the number of the ornamenting elements. The exopodites present a much more complex picture. The asymmetry may, rarely, be expressed only in the number of segments and ornamenting elements. More commonly the expodite is reduced to a single segment to begin with, and on this modification is superimposed a striking difference in configuration on the two sides, and, also very commonly, by a striking dimorphism of the corresponding ornamenting elements on the two sides. The most extremely modified exopodite is like nothing seen elsewhere in ascidicole copepods. In the genus *Schizoproctus* the phenomenon has not so far been noted, and it certainly is not present in *S. inflatus* nor, apparently, in Sars' *S.* (= *Pteropygus*) *vestitus*; this latter fact remains to be corroborated.

There is no evidence whether Hesse noted the phenomenon, although he described several species in his genus. Stock (1970, p. 21) refers to material in his possession he considers as topotypes of *B. ruber*, and points out the legs 1-4 are asymmetrical, the condition extending to differences in numbers of ornaments on most of the rami.

One of the most extended discussions of *B. ruber* is that of Lang (1949), in which among other things the problem of asymmetry was discussed and dismissed with the conclusion that essentially all forms described in the genus *Botryllophilus* were referrable to the single species, *B. ruber*. The material of Lang was from the Swedish west coast, from *Botrylloides leachi*. Since he compared his material to types of Sars' *B. brevipes* and found a good substantiation of the original description, the conspecificity seems established. It is not at all certain that these specimens refer to the *Botryllophilus ruber* of Hesse, contrary to Lang's conclusion. Lang found in most of his specimens and one of Sars' that the legs 1-4 are asymmetrical, but it is very likely that the condition he found is at a different level from what Stock referred to in his specimens. Sars depicted the appendages of his form as very simple with ornaments little modified, except perhaps as to length, and, indeed, in the direction of some general reduction. Lang considers the differences he found in most legs to amount to a very marked asymmetry. His drawings and indeed his discussion do not convey a great deal of information but would lead one to conclude that Lang did not really appreciate the nature of asymmetry as it is found in the majority of species. He found that sometimes a weak articulation conveyed a 2 articled aspect to a ramus, and he found some variability in the numbers of elements. Actually his material would seem to us to represent a species with a very low level of asymmetry. As he more or less directly pointed out himself, he was dealing with a rather exceptional order of individual variation. His conclusions therefore have little bearing on the problems of asymmetry in the majority of species. Doubtless his misunderstanding of this basic point was crucial to his completely unacceptable sweeping conclusion as to the conspecificity of all previously described material.

The literature on asymmetry is useful to some degree in providing a few clues with regard to older species. Hesse did not make any allusion and his figures and descriptions are too uninformative to allow any inference as to whether he was or was not aware of the phenomenon. Della Valle certainly was aware, and invoked the asymmetry of the legs in his description of *B. notopus*. Canu (1892) knew of the situation from Della Valle's paper and expressly stated that all of the legs of his *B. macropus* were symmetrical. Such authors as the Scotts and a fairly long list of others of the epoch did not seem to appreciate the phenomenon.

Brément (1909) invoked asymmetry and " resemblance " in his descriptions of *B. brevipes* and *B. banyulensis*, referring to differences in configuration in the successive pairs of limbs as well as to differing numbers of segments and ornaments. He understood the phenomenon very well and had a good grasp of the taxonomic problems in the genus.

Schellenberg (1922) considered the matter carefully and obviously noted aspects of the condition in his own material. He carefully described some details and made some speculations as to possible underlying influences. We are inclined to agree he was right in this regard to the extent that some features in the behavior of the animal in relation to its natural history as a symbiont may very well depend on the well developed morphological differentiation. Lang's airy dismissal of Schellenberg's careful observations and clearly tentative conclusions reflects only his own lack of precise information.

We are firmly of the opinion already stated by Stock, 1970, that Lang went much too far in synonymizing so many species in *B. ruber*. There are some morphological features of sufficient reliability to differentiate a considerable of the recorded forms. On the other hand, as we have found throughout the ascidicolids, but here even more pronouncedly, there are some consistent morphological plans of suspiciously wide geographic dispersion and diversity of hosts. Superimposed in *Botryllophilus* is a strong tendency to great individual variability of various characters, particularly those deriving from the thoracic appendages. It will be necessary to study in detail large suites of specimens and probably, also, to scrutinize closely, in selected strategic localities, the entire complement of species to place the genus in a sound taxonomic state. Our intensive studies were in a locality (San Juan Archipelago, Washington) fortunate for many features of occurrence of simple ascidians and a great variety of ascidicoles, but it is a less than ideal locality for botryllophilins because the fauna of compound ascidians is impoverished and in various regards somewhat anomalous. Further, the occurrence of several botryllophilins in hosts of decided immaturity leads us to suspect that for such species we have not yet located the most characteristic hosts. We have not been able to assign a satisfactory identification to the most common species available to us because it corresponds morphologically to the group of forms from the west coast of Europe centered around *B. ruber* Hesse and " *B. brevipes* " Sars. We await the resolution of this taxonomic problem before we feel we can present our anatomical findings and a description we have compiled of a suite of the developmental stages. The material from Europe at our disposal is insufficient for us to attempt the disposition of a majority of the species in the genus. We have some specimens which lead us to conclude a number of the species described have substantial validity. We list below the species so far described with our comments.

BOTRYLLOPHILUS RUBER Hesse, 1864

Botryllophilus ruber Hesse, 1864, p. 345-347, pl. 12, fig. 1-12 (type locality Rade de Brest, France, from *Bothyllus* (sic) *stellatus*). — Bate, 1864, p. 308. — Gerstaecker, 1870-1871, p. 719, 774. — Canu, 1892, p. 205, 207. — (?) Thompson & Scott, 1903, p. 255, 273. — Norman & Scott, 1906, p. 203. — Brément, 1909, p. LXXIV, LXXVII, LXVIII. — Hartmeyer, 1911, p. 1734. — Schellenberg, 1922, p. 283, 294. — Harant, 1931, p. 370. — Leigh-Sharpe, 1935, p. 48. — Lang, 1948, p. 3, 9, 10, 11-14, 15-16, ? figs. 1-6 (part). — Sewell, 1949, p. 145, 170, 177, 188. — Gotto, 1952, p. 674; 1954, p. 666; 1960, p. 216, 221; 1961, p. 153. — (?) Bresciani & Lützen, 1962, p. 374-376, text-fig. 2. — Gotto, 1966a, p. 193. — Stock, 1970, p. 21-22, 24. — Hamond, 1973, p. 350.

non B. ruber T. Scott, 1900, p. 388; 1901b, p. 242-245, pl. XVII, fig. 15-27 (= *B.* sp., Sars, 1921, p. 68).

This species requires extended redescription and illustration and estimation of the range of variation in the morphological characters and host incidence. STOCK (1970, p. 21-22) has provided a number of details from topotypes but a fuller treatment is needed. With this uncertain base of comparison it becomes difficult or impossible to allocate a substantial number of the subsequently described species.

BOTRYLLOPHILUS MACROPUS Canu, 1891

Botryllophilus macropus Canu, 1891a, p. 473 (type locality, Wimereux, France, from *Lithonephria eugyranda* Giard); 1892, p. 66, 67, 206-208, pl. 16, fig. 1, 3, 5-14). — Brément, 1909, p. LXVI, LXVII, LXVIII. — Chatton & Brément, 1915, p. 145. — Schellenberg, 1922, p. 283, 194. — Harant, 1931, p. 370. — Sewell, 1949, p. 145, 188. — Stock, 1970, p. 21, 24.

Botryllophilus ruber, Lang, 1948, p. 9, 10, 13, 14, 15 (part). — Bresciani & Lützen, 1962, p. 374 (part).

(?) *Botryllophilus canopus* Canu (*sic*), Hartmeyer, 1909-1911, p. 1734.

CANU characterized this species well and there is no difficulty in maintaining its status. It is interesting in departing from the asymmetrical pattern, and again, perhaps in correlation, for occurring in a species of solitary ascidian.

BOTRYLLOPHILUS BANYULENSIS Brément, 1909

Botryllophilus banyulensis Brément, 1909, p. LXXI-LXXVIII, fig. IX-XI (type locality, Port-Vendres, Golfe du Lion, France, from *Parascidium areolatum* della Chiaje). — Schellenberg, 1922, p. 282, 293. — Harant, 1931, p. 370. — Sewell, 1949, p. 183.

Botryllophilus ruber Lang, 1948, p. 9, 10, 14, 15 (part).

The description and figures by BRÉMENT are excellent ; it would appear to be a valid species.

BOTRYLLOPHILUS BREVIPES Brément, 1909

Botryllophilus brevipes Brément, 1909, p. LXX-LXXII, fig. VI-VIII (type locality, Port-Vendres, Golfe du Lion, France, from *Amaroucium lacteum* Drasche). — Hartmeyer, 1911, p. 1736. — Schellenberg, 1922, p. 282. — Harant, 1931, p. 370. — Sewell, 1949, p. 183.

Botryllophilus ruber, Lang, 1948, p. 9, 10, 14, 15 (part).

The description and figures by BRÉMENT are excellent ; we consider it a valid species.

BOTRYLLOPHILUS BERGENSIS Schellenberg, 1921

Botryllophilus bergensis Schellenberg, 1921, p. 9-11, fig. 8-9b (type locality Bergen, Norway, from *Leptoclinides faeröensis* (Bjerkan)) ; 1922, p. 282, 293.

Botryllophilus ruber, Lang, 1948, p. 9, 10, 14, 15 (part).

The asymmetrical thoracic appendages depicted by the author indicate some correspondence with statements of STOCK about *B. ruber.* Fuller description of both forms will be necessary to establish if this species can be maintained as a valid one.

BOTRYLLOPHILUS NORVEGICUS Schellenberg, 1921

Botryllophilus norvegicus Schellenberg, 1921, p. 6-9, figs. 5-7 (type locality, Trondhjemfjord, from *Pelonaia corrugata* Goodsir) ; 1922, p. 282, 294. — Harant, 1931, p. 370. — Lang, 1948, p. 9, 10, 13, 16. — Gotto, 1960, p. 225.

Blakeanus corniger Wilson, 1921, p. 11-13, pl. 5, fig. 39-43 (type locality, Long Island Sound, U.S.A., from *Cynthia carnea* Verrill). — Wilson, 1932, p. 391, fig. 240.

Blakeanus groenlondicus Hansen, 1923, p. 24-25, pl. II, fig. 8a-8d, pl. III, fig. 1a-1h (type locality, West Greenland, from *Cynthia rustica* L.). — Préfontaine, 1936, p. 76. — Sewell, 1949, p. 194. — Préfontaine & Brunel, 1962, p. 253.

This striking species is valid. We have a number of collections indicating it is rather widespread in northern waters. It is a very large form, perhaps to some degree in correlation with its occurrence in the branchial cavity of solitary ascidians. A degree of asymmetry is persistent, although not as extreme as in some of the small species.

BOTRYLLOPHILUS BREVIPES Sars, 1921

Botryllophilus brevipes Sars, 1921, p. 68-69, pl. 33 (type locality, Espevaer, Norway, from *Botryllus* sp.). — (?) Wilson, 1932, p. 392, fig. 241. — Sewell, 1949, p. 145, 157, 158, 192.

Botryllophilus ruber, Lang, 1948, p. 8, 9, 10, 11, 12, 13, 14, 15 (? fig. 1-6) (part). — Bresciani & Lützen, 1962, p. 374-376, fig. 2.

As was usual with SARS this form is very well illustrated and his presentation seems well substantiated by the subsequent reports of LANG and of BRESCIANI & LÜTZEN. LANG's synonymy of this form with *B. ruber* does not seem to us justifiable, but the question must remain open until *B. ruber* is better known. BRÉMENT's specific name has precedence over that of SARS. It seem to us unlikely that the species of the two workers are conspecific. It may well be that *B. bergensis* Schellenberg may turn out to be a synonym, in which case his name, as older, would take precedence.

BOTRYLLOPHILUS ASPINOSUS Schellenberg, 1922

Botryllophilus aspinosus Schellenberg, 1922, p. 282-284, 293, fig. 1-2 (type locality, Plymouth, from *Polycarpa pomaria* (Savigny) ; Angola, from *Styela hupferi* Michaelsen). — Harant, 1931, p. 370. — Sewell, 1949, p. 188. — Barnard, 1955, p. 240-241, fig. 7, 9.

Botryllophilus ruber, Lang, 1948, p. 9, 10, 14, 15 (part).

This appears to us to be a valid species, well characterized for the period at which it was described. Redescription on a more detailed basis is now necessary to allow for treatment of the genus.

BOTRYLLOPHILUS INAEQUIPES Hansen, 1923

Botryllophilus inaequipes Hansen, 1923, p. 25-26, pl. III, fig. 2a-2f (type locality, Davis Strait, West Greenland, bottom sample). — Sewell, 1949, p. 194.

Botryllophilus ruber, Lang, 1948, p. 9, 14, 15 (part).

This species is probably not *B. ruber* Hesse, so it becomes another possibility in the disposition of SARS' *B. brevipes.* A much more detailed description of the Greenland form and determination of its normal host will be required.

BOTRYLLOPHILUS RANDALLI Stock, 1970

Botryllophilus randalli Stock, 1970, p. 17-22, fig. 14-18 (type locality, Puerto Rico, from *Eudistoma olivaceum* (Van Name).

STOCK, well aware of the problems in the genus, referred to topotypic specimens of *B. ruber* in establishing the substantial differentiation of his valid species.

INDETERMINABLE SPECIES

The remaining species in the genus are indeterminable by us with present information. It is possible that full redescriptions of some of the species from remoter localities, such as those of SCHELLENBERG and SEWELL, will validate their species. DELLA VALLE's form possibly could be maintained with fuller information. The species described by HESSE seem to offer no possibility for constructive treatment except for *B. ruber.* The other names should be dealt with by the protocol for disposing of forgotten names (International Code of Zoological Nomenclature, 1961) and suppressed as far as future nomenclatural considerations are concerned.

BOTRYLLOPHILUS VIRESCENS Hesse, 1864

Botryllophilus virescens Hesse, 1864, p. 347-348 (type locality, côtes de France [rade de Brest], host not specified). — Bate, 1864, p. 308. — Gerstaecker, 1870-1871, p. 774. — Canu, 1892, p. 207. — Hartmeyer, 1911, p. 1734. — Sewell, 1949, p. 145.

Botryllophilus ruber, Lang, 1948, p. 9, 14, 15 (part).

?Botryllophilus vert, nobis, ? B. viridis, nobis, Hesse, 1865, p. 223-224 ; 1866, p. 79-80, pl. 4, fig. E, E1-E7. — *B. viridis* Gerstaecker, 1870-1871, p. 774. — Hartmeyer, 1911, p. 1734.

BOTRYLLOPHILUS PALLIDUS Hesse, 1865

Botryllophilus pallidus Hesse, 1865, p. 224-225 (type locality, Rade de Brest, France, in " *Botrylle* ", attached to *Fucus serratus*). — Gerstaecker, 1870-1871, p. 774. — Hartmeyer, 1911, p. 1734.

Botryllophilus ruber, Lang, 1948, p. 9, 14, 15 (part).

BOTRYLLOPHILUS ARMATUS Hesse, 1869

Botryllophilus armatus Hesse, 1869, p. 293-294 (type locality, " côtes de France ", in " *Botrylle* " on frond of *Fucus vesiculosus*). — Gerstaecker, 1870-1871, p. 774. — Hartmeyer, 1911, p. 1734.

BOTRYLLOPHILUS BREVIS Hesse, 1869

Botryllophilus brevis Hesse, 1869, p. 295 (type locality, from " *Botrylle* " on a *Pecten*). — Gerstaecker, 1870-1871, p. 774. — Hartmeyer, 1911, p. 1734.

BOTRYLLOPHILUS PURPURESCENS Hesse, 1869

Botryllophilus purpurescens Hesse, 1869, p. 294-295 (type locality, rade de Brest, France, from a " *Botrylle* ", on an annelid tube). — Gerstaecker, 1870-1871, p. 774. — Hartmeyer, 1911, p. 1734.

BOTRYLLOPHILUS PROPINQUUS Hesse, 1872

Botryllophilus propinquus Hesse, 1872, p. 25-27 (type locality, Rade de Brest, France, from compound tunicate attached to *Pecten maximus*). — Hartmeyer, 1911, p. 1736.

BOTRYLLOPHILUS NOTOPUS (Della Valle, 1883)

Kossmechthrus notopus Della Valle, 1883, p. 248-252, 253, fig. 11-23 (type locality, Naples, from *Distoma panceri* Della Valle).

Kossmechthrus notopus, Canu, 1886a, p. 311 ; 1886b, p. 1025.

Botryllophilus notopus, Canu, 1892, p. 207. — Brément, 1909, p. 74, 78. — Hartmeyer, 1911, p. 1735, 1736. — Schellenberg, 1922, p. 282, 294. — Harant, 1931, p. 370. — Sewell, 1949, p. 145, 183.

Botryllophilus ruber, Lang, 1949, p. 9, 10, 14, 15 (part).

BOTRYLLOPHILUS AFRICANUS Schellenberg, 1922

Botryllophilus africanus Schellenberg, 1922, p. 284-285, 293, fig. 3-4 (type locality, Angola, from *Macroclinum angolanum* Michaelsen). — Barnard, 1955, p. 240. — Stock, 1970, p. 21, 24.

Botryllophilus ruber, Lang, 1948, p. 9, 10, 14, 15 (part).

BOTRYLLOPHILUS INDICUS Sewell, 1949

Botryllophilus indicus Sewell, 1949, p. 146 (type locality, Nankauri Harbour, Nicobar Islands, weed washings). — Stock, 1970, p. 22, 24.

There seems a strong possibility that this species can be maintained, but a much more detailed description and clearer illustrations of the appendages are needed.

BOTRYLLOPHILUS sp. Brément, 1909

Botryllophilus sp. Brément, 1909, p. LXXVIII. — Schellenberg, 1922, p. 294. — Lang, 1948, p. 16.

BOTRYLLOPHILUS sp. Sars, 1921

Botryllophilus sp. Sars, 1921, p. 68 for.

Botryllophilus ruber, T. Scott, 1900, p. 388 (Loch Fyne, Scotland, from debris) ; 1901b, p. 242-245, 352, pl. XVIII, fig. 15-27. — Lang, 1948, p. 16 (part). — Sewell, 1949, p. 145.

BOTRYLLOPHILUS sp. Schellenberg, 1922

Botryllophilus sp. Schellenberg, 1922, p. 294 (from Plettenberg Bucht, S. Africa, from *Polycitor renieri* Hartmeyer). — Lang, 1948, p. 16.

BOTRYLLOPHILUS sp. Schellenberg, 1922

Botryllophilus macropus (" petits ") Canu, 1892, p. 206, pl. XVI, fig. 4, 5 (Boulonnais, English Channel, from *Polyclinum luteum* Giard).

Botryllophilus sp. Schellenberg, 1922, p. 294.

Botryllophilus ruber, Lang, 1948, p. 13, 15 (part). — Bresciani & Lützen, 1962, p. 374 (part).

BOTRYLLOPHILUS sp. Dudley, 1966

Botryllophilus sp. Dudley, 1966, p. 157, 160 (Friday Harbor, Washington, from *Aplidium* sp.).

BOTRYLLOPHILUS sp. Stock, 1970

Botryllophilus sp. Stock, 1970, p. 22-24, fig. 19-21 (from Puerto Rico, in *Didemnum* sp.).

SCHIZOPROCTUS Aurivillius, 1885

Schizoproctus Aurivillius, 1885a, p. 247-248 (type species, by monotypy, *S. inflatus* Aurivillius, 1885a) ; 1886, p. 44-46. — Sars, 1921, p. 71-72. — Hansen, 1923, p. 26. — Neave, 1940, p. 137. — Wilson, 1932, p. 600. — Lang, 1948, p. 8. — Gotto, 1960, p. 225. — MacGinitie, 1955, p. 114, 150. — MacGinitie & MacGinitie, 1968, p. 48.

Botryllophilus (part) Canu, 1892, p. 203. — Brément, 1909, p. 75, 76, 78. — Hartmeyer, 1911, p. 1734. — Schellenberg, 1922, p. 281. — Harant, 1931, p. 370.

Pteropygus Sars, 1921, p. 70 (type species, by monotypy, *P. vestitus* Sars, 1921). — Wilson, p. 600. — Neave, 1940, p. 1029. — Sewell, 1949, p. 191. — Gotto, 1960, p. 225.

Schizoproctus is a well established genus, readily recognizable since its establishment. It shows a high degree of correspondence to *Botryllophilus* and the differences between the 2 genera are those of degree rather than of kind. A number of perceptive workers did not hestiate to synonymize the 2 genera. Sars maintained the separation and went so far as to establish a new genus, *Pteropygus*, for a related form he found in Sweden. We feel that maintaining a third genus in this situation is not supportable. Further, adding *P. vestitus* Sars to *Schizoproctus* re-enforces the generic concept and also emphasizes the differentiation between the 2 sets of species. It is of interest that both the species we assign to *Schizoproctus* come from solitary ascidians, from northern localities, and do not show the asymmetry encountered in so many species of *Botryllophilus*. They are also among the giants of the ascidicole copepods. The species are readily differentiated, following characters presented by Sars.

KEY TO THE SPECIES

1. Urosome including 5 articles posterior to the genital complex........ *inflatus*, Aurivillius
1′. Urosome including 3 articles posterior to the genital complex................ *vestitus*, Sars

Schizoproctus inflatus Aurivillius, 1885

Schizoproctus inflatus Aurivillius, 1885a, p. 248-250, pl. 9, fig. 21-32 (type locality, Hackluyts Heade, Spitzbergen, from *Phallusia* sp.) ; 1886, p. 44-46, pl. 1, fig. 7. — Hartmeyer, 1911, p. 1735. — Sars, 1921, p. 72-73, pl. xxxiv. — Hansen, 1923, p. 26-27. — Stephensen, 1932, p. 3-4. — Lang, 1948, p. 8. — Sewell, 1949, p. 192, 193, 194. — Gotto, 1960, p. 225. — MacGinitie, 1955, p. 114, 150. — MacGinitie & MacGinitie, 1968, p. 450.

Botryllophilus inflatus, Canu, 1892, p. 207-208. — Brément, 1909, p. 75, 76, 78. — Schellenberg, 1922, p. 283, 293. — Harant, 1931, p. 370.

Doropygus gibber, Vanhöffen, 1897, p. 292.

Distribution : Arctic Ocean, Atlantic : Greenland, Norway.

Hosts : *Phallusia* sp., *Ascidia dijmphniana* (Traustedt), *A. obliqua* Alder, *Boltenia ovifera* (Linnaeus), *Molgula groenlandica.*

This species was described from the Arctic Ocean and subsequent records show it ranges fairly widely there. Sars' record added it to the fauna of Norway and we have other evidence of its occurrence in the northern Atlantic fauna.

Schizoproctus vestitus (Sars, 1921), New Combination

Pteropygus vestitus Sars, 1921, p. 70-71, pl. xxxiii (type locality, Risör, Norway, from *Phallusia obliqua*). — Sewell, 1949, p. 191. — Gotto, 1960, p. 225.

INDETERMINABLE GENUS, BOTRYLLOPHILINAE

PARABOTRYLLOPHILUS Leigh-Sharpe, 1934

Parabotryllophilus Leigh-Sharpe, 1934, p. 216 (type species, by monotypy, *P. arrisio* Leigh-Sharpe, 1934).

The animal as described cannot be assigned to the Botryllophilidae, although placed there by the author. We know of no other place in the classification to receive it. The description seems to us to be a chimaera of some sort; perhaps drawings of 2 organisms were somehow combined. We find the presentation insufficiently detailed to place the animal anywhere in the Ascidicolidae.

ENTEROGNATHINAE, New Subfamily

Ascidicolidae, Gieshrecht, 1901, p. 77 (part). — Calman, 1908, p. 172, 182 (part); 1909, p. 103 (part). — Stebbing, 1910, p. 550 (part). — Gravier, 1912b, p. 70 (part); 1913, p. 66 (part). — Chatton & Brément, 1915, p. 143 (part). — Brehm, 1927, p. 490 (part). — Stock, 1959, p. 74 (part); 1966, p. 211 (part).

Ascidicolinae, Schellenberg, 1922, p. 227-230 (part).

Enterocolinae, Chatton & Harant, 1924b, p. 361 (part).

Female :

The body is inflated and the shapes suggest those found among the haplostomins and enterocolins, with prominent pediform projections corresponding to the fifth legs and tending to enclose the anterior ends of the egg sacs. The segmentation of the body varies from very clear cut to much reduced, with only indications by distributions of the appendages and a number of vague cuticular inflections.

The antennules and antenna conform in a basic way to the ascidicolid generalized type but with the modifications deriving essentially from extreme reduction in segmentation and ornamentation. There is little or no representation of a rostrum. There is a mouth cone apparently representing the labrum and labium. Essentially there is a mandible with well-developed masticatory lamella (*Enterognathus*), this appendage possibly graduating to obsolescence or disappearance (*Zanclopus*).

The maxillule and maxilla vary from retrgressed but recoignizable ascidicolid derivation (*Enterognathus*) to a single pair, much reduced (*Zanclopus*). Maxillipeds are probably absent. The single pair of conspicuous mouthparts of *Zanclopus* are entirely problematical. There is no evidence for determining exactly their identity. They could as well represent maxillae or maxillipeds, but in any case are much modified by reduction.

The legs of pairs 1 to 4 are much modified, but show ascidicolid features. They are biramous but with much suppression of segmentation. Intercoxal plates are not developed. The usual lateral setae of the coxopodites are present (but not so in one of the species of *Zanclopus*, and in *Enterognathus* the medial spine of the first basipodite is present). The exopodites terminate in falciform hook-processes, not unlike some seen elsewhere among ascidicolids. The much modified endopodites, ornamented with processes which somehow probably represent some of the usual elements of armature, are distinctive, but not exceptional when considered in relation to the family as a whole.

The pediform processes involving the fifth legs are expanded curved lamellae such as are found in many ascidicolids. In the case of *Enterognathus* the ornamentation is unique, consisting of 4 well-formed setae. The insemination apparatus of the segment next posterior is comparable to that found throughout the ascidicolids.

The caudal rami are not greatly distinctive ; they are somewhat modified in having a reduced armature — but there are perhaps 4 elements represented in the complement of *Zanclopus cephalodisci.*

Male :

The males are rather generalized cyclopiform in appearance, but with specializations. As in many of the ascidicolids the antennules are more developed than in the females, with 6 to 8 segments present. There are fairly numerous setae, but no distinctive feature among them and no notably salient development of aesthetascs. In both *Enterognathus* and *Zanclopus* this appendage could be claimed as offering strong support for inclusion of the genera in the Ascidicolidae. The antenna is 3-segmented and suggests that of some of the more derivative ascidicolids, especially that of *Enterocola.* There is a well-developed seta on the basal segment in *Enterognathus,* also a feature of *Enterocola.* The second segment is unornamented. The third bears terminal elements, somewhat between spiniform and setiform. In *Zanclopus cephalodisci* there is an apical trio of distinctly curved strong setae. The presence of a curved or clawed element apically on the antenna is rare in ascidicolids and a very strong character in the Notodelphyidae. The persistence in *Enterocola* and *Enterognathus* could quite possibly be regarded as a conservative character.

The mouthparts are reduced to lacking, totally so in *Enterognathus.* There remains Calman's so far unverified representation of a pair of mandibles in *Zanclopus cephalodisci* and a pair of protuberances more or less in the position of the more posterior mouthparts. In any case the diagnostic fact for the males of the subfamily is a very great reduction of mouthparts, a feature widespread in the family.

Legs 1 to 4 are biramous with the rami trimerous. The ornamentation as depicted so far shows some slight variation from a typical cyclopoid pattern but there does not appear to be any diagnostic feature deriving from this which could be presented with any comfortable degree of reliability.

Fifth and sixth legs conform well enough to a general characterization for ascidicolids and do not offer distinctive features. The fifth legs are bimerous basically, each article set with at least one prominent seta. There are supplementary spiniform processes of the distal article in *Enterognathus,* these replacing setiform elements of earlier developmental stages. If indeed, 3 setae are represented this would be a rather primitive expression. The sixth legs of *Enterognathus* seem to have 3 setae, an exceptionally high number.

The caudal rami are again very generalized, with 6 elements of armature, 4 of these terminal, as in typically cyclopoid males.

Various observers pointed out strong similarities of *Enterognathus* with the Enterocolinae, but the conformity is contradicted by the presence of the substantial mandibular lamella and vestigial palp in *Enterognathus.* Enterocolinae lack the mandible. *Zanclopus* is in a more ambiguous position because the nature of the mouthparts is not apparent, but it should in any case accompany *Enterognathus* in the classification.

KEY TO GENERA (BASED ON FEMALES)

1\. Body with segmentation distinctly apparent ; mouthparts for the most part well-developed, with some apparent setiferous lobes.............................. *Enterognathus* Giesbrecht

1'. Body inflated, with segmentation not strongly demarcated ; mouthparts much reduced, no setiferous lobes apparent.. *Zanclopus* Calman

Enterognathus Giesbrecht, 1900

Enterognathus Giesbrecht, 1900, p. 61, 76-78 (type species, by monotypy, *E. comatulae* Giesbrecht, 1900). — Calman, 1908, p. 171, 182 ; 1909, p. 123. — Gravier, 1912b, p. 70 ; 1912c, p. 244, 245 ;

1913, p. 59, 70-74. — Farran, 1913, p. 19. — Chatton & Brément, 1915, p. 143, 145. — Schellenberg, 1922, p. 295. — Chatton & Harant, 1924b, p. 361. — Brehm, 1927. — Wilson, 1932, p. 596 — Neave, 1939, p. 241. — Grainger, 1950, p. 636. — Changeux & Delamare-Deboutteville, 1956, p. 106-107, 155. — Stock, 1959, p. 74 ; 1966, p. 211, 215-216.

The inflated body and the salient appendages of this form strongly evoke the concept of an ascidicolid. The reduction of the thoracic legs is very similar to the pattern in enterocolins. The antennule has few segments, but is setiferous. The antenna is trimerous and rather ascidicolid in one species, more reduced in the other. There are labrum, labium and paragnaths. The mandible is reduced but maintains a well-developed masticatory lamella. There is a reduction in the remaining mouthparts but the hindermost has a somewhat prehensile aspect, with an articulated terminal spiniform piece set on a massive basal segment. The 2 species so far known can be readily separated by a number of salient characters.

1\. Antenna 3-segmented ; pediform processes involving the fifth legs set with 4 setae on the distal margin .... *comatulae* Giesbrecht

1'. Antenna 2-segmented ; pediform processes involving the fifth legs set with 3 setae on the distal margin .... *lateripes* Stock

ENTEROGNATHUS COMATULAE Giesbrecht, 1900
(Figures 53, a-c)

Figured, but not described : McIntosh, 1866, p. 611, fig. 5 ; 1875, p. 140.

Enterognathus comatulae Giesbrecht, 1900, p. 62-73, pl. 5, fig. 1-33 (type locality, Gulf of Naples, Italy, from *Antedon rosaceus*). — Calman, 1908, p. 177. — Gravier, 1912b, p. 70 ; 1912c, p. 243 ; 1913, p. 70, 74. — Farran, 1913, p. 19. — Chatton & Brément, 1915 p. 145,. — Schellenberg, 1922, p. 295. — Grainger, 1950, p. 636. — Changeux & Delamare-Deboutteville, 1956, p. 155. — Stock, 1959, p. 74 ; 1966, p. 215, 216.

Distribution : Mediterranean, British Isles.

Hosts : *Antedon bifida* (Pennant), *A. rosacea* (Linck), *A. mediterranea* Lamarck.

We have reviewed specimens and the literature on the species of *Enterognathus*. The first described species, *E. comatulae* was so well illustrated by GIESBRECHT and some later workers that we are not presenting further figures. The appendages conform without difficulty to the range of variation found within the ascidicolids, but with indications of derivation from a very primitive condition for some of the characters. As is usual there is great dimorphism and the characters of the female are much more distinctive than those of the male, which is a very generalized gnathostome type. Both male and female lack the eye. The head is perhaps somewhat produced between the antennular bases, but there is not really a rostrum. The labrum is a prominence with a posteriorly directed rounded lobe, but without ornamentation. There is a labium-like structure, called by GIESBRECHT the lower lip, and on the sides, at the bases of the mandibles are prominent paragnaths. These latter are well known in the notodelphyids ; we have now seen a very similar type in an archintodelphyid species ; and above we have recorded the presence of paragnaths in *Ascidicola rosea*. They seem to be lacking in most of the ascidicolid subfamilies, although it is difficult to determine just how they might be represented in the very modified and complex mouth apparatus of most forms. In possession of the paragnaths and some other features we would say the mouth region of *Enterognathus* shows some generalized characters, these tending, however, to modification in the direction of regression.

In the female the antennules are very reduced, but without other specialization, and give little

Fig. 53. — *Enterognathus comatulae* Giesbrecht, nauplius (a-c) ; *Zanclopus cephalodisci* Calman, female (d-o) ; male (p-r) : a, antennule ; b, antenna ; c, mandible ; d, habitus, dorsal ; e, urosome ; f, head, *en face*, showing cephalic structures and appendages ; g, head, *en face*, another specimen ; h, antennule ; i, antenna ; j, antenna of opposite side ; k, first leg ; l, second leg ; m, third leg ; n, fourth leg ; o, urosome and pediform projection ; p, antennule ; q, antenna ; r, head and mouth area *en face*.

information as to the systematic position. They could well be referred to an early copepodid stage of various of the ascidicoles we have studied. The antennae are also much simplified but could also be derivable from a generalized developmental form. They are much like those seen in the male of *Enterocola* species. The mandibles furnish the strongest grounds for our disposition of the genus in the Ascidicolidae. The strong coxa with very effective masticatory lamella is of basic gnathostome type. Paradoxically, the palp is reduced to a minuscule projection, probably incorporating a single reduced seta. This aspect might readily be derived from a stage like that seen in *Ascidicola*, and is close to the condition of *Buprorus*. The position of the latter in our scheme is somewhat ambiguous, but basing our argument on the condition of the mandible, we might argue that both the *Buprorus* line and the *Enterognathus* line represent very early derivative offshoots of a basic ascidicolid stock, the daughter series taking rather independent evolutionary pathways of morphological adaptation. The maxillule is bilobed, as in some ascidicolids, with a medial portion, probably the endite, bearing a few setae, and with the palp reduced to an unsegmented setiferous knob. The bimerous maxilla is much specialized, and certainly reduced, but retains a strong indication of a very basic structural pattern among the ascidicoles. The massive basal segment bears a single setiferous process which corresponds well to one of the endites of a more developed maxilla. The terminal piece doubtless represents a coalescence of distal elements and retains the strong medially directed claw process of the primitive third segment (as in *Notodelphyopsis*) or the usual second segment of somewhat modified forms (*Notodelphys*, many other notodelphyids. The condition is strikingly similar to that in *Ascidicola*. The lack of the maxilliped is a character of two other ascidicolid subfamilies, the Enterocolinae and the Enteropsinae. In both of these, however, the mandible is also lacking in the adult. The observation of Stock, 1966, p. 215, fig. 1, h) that the pair of appendages we are calling maxillae are united by a connecting lamella in his species *E. lateripes*, injects a somewhat perplexing note in attemps to identify the mouthparts. From all past experiences with copepod anatomy, as Stock points out, a pair of mouthparts so constructed should be the maxillipeds. We lack the information from development necessary to decide the exact position, and therefore, the identity of these appendages in the mouthpart series. Stock elected to leave the resolution for future investigation and called the appendage the posterior mouthpart. In the subfamilies which lack the maxilliped, the maxilla is built with very convincing resemblance to this mouthpart of *Enterognathus*. Maxillipeds of somewhat similar aspect occur in the Haplostominae and Botryllophilinae, but the resemblance would be rather far-fetched. We continue the tradition of the older observers but acknowledge the weight of Stock's observation. As to the utility of the appendage as a taxonomic character we would say it serves very well in either case to place *Enterognathus* in the ascidicolid series. The potential for modification of either the maxilla or the maxilliped to evolve into such a structure seems to us well demonstrated by the anatomies now known. The thoracic legs show many elements seen among ascidicolids, but the exact pattern is unique. The remarkable exopodites have a striking resemblance to those of *Stylicola lighti*, this aspect enhanced by the similar development of a very large seta adjacent on the lateral margin of the basipodite. The ramus of *S. lighti* has a much more complex articulation and doubtless functions in a very different manner. The endopodites suggest very much the condition found in some enterocolins. The so-called fifth leg probably incorporates a portion of the body proper as is the case in the enterocolins. There is no other instance of similar ornamentation among the other ascidicolids. However, the evidence from development of the male, as presented by Giesbrecht, would seem to indicate that early stages show a fifth leg very comparable to that seen in other ascidicoles ; in the female, however, the arrangement is unique from an early stage. There is no appearance of a basal seta, so usual among the ascidicoles, and occurring here in the male, and the free element is ornamented with 4 setae, an unusual, and probably very primitive feature. The insemination pore, canals and associated apparatus of the female are very much as in the majority of the ascidicolids. The habitus and the appendages of the male which are present correspond very well to the structural characteristics of generalized ascidicolids without any difficulty. There are no mouthparts. The plans of the fifth and sixth legs conform very well to those of a number of ascidicolids.

It would be very useful to have a full account of the development of this form. At Naples, Dudley was able to make some observations on nauplii and obtained some copepodids, but there was insufficient material for a thorough study. GIESBRECHT presented some information from late copepodids. Our nauplius showed many primitive characteristics, and as in most ascidicoles the development was lecithotrophic. In the first nauplius the larva was of good size (0.264 mm in length) and the features of the appendages were very suggestive of those of a primitive notodelphyid, such as *Notodelphys.* The general impression would be of a somewhat more generalized nauplius than has so far been seen in ascidicolids. However, such observations as we have indicate a very fast passage through the naupliar sequence, and very probably an abbreviated number of naupliar stages, perhaps about 4. The nauplius contains a substantial amount of yellow pigment, some of it associated with the yolk, and lacks an eye. The uniramous antennule (fig. 53, a), very much like that of *Notodelphys*, is trimerous, uniramous. The basal article lacks armature, but there is a short ventral row of fine spinules on the distal margin. The second article has a distal ventral plumose seta of moderate length, two small thorn-like spines inserted on the ventral margin at about equal intervals, and 3 short rows of fine spinules on the surface. The distal article is the longest, substantially longer than wide. It bears 2 apical setae, very unequal in length. The major seta, about 3 times as long as the other, bears a short projection near its base, which probably is an aesthete. Both setae are plumose.

The antenna (fig. 53, b) is biramous, with the segmentation obscure. The protopodite is possibly bimerous, with an articulating hasal element, which however may only represent a protrusion of tbe surface of the head. The major article of the protopodite is J-shaped, so that although the unimerous endopodite forms a sharp articulation, the positions of the setae indicate that the hasal article of the exopodite is directly continuous with the longer arm of the protopodite. There are ornamenting rows of spinules and 2 short thorn-like spines equispaced on the medial margin. The somewhat ovoid endopodite bears a short seta at about midway on the medial margin and 2 subequal long plumose setae at the apex, which is constricted to a rounded contour. There are 3 clearly set off exopodite articles, each bearing a long plumose seta at the mediodistal corner, as does also the fused basal article. The distal article bears 3 setae, a proximal medial one very slender and rather short, and a long terminal seta accompanied by a much shorter rather stout lateral seta. All these setae are plumose.

The mandible (fig. 53, c) has somewhat the appearance of the antenna, with J-shaped protopodite, this also with a possibly basal article. The distal article of the protopodite bears 2 short thorn-like setules equispaced on the medial margin, with a short row of spinules at the base of the distal one. The endopodite is bimerous, the distal article much the longer, although the width is uniform throughout the ramus. On the basal article there is a short spine at about midway on the medial margin. There is a short row of fine spines on the surface just distal to this. The distal article bears a short setule, without ornament, on the medial margin well distal to the midpoint, and 2 subequal apical plumose long setae. The exopodite is probably tetramous, as indicated by the setation, but there is no articulation between the basal portion and the exopodite. At the distal medial corner of the basal article portion there is a long plumose seta, corresponding to 3 more equivalent setae, progressively slightly shortened, each inserted distomedially on its article. Accompanying the seta of the terminal article there is a very short acute apical setule.

Reference to our studies of *Enterocola* and *Enteropsis* have demonstrated many points of similarity with the nauplius of *Enterognathus* and with very few substantial differences, if any.

ENTEROGNATHUS LATERIPES Stock, 1966

Enterognathus lateripes Stock, 1966, p. 211-216, fig. 1-2 (from Eilat, Gulf of Aqaba, Red Sea, from *Heterometra savignyi* (J. Müller) ; *Oligometra serripinna* (P. H. Carpenter) ; *Decametra chedwicki* A. H. Clark.

Distribution : Red Sea.

Hosts : *Heterometra savignyi* (J. H. Müller), *Oligometra serripinna* (P. H. Carpenter), *Decametra chedwicki* A. H. Clark.

ZANCLOPUS Calman, 1908

Zanclopus Calman, 1908, p. 178, 182 (types species, by monotypy, *Z. cephalodisci* Calman, 1908). — Stebbing, 1910, p. 550. — Gravier, 1912a, p. 1440 ; 1912b, p. 243 ; 1913, p. 68, 69, 73. — Chatton & Brément, 1915, p. 143, 145. — Schellenberg, 1922, p. 295. — Chatton & Harant, 1924b, p. 361. — Brehm, 1927, p. 490. — Wilson, 1932, p. 601. — Neave, 1940, p. 691. — Barnard, 1955, p. 237, 242.

Zanelopus (lapsus) Gravier, 1913, p. 74.

This interesting copepod, an internal parasite of *Cephalodiscus*, was assigned by the author to the Ascidicolidae and he emphasized the resemblance to *Enterognathus*. The genus is readily differentiated because of the great reduction of mouthparts, none of them being positively identifiable. CALMAN claimed to find a rudimentary mandible terminating in a scythe-shaped blade. The general aspect of the animal and the thoracic appendages are more or less ascidicolid. We will discuss more in detail below the observations we have been able to make on CALMAN's types.

The 2 species so far described are similar to each other, confirming the generic diagnosis of CALMAN. They are readily separated, as GRAVIER, the describer of the second species points out, by substantial differences in the oral appendages and slighter differences in the ornamentation of the thoracic legs. GRAVIER did not find identifiable mandibles in his species. The position of the genus therefore becomes ambiguous. Collection of fresh material and more detailed dissection and examination of the appendages will be necessary before the genus can be firmly assigned as to taxonomic position.

ZANCLOPUS CEPHALODISCI Calman, 1908
(Figures 53, d-r)

Zanclopus cephalodisci Calman, 1908, p. 178-182, pls. 18, 19 (type locality, Agulhas Bank, off Cape of Good Hope South Africa, from *Cephalodiscus gilchristi* Ridewood). — Stebbing, 1910, p. 550. — Gravier, 1912b, p. 70 ; 1912c, p. 243-245 ; Gravier, 1913, p. 72-74. — Schellenberg, 1922, p. 295. — Barnard, 1955, p. 242, figs. 7d, 7e.

Distribution : Off Cape of Good Hope, S. Africa.

Host : *Cephalodiscus gilchristi* Ridewood.

This interesting copepod was fairly well described as to superficial characteristics by the author. We have made some observations on his material now deposited in the British Museum (Natural History). Unfortunately, the state of preservation does not allow exact determination of a number of details, particularly of the appendages.

There are some females preserved entire. In these the body is seen to conform well enough to CALMAN's presentation (fig. 53, d : female, dorsal view ; fig. 53, e : urosome). We are able to present some information about the head appendages (fig. 53, f : female, apex of head and mouth area, ventral ; 53, g : another specimen, similar). The dissected material includes antennules (fig. 53, h) and antennae (figs. 53, i, j). We corroborate these are extremely reduced, and by this fact indicate the affinity, but hardly offer substantial evidence for the position of the animal in the general scheme. CALMAN reported he made out in satisfactory fashion a rudimentary mandible. His statements and figures only indicate the position and some rather general outlines. The state of the material did not offer our examination further details ; in fact we cannot actually confirm the existence of the mandible. We find (figs. 53, f, g) the presence of only a single pair or mouthparts, these situated well posterior to the well-developed oral cone.Without anatomical details or observations on development it is impossible to fix an exact identification on these appendages.

The thoracic legs (figs. 52, k-n, first to fourth legs), in our examination, confirmed Calman's presentation. As he suggested they most closely approach those of *Enterognathus*, with indeed quite remarkable conformity. We present in our figures what we could make out in additional details of apparent articulations and the insertions of setae and spines. In the figures of the endopodites some of our lines would seem to indicate that the spine-like ornaments are articulated on their articles; such is not the case, all are in direct continuation with the supporting element.

On a rather crumpled preparation of the urosome (fig. 52, 0) we confirmed that the so-called fifth leg is as was described, and that it bears 2 well-developed but small setae on the margin. The caudal ramus bears an apical assemblage of 4 somewhat differentiated elements.

On the preparations of the males we could confirm some of Calman's presentations in general. The antennule (fig. 53, p) offers no problem in placement in the ascidicolid series. The antenna (fig. 53, q) is also a reasonable example of an ascidicolid general type, with an interstingly differentiated set of apical elements. In the mouth area (fig. 53, r) we could not confirm the claim of presence of mandibles, indeed are not certain there is any definitely developed oral appendage. The labrum and labium form a strong oral cone. It must be said that the material is in very poor condition and our observations are in no way conclusive. We could not find preparations to make observations on the thoracic appendages and urosome of the male, but see no reason at all to contest Calman's quite reasonable presentation. The legs do not offer strong evidence for the position of the genus, but there is no apparent fact contradictory to Calman's conclusion.

Zanclopus antarcticus Gravier, 1912

Zanclopus antarcticus Gravier, 1912a, p. 1440 (type locality, Ile Jenny, [Marguerite Bay], latitude 68° S., Longitude [Paris] 70.20° W., from *Cephalodiscus anderssoni* Gravier, 1912); 1912c, p. 240-245, fig. 1-4; 1913, p. 68-74, fig. 53-62. — Schellenberg, 1922, p. 295.

Distribution : Antarctic.

Host : *Cephalodiscus anderssoni* Gravier.

In his description Gravier characterizes this form very well and corroborates Calman's diagnosis of the genus as far as the generalities of body outline and form of thoracic legs are concerned; his idea of the presence of mouthparts and the possible identities substantially differs. The resolution of the situation is not possible with present information.

The addition of Gravier's species adds a certain confirmation to the long-standing assignment of the genus to the Ascidicolidae. From information now available it does not belong to any of the ascidicolid subfamilies previously proposed and its position remains, as originally suggested in close relation to *Enterognathus*. We tentatively assign it to the subfamily of the latter, a solution which at least has the merit of finding a place in the overall copepod scheme for this interesting animal. We maintain the serious reservation that future thorough investigation may well challenge this disposition. We agree with the assertion of Gravier that the many parallels with the annelidicole poecilostome genera leave the question a very open one. However, finally, there remains the very firm suggestion toward ascidicolid affinity provided by the antennule of the male of *Zanclopus cephalodisci*.

III. — DEVELOPMENT

In his revisionary treatment of the former Notodelphyoida, Lang (1948) suggested that the Enterocolidae and its relatives should be incorporated into the Cyclopoida Poecilostoma. Among his substantiating evidence, he presented a comparison of the biology and development of *Mychophilus roseus*, first nauplius stage, *Notodelphys agilis* and *Ascidicola rosea*. He stated " the first nauplius stage in *Mychophilus* differs in one or two respects from the corresponding stage in *Notodelphys* and *Ascidicola* and seems to show greater similarity to the first nauplius stage of the poecilostomes. It cannot, however, be determined with certainty how this likeness is, as the first nauplius stage of the poecilostomes is only known in a few forms and as the figures relating to this stage given by various zoologists differ from each other in more than one respect ". We thoroughly agree that the study of the poecilostomes is incomplete. Some original observations made by us (Dudley, Ph. D. thesis, 1957; 1966, p. 155-156) show immediately that important differences exist among poecilostomes, as well as among gnathostomes, because of a differentiation in either series of planktotrophic and lecithotrophic developmental forms. Since all ascidicolous copepods known in development so far are lecithotrophic it is important to compare these with lecithotrophic poecilostomes. Such forms are rare, and we have been able to study only one. The literature has furnished only preliminary information on such forms. At this point, therefore, the position of the lecithotrophic poecilostomes is uncertain, on developmental evidence. Further, there is no appendage in the oral apparatus of the adult poecilostomes which actually corresponds structurally to the appendages of the ascidicolids. The mere lack of an appendage in either series is not a positive relating character. Furthermore, the lack of the prehensile modification of the antennule in ascidicolid males is equally uniformative (cf. Dudley, 1966, p. 156-157). The fact that the nauplii of the ascidicolids (all lecithotrophic) have certain definite similarities with poeciolostome lecithotrophic nauplii is principally a result of parallel adaptations in this pattern of development.

All lecithotrophic cyclopoid nauplii that have been reported or that we have studied have definite characteristics in common : The development is consistently extremely rapid, ranging from 1 1/2 days for completion of the entire naupliar sequence (*Enteropsis capitulatus*) to 6 days (*Pseudomyicola* sp.). All such nauplii are distinctive for the very thin cuticle which shows little or no external evidence of internally developing postmandibular appendages during the later naupliar stages. There are actually postmandibular rudiments present from the first naupliar stage, and by late stages the appendages through the third legs are very definitely differentiated, but the external expression is in simple fold-like protrusions of the exuviae, indicative only of the margins of the appendages. The basic naupliar appendages (antennule, antenna, mandible) have a particularly simple pattern of structure, notably expressed in the lack of feeding modifications or accessory structures. Probably the function of these appendages combines sensory and locomotor considerations. In the notodelphyids the gut, although fully developed, is not patent, nor in direct communication with the stomodaeum or proctodaeum, and we assume from external observations that this feature is consistent throughout the lecithotrophic nauplii of the ascidicolids.

Further studies of the diversity of naupliar characters in the ascidicolids as we presented them above, show a sofficient range of variability that generalizations about the nauplii of the ascidicole series (notodelphyids plus ascidicolids) will doubtless come to show extensive overlap with a similar generalization for the lecithotrophic poecilostomes when they come to be equivalently analyzed. In our comparison below of the descriptive features of the appendages of the first nauplius of ascidicolids our inclusion of notodelphyids and the poecilostome *Pseudomyicola* sp. will demonstrate such an overlap.

So far there exist reports on accurate determinations of the numbers of naupliar stages only for the genus *Ascidicola* (4 stages, Gotto, 1957), various genera of Notodelphyidae (5, rarely 4, Dudley, 1966), and for a few lecithotrophic poecilostome forms, namely *Mytilicola* (2, Pesta, 1907 ; Caspers, 1939) and the genera *Sabellacheres* (4) and *Gastrodelphys* (2) in the Gastrodelphyidae (Dudley, 1964). Excellent partial accounts of life histories have been recorded, including details of one or more naupliar stages, as in the monograph of Canu (1892). Our findings are also fragmentary, but with the existing background we have indications of the major features. There seems to be a strong tendency to persistence of a sequence of naupliar stages. For many cases, 4 or more definite naupliar stadia have been determined.

Naupliar appendages of *Botryllophilus* sp., " *Aplostoma* ", *Notodelphys* sp., *Pseudomyicola* sp. (Dudley, 1966) and *Ascidicola, Enterocola, Enteropsis,* above : The antennule is 3-segmented in the first nauplius throughout the series of lecithotrophically developing cyclopoids. The basal 2 segments approximately equal the length of the terminal. The basal article is unarmed. The second article bears 3 setae in *Notodelphys* and *Pseudomyicola,* 3 setules in *Ascidicola,* 2 setae in " *Aplostoma* ", 1 seta and 2 setules in *Enteropsis,* 1 seta and 1 setule in *Enterocola* and 1 seta only in *Botryllophilus.* The terminal article bears 1 long and 1 shorter seta in all forms and an aesthete in all except " Aplostoma ", *Ascidicola, Enterocola,* and *Pseudomyicola.*

The antenna is composed of a bimerous protopodite without any gnathal modifications, throughout and the segmentation of the rami varies. The exopodite is tetramerous (some *Enterocola, Botyllophilus* " *Aplostoma* ", *Pseudomyicola*), or obscurely tetramerous, that is, with the basal article completely fused with an extension of the basipodite (*Notodelphys, Enteropsis, Ascidicola, Enterocola*). The endopodite is unimerous.

The coxopodite is unarmed throughout. The basipodite has 1 medial setule in *Notodelphys* and *Ascidicola* and 2 medial setules in *Pseudomyicola.* In the others it is unarmed. Each of the 3 basal articles of the exopodite bears 1 long medial seta in all cases. The terminal article of the exopodite bears 2 short setae or setules and 1 long seta in *Notodelphys, Enterocola,* " *Aplostoma* ", *Botryllophilus* and *Pseudomyicola.* There is only 1 short seta or setule and 1 long seta in *Enteropsis* and *Ascidicola.* The endopodite bears 1 medial setule and 2 terminal setae in all. In *Pseudomyicola* the medial seta and 1 terminal seta are stiffened and are margined by a hyaline flange.

The mandible is composed of a bimerous protopodite, without gnathal modifications, tetramerous exopodite and bimerous endopodite in *Notodelphys, Enterocola,* " *Aplostoma* ", *Botryllophilus, Ascidicola,* and *Pseudomyicola.* In *Enteropsis* the exopodite is unsegmented and fused with the basipodite.

The coxopodite bears a medial spine-like element in *Ascidicola* and is unarmed in all others. The basipodite in *Notodelphys* bears 1 setule and 1 minute pointed process. In *Enterocola* there is 1 medial unarticulated pointed process. In *Pseudomyicola* there is 1 setule and 1 spine. In all the others the basipodite is unarmed. The exopodite bears 4 long setae and 1 short terminal seta in *Notodelphys* ; 4 long seta and 1 unarticulated spiniform process in *Enterocola.* In all the others this ramus bears only 4 long setae. The basal article of the endopodite bears 1 medial setule in all except *Pseudomyicola,* in which the article is unarmed. The second article bears 2 setules and 1 seta in *Notodelphys* ; 1 setule and 2 setae in *Enteropsis, Enterocola,* and *Botryllophilus* ; 1 seta and 2 flanged spines in *Pseudomyicola* ; 2 setae in " *Aplostoma* ". In *Notodelphys,* and all other notodelphyids, the mandibular endopodite has a very characteristic form ; the endopodite is only as long as the basal article of the exopodite and the setae are very reduced. In all the others the endopodite is much longer, reaching to the second or even to the end of the third article of the exopodite and the terminal setae are as long as those of the exopodite.

Lang's (1948) presentation for the first nauplius of *Mychophilus* is in essential agreement in terms of the basic pattern of segmentation.

Although, as demonstrated by Dudley (1966) there is a very reliable salient characteristic for recognition of notodelphyid nauplii, namely a distinctive outline of the endopodite of the mandible, there is no equally reliable differentiating character for the first nauplii of the ascidicolids, nor can they be easily separated from the poecilostome series. However, it can be shown by use of the characters of the early copepodids that the ascidicolid group is cohesive and shows a greater affinity with the notodelphyids than with any poecilostome genus.

In the poecilostomes (*Mytilacola*, Pesta, 1907; Caspers, 1939; *Sabellacheres*, Dudley, 1964; *Pseudomyicola* sp., Dudley, 1966) the identifying cephalic mouthparts appear at the first copepodid stage and immediately establish the divergence from all the gnathostomes. It is interesting to note in *Sabellacheres* there is a vestige of the antennal exopodite in the first copepodid, which is lost in the next molt. This feature is also characteristic of all notodelphyids and ascidicolids for which we have information, and also occurs in *Cyclops* (*s. lat.*) and in *Oithona*, so might be regarded as a generalized cyclopoid characteristic, although it definitely does not occur in some poecilostomes. The mandible undergoes metamorphosis during the last naupliar stage in typical peocilostomes and is lost entirely in the last naupliar molt in *Mytilicola*.

The resulting condition of the appendage, in any case, is similar to that in the adult. In the notodelphyids and ascidicolids, the mandible of the first copepodid is characteristic for each particular genus, and represents a transformation from the naupliar appendage, but always undergoes subsequent modification through ensuing copepodid stages to attain the adult characteristics. This modification may indeed be as extreme as the complete loss of the mandible at the third copepodid stage in *Enteropsis* and *Enterocola*. Other characteristic modifications of the mandible and of the legs tend also to appear at the third copepodid, a feature of the whole assemblage, representing a second major metamorphosis, related to the event of infection of the host. This is a different pattern from the sequence of poecilostome development at all stages.

Tracing further development of lecithotrophic poecilostomes shows distinct differences emerging from the pattern of development in ascidicolids, particularly with the appearance at the first copepodid of the identifying mouthparts. *Pseudomyicola* does not possess any evidence of an antennal exopodite at the first copepodid stage) we know some poecilostomes do (*Sabellacheres*, Dudley, 1964). *Mytilicola* goes further than *Pseudomyicola* in reductions before the molt to the first copepodid stage, since in this molt it loses the mandible. *Mytilicola* and *Pseudomyicola* also show similarities in not further modifying the appendages of the cephalosome appeciably after the first copepodid except for the differentiation of the dimorphic maxilliped in the late male stages. Ascidicolids, then, show trends of reduction that are distinctly different from those in *Mytilicola* and *Pseudomyicola*, representing the poecilostomes.

Such nauplii demonstrate there is never any sign of a maxilliped in the species of *Enterocola* shown by Canu and us, and in the *Enteropsis* species studied. The mandible can be traced into the first copepodid stage and it can be shown that this appendage disappears during copepodid molts in *Enteropsis* and *Enterocola*. The exopodite of the antenna is similarly lost during the first copepodid stage in all notodelphyids and ascidicolids we have studied. Exactly this also happens in *Cyclops* (Dietrich, 1915) this feature thus serving to tie all the gnathostomes together. Further strong evidence for relating the ascidicolids and the notodelphyids would come from the following : In *Notodelphys*, *Ascidicola*, *Enterocola*, *Botryllophilus*, *Enteropsis*, and " *Aplostoma* " (Canu) the naupliar appendages are strikingly similar. The antennule has 3 segments ; the antenna has a protopodite of 2 segments, a basically tetramerous exopodite and a unimerous endopodite ; the mandible is biramous with bimerous protopodite, basically tetramerous exopodite and bimerous endopodite. Lang's presentations concerning the nauplii of *Mychophilus* incline us to believe these are in essential agreement. The patterns of setation throughout, while showing some minor differences are sufficiently consistent as to offer to us reinforcement of this agreement.

Although the above references furnish some indications of the structure of nauplii and late copepodids of some of the species in the Ascidicolidae, the only early substantial published study of development is that of Canu (1892). He furnished basic and significant information on the life histories of *Enterocola fulgens* and " *Aplostoma* " *brevicauda*. The literature has furnished some descriptions of males based on subadult stages, and these refer in part then to life history features. We refer to such information under the individual general above.

In collections from the host ascidians and from cultures from developing egg masses we have been able to obtain the first nauplius and the first three copepodid stages of *Ascidicola rosea* ; the first nauplius and first 2 copepodids of *Enterocola fertilis* ; the first nauplius and a fourth copepodid of *Enterocola laticeps* ; the first nauplius and first 2 copepodids of *Enteropsis capitulatus* ; and the fourth and fifth copepodids of *Enteropsis superbus*. Although we have not observed a complete life history, the descriptions below show great basic conformities and give additional evidence for our concept of the family Ascidicolidae.

Development of *Ascidicola rosea*
(Figures 54, 55)

The nauplius is a lecithotrophic larva and has the basic characteristics of cyclopoids of non-feeding type. The antennule (fig. 54, a) is uniramous and functionally trimerous. The basal article lacks armature and ornamentation ; it may be only a mechanically differentiated element. The second article bears a seta, which is about 1/3 the length of the article, on the ventral face, at the distal margin. Proximal to this, on the ventral margin, there are 2 shorter, equispaced setae on projections of the margin. Three rows of spinules ornament the medial surface. The terminal article is somewhat longer than the second and tapers slightly. On the apical margin there is a long, ventral seta and somewhat removed from this there is a dorsal seta which is about 1/3 as long. There is no aesthete.

The antenna (fig. 54, b) is biramous, the protopodite bimerous, the endopodite unimerous, and the exopodite tetramerous, but not articulated on the protopodite. The basal article of the protopodite lacks armature and ornamentation. The distal article has a small marginal setule near the articulation with the endopodite. The endopodite, which reaches only slightly beyond the distal end of the basal article of the exopodite, bears 1 setule in an emargination at the middle of the medial margin, and 2 long terminal setae. The basal article of the exopodite shows no clear articulation with the protopodite but probably is represented by an extension of the latter terminating in a long, articulated medial seta. This extension is longer than the 3 terminal articles of the exopodite. The second and third articles of the exopodite are wider than long and each bears a long seta at the distal medial corner. The terminal article is rounded, with an emargination on its medial face ; a short seta is inserted in this. Apically there is a long seta. Rows of spinules are found on the articles of the ramus.

The mandible (fig. 54, c) is biramous, with bimerous protopodite, bimerous endopodite and tetramerous exopodite. The basal article of the protopodite has a distal medial setule. The second article is unarmed. The endopodite is long, subrectangualar and reaches to the end of the third article of the exopodite. The basal article bears a small setule at the distal medial corner. The second article bears a minute setule just beyond the middle of the medial margin and 2 long apical setae. The exopodite is poorly articulated with the protopodite. The first 3 articles each bear a long seta at the distal medial corner. The terminal article is rounded and bears a long apical seta. There is a row of spinules on the basal article of the exopodite. All of the long setae of the antenna and mandible bear long coarse hairs.

In the successive naupliar stages, setae are added to the antennule, and the other appendages begin the regression which leads to the form of the appendage in the copepodid stages. In the last nauplius, containing internally the structures of the first copepodid, the following cuticular structures, which are still naupliar, can be made out.

The antennule is still trimerous, the basal article unornamented ; the second article has reduced setae, consisting of a very short seta at the distal end of the article and 1 setule. Therefore, during the naupliar stages, 1 seta has been lost from this article. The terminal article still bears a distal elongate seta, accompanied by a short seta, but 5 or 6 setules have been added to the ventral terminal margin and 1 short setule to the dorsal terminal margin.

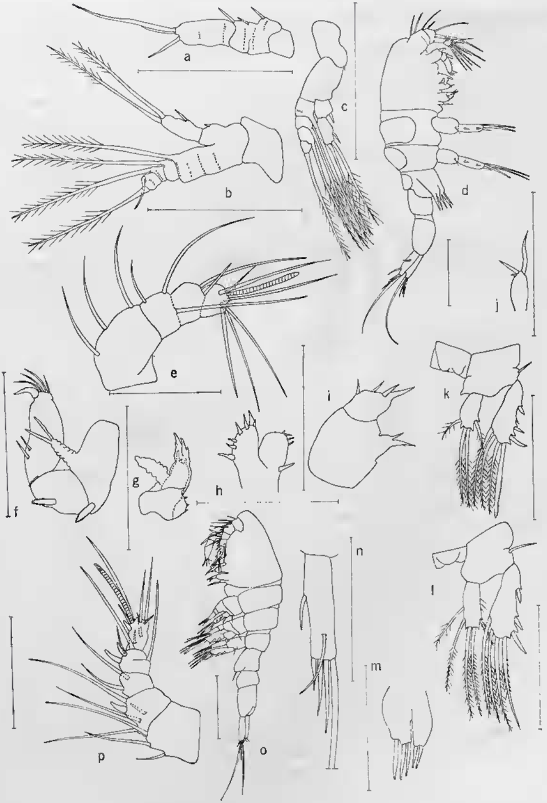

FIG. 54. — *Ascidicola rosea:* first nauplius (a-c) ; first copepodid (d-n) ; second copepodid (o-p) : a, antennule ; b, antenna ; c, mandible ; d, habitus, lateral ; e, antennule ; f, antenna ; g, mandible ; h, maxillule ; i, maxilla ; j, maxilliped ; k, first leg ; l, second leg ; m, third leg ; n, caudal ramus ; o, habitus, lateral ; p, antennule. Scales for a, b, c, d, k, l, m, n, 0 = 0.1 mm ; scales for e, f, g, h, i, j = 0.05 mm.

Source : MNHN, Paris

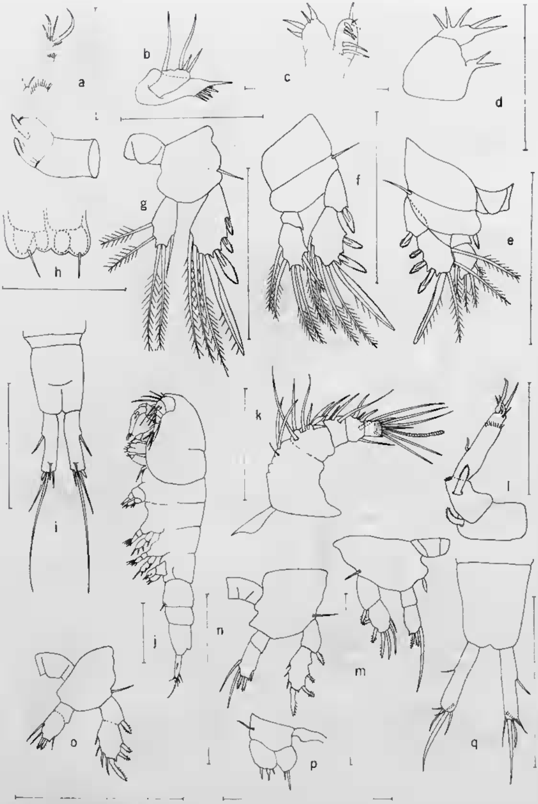

FIG. 55. — *Ascidicola rosea* : second copepodid (a-i) ; third copepodid (j-q) : a, antenna ; b, mandible ; c, maxillule ; d, maxilla ; e, first leg ; f, second leg ; g, third leg ; h, fourth leg, with dotted line indicating forming fourth leg of third copepodid ; i, terminal somite of urosome and caudal rami, dorsal ; j, habitus, lateral ; k, antennule ; l, antenna ; m, first leg ; n, second leg ; o, third leg ; p, fourth leg ; q, terminal somite of urosome and caudal rami, ventral. Scales for a, b, c, d, k, l = 0.05 mm ; other scales = 0.1 mm.

In the antenna, the protopodite and exopodite are the same as in the first naupliar stage, the medial seta of the endopodite has been much reduced.

In the mandible the protopodite and exopodite are the same as in the first stage, the medial seta of the endopodite is reduced.

Cuticular lines indicate the margins of the maxillule, maxilla and maxilliped, which are developing internally. The first and second legs are visible on the cuticle as protruding sacs within which the well-formed legs are differentiating. The posterior end of the last nauplius is bilobed. Each lobe bears 1 long seta and 5 short setae.

When the late last nauplius is examined in life, features of the first copepodid can be seen internally. It would appear that the antennule will have 5 articles. The terminal article of the naupliar appendage will divide into 2 articles in the copepodid. Details of the first 2 legs, the presence of third leg rudiments and the developing caudal rami are visible. All the naupliar stages lack an eye. This feature has been remarked on both in regard to the adult and the nauplius by various authors, and we can confirm the observation.

In this species we have been able to study the first 3 copepodids which were obtained by rearing the nauplii. We obtained large numbers of first and second copepodids, but only a single third copepodid. The first copepodids were molting to second stages after about 24 hours. The single copepodid to molt to the third did so after about 96 hours. We are convinced that the second copepodid is the infective stage.

In the first copepodid the body (fig. 54, d) is composed of the cephalosome, metasome and urosome. The overall length is 0,35 mm. By analogy with later developmental stages and the observed anatomy we concluded the cephalosome to include the portion of the body anterior to the segment of the first legs and there appears to be an actual articulation. The metasome has 2 leg-bearing segments, these very well-defined and each with a dorsal plate-like sclerotization. The urosome consists of a segment bearing rudimentary third legs, 1 leg-less segment and the anal somite with its terminal caudal rami. There is no salient rostrum. The antennule (fig. 54, e) is obscurely 4-segmented. There is a slight taper from base to apex. The basal segment is about twice as long as any other. The armature is as follows : article I — 3 setae ; II — 3 setae ; III — 2 setae ; IV — 6 setae, 1 aesthete. There is no vestigial seta on the apical segment as seen in the first copepodids of *Enterocola* and *Enteropsis*.

The antenna (fig. 54, f) is obscurely trimerous and early in the stage is clearly biramous, but very soon the internal tissue of the expodite regresses and the cuticle crumples as shown in the figure. The basal article has a large flattened spinulose seta at about the middle of the outer margin, and there is a row of spinules distally on the outer margin. The terminal segment, approximately equal in length of the other 2 combined, bears 1 terminal flexible hook-like element and 4 fine setae. In addition there are 2 setae at the proximal third of the outer margin.

The mandible (fig. 54, g) early in the stage is biramous, but very soon the tissue in both rami regresses and the cuticle tends to crumple. However, in the later portion of the same stage one can discern the palp of the second copepodid forming within the cuticle, demonstrating that this palp includes the endopodite of the appendage, and there is also a possibility that the basal portion of the palp is the basipodite. The coxopodite has a toothed medial margin, but the teeth are not so complex as in later stages and the article is narrow.

The maxillule (fig. 54, h) is bilobed and has an outline similar to that of the adult. Near the distal medial corner of the basal segment there is an endite bearing 2 unarticulated setae. The apical segment is drawn out medially as a narrow setiform process and there are 3 setae on the apical margin. The apical segment thus lacks three setae present on this segment in the adult.

The maxilla (fig. 54, h) is bimerous, the distal article about 1/4 the mass of the basal. On the latter the medial margin is produced at about its middle to a rounded process terminated in 2 unequal pointed processes. The distal article has a sloping anterolateral margin. This terminates at the anterodistal corner as a pointed process. A slightly smaller spiniform seta is set on the base of the process and 2 somewhat smaller spiniform setae are set at intervals on the distal margin.

The maxilliped (fig. 54, j) is a very small, narrow lobe with 2 apical setae and a medial setule.

The first leg (fig. 54, k) is biramous, with unimerous protopodite and rami. The subquadrate intercoxal lamella is well developed. The protopodite has a small seta at the distal lateral corner near the articulation of the exopodite. There is also a pointed protrusion at the distal medial corner; but no articulated spine is present as yet. The exopodite, flattened and considerably longer than the endopodite, has 3 short lateral spines, 1 very long terminal spine, 1 terminal seta and 2 medial setae. The endopodite has 1 lateral seta, 2 terminal setae and 1 distal medial seta.

The second leg (fig. 54, l) is biramous with unimerous rami. The intercoxal lamella is subquadrate. There is a relatively long seta on the lateral margin of the protopodite, proximal to the articulation of the exopodite. The exopodite bears 3 lateral spines, 1 terminal spine, 1 terminal seta and 2 medial setae. The endopodite, about 2/3 as long as the exopodite, bears 1 distal lateral seta, 2 terminal setae and 2 distal medial setae.

The third leg (fig. 54, m) is non-functional and the basal articulation with the body is undeveloped. Each leg consists of 2 flaps which encapsulate the developing rami of the leg of the second copepodid. The exopodal portion has 3 setiform projections and the endopodal 2.

The second urosomal segment and the anal somite proper have no ornamentation. The caudal ramus (fig. 54, n) is slightly shorter than the anal somite and subrectangular in outline. There are 6 setae on the ramus, 1 at the proximal lateral third, 1 on the dorsal surface at about the distal third and 4 terminal. The medial terminal seta is the longest, and is slightly more than twice the length of the ramus.

The second copepodid (fig. 54, o) has the body composed of cephalosome, bearing appendages through the maxilliped, metasome of 3 leg-bearing segments, and a urosome of 2 segments and the anal somite; with terminal caudal rami. The overall length is 0.36 mm. There is no defined rostrum.

The antennule (fig. 54, p) is clearly 5-segmented, with only a slight taper. The basal segment is the longest. The armature is a follows: Article I — 3 setae; II — 4 setae and a hook; III — 2 setae; IV — 3 setae, 2 hooks; V — 6 setae, 2 aesthetes and 1 hook.

The antenna (fig. 55, a) is trimerous and uniramous. The exopodite has been lost at the molt. Each of the 2 basal segments bears an outer distal spatuliform spinulose seta and a row of spinules on the distal external margin. The apical segment, about equal to the combined lengths of the 2 basal segments, and somewhat narrower, has 4 apical setae and a narrow hook, articulated terminally. At the proximal third there are 2 short setae. Curved rows of spinules ornament the surface at the proximal third and distal fifth. The mandible (fig. 55, b) is similar to that of the adult. There is a coxal lamella, with complex articulated spines directed medially, and a unimerous palp, which bears 4 unequal setae on its flattened anterior margin. The setation of the palp thus conforms to the adult in number but not in the form of the setae.

The maxillule (55, c) is bilobed, with a poorly defined articulation between the base and the palp lobe. An endite-like lobe continues directly from the base without articulation. The palp bears 7 setae and a setule on the lateral and apical margins. The endite has only 4 setae and thus has lost the basal seta seen in the appendage of the first copepodid. This basal seta is also absent in the adult, but several marginal setae are added.

The maxilla (fig. 55, d) is very similar to the appendage of the first copepodid except that the setae have lengthened appreciably.

The first leg (fig. 55, e) is biramous with bimerous protopodite and rami. The trapezoidal intercoxal lamella is well developed. The coxopodite is unarmed and unornamented The basipodite bears a relatively long seta on the lateral margin and an articulated spine at the distal medial corner. The exopodite bears 1 spine at the distal lateral corner of the basal segment. The distal article bears 3 lateral spines, 1 terminal spine, 1 terminal seta and 2 medial setae. The basal segment of the endopodite bears no armature. The terminal segment bears 1 lateral seta, 2 terminal setae and 1 medial seta. It should be noted that the appendage has gained no element of armature at this stage from the condition seen in the first copepodid. The setae all are plumose, but there has been a shortening of the setae of the endopodite.

The second leg (fig. 55, f) has a bimerous protopodite and rami. The coxopodite is unarmed. There is a relatively long seta laterally on the basipodite. The basal segment of the exopodite bears 1 distal lateral spine. The terminal segment bears 2 lateral spines, 1 terminal spine, 1 terminal seta, and 3 medial setae. Thus 1 medial seta has been added at this stage. The basal segment of the endopodite has no armature. The terminal segment has 1 distal lateral seta, 2 terminal setae and 2 distal medial setae. Thus no element of armature has been added at this stage. The setae do not show the pronounced shortening seen in the endopodite of the first leg.

The third leg (fig. 55, g) has a unimerous protopodite and rami. A subrectangular intercoxal lamella connects the protopodites. A seta articulates on the distal lateral margin of the protopodite. The exopodite bears 3 lateral spines, 1 terminal spine, 1 terminal seta and 2 medial setae. The endopodite bears 1 distal lateral seta, 2 terminal setae and 2 distal medial setae.

At the posterior margin of the first segment of the urosome are found the rudimentary fourth legs (fig. 55, h). Each consists of a bilobed pad with a single seta articulating on the lateral lobe. In the late second copepodid one can discern the outline of the biramous leg of the subsequent stage developing within the cuticle, as figured.

The second urosomal segment and the anal somite have no ornamentation. The caudal rami (fig. 55, i) are approximately as long as the anal somite. Each bears 6 setae, 1 of these just posterior to the proximal third of the lateral margin ; 1 dorsally at the distal fifth ; and 4 apical. The medial seta is greatly reduced over the condition of the previous copepodid and that next lateral is now the longest, approximately twice as long as the ramus. The most lateral seta on the apex has been reduced to a spiniform element.

The third copepodid (fig. 55, j) shows some modifications, with partial fusions of body segment and a general shortening of all the setae of the appendages. Because we had only a single specimen we could not completely make out all the appendages. The antennule (fig. 55, k) is obscurely pentamerous. The basal portion shows indications by indentations in the cuticle that 2 segments, clearly demarcated in the second copepodid, are incorporated by a considerable degree of fusion. The portion of this basal complex corresponding to the first segment of the second copepodid bears 2 setae and a setule. The distal portion of the complex bears 5 setae and 3 thick hook-like elements. The remaining formula for the antennule : Article III — 2 setae, 1 aesthete ; IV — 2 setae, 2 hook-like elements, 1 aesthete ; V — 6 setae, 1 hook-like element, 1 aesthete.

The antenna (fig. 55, l) is very similar to that of the second copepodid. It is trimerous ; the 2 basal articles and the apical armature of the terminal article are exactly as in the second copepodid. One seta on the inner margin of the terminal article and 1 curved row of spinules on the face appear to have been lost.

The mouthparts are not illustrated, but dissection showed that they were very similar to those of the second copepodid.

The first leg (fig. 55, m) has a unimerous protopodite and bimerous rami. There is no articulative line between the coxopodite and basipodite, this having been lost in the transformation from the second copepodid. There is a seta at the distal lateral corner and a spine on the distal medial corner of the protopodite. The exopodite has 1 spine at the distal lateral corner of the basal article, 2 lateral spines, 1 terminal spine, 2 terminal setae, and 1 medial setule on the distal article. All of these elements have been greatly reduced from the condition of the second copepodid, and 1 medial seta has been lost. The basal article of the endopodite bears no armature ; the terminal article bears 1 distal lateral setule, 2 terminal spines, and 2 distal medial setae. Although the number of elements of this ramus is the same as in the second copepodid, the setae have been greatly reduced in size and the 2 terminal setae have been transformed into spines.

The protopodite of the third leg (fig. 55, o) is as in the second leg. The rami are now obscurely bimerous rather than unimerous as in the previous stage. The basal article of the exopodite bears a single distal lateral spine. The terminal article bears 2 lateral spines, 1 terminal spine, 1 terminal setule, and 3 medial setules. One setule has been added to the medial margin. The setae of the ramus have been greatly reduced from the condition of the second copepodid. The poorly defined basal article of the endopodite bears no armature. The distal article bears 1 distal lateral setule, 2 terminal spines and 2 distal medial setules. Numerically the elements of armature correspond to the second-copepodid but the setae are greatly reduced and the terminal elements of the ramus have been transformed from setae into spines.

The fourth legs (fig. 55, p) which were markedly rudimentary in the previous stage now consist of a unimerous protopodite, with a lateral seta, and unimerous rami; the exopodite bears 3 setiform elements and the endopodite 2.

The urosome consists of only 2 segments and the anal somite. The first segment bears 2 distal setae, 1 on either side. Each is the rudiment of a fifth leg. The caudal rami (fig. 55, q) are approximately as long as the anal somite. Each bears 6 setae, 1 at the middle of the lateral margin, 1 on the dorsal surface at the distal eighth, and 4 terminal setae. The medial terminal and the 2 lateral terminal setae are very short; the second medial seta is the longest but it is shorter than the ramus at this stage, thus showing a great reduction in length from the condition of the second copepodid.

We did not collect fourth or fifth copepodids.

Development of *Enterocola fertilis*

(Figures 56, 57)

The first nauplius is a lecithotrophic larva, with the basic characteristics of other non-feeding nauplii. We have drawn the habitus (fig. 56, a) from an exuvia. The body is somewhat globose and not markedly pyriform, as in the Notodelphyidae. There is a protrusion at the anterior end which is possibly homologous with the rostrum. Three pairs of appendages, the antennules, antennae and mandibles, articulate distally to the anterior third. There is a subcircular supraoral plate and the cuticular remnant of the inner stomodaeal lining protrudes from the mouth. This latter is closed and the gut is not patent at this stage. The posterior end of the exuvia has 2 sectors, a ventral truncated abdominal end which bears 2 lateral setae, and the dorsal shield, which extends over the end of the abdomen and which appears to be the precursor of the anal shield of the copepodids. The antennule (fig. 56, b) is trimerous, uniramous. The basal " article " is simply a scleritic ring that articulates the appendage with the body. It bears no armature or ornamentation. The second article bears a single long seta near the distal margin on the ventral face. Proximal to this on the ventral face and at the middle, set on a lobe, is a very small setule. The terminal article is slightly longer than the second and shows a certain amount of taper. On the apex there is a long ventral seta accompanied by a dorsally placed seta which is about 1/3 as long. All the setae are plumose. It should be noted that the apical aesthete present in other subfamilies described here is missing, an interesting feature in contrast to the case in *Enterocola laticeps*, described below.

The antenna (fig. 56, c) is biramous with bimerous protopodite, tetramerous exopodite and unimerous endopodite. The basal and second articles of the protopodite lack armature and ornamentation. The second article shows some coalescence with the basal article of the exopodite. This basal article of the exopodite is longer than the other articles combined. Each of the 3 basal articles of the exopodite bears a seta at the distal medial corner. The terminal article is rounded apically, but with a lateral and a medial emargination, in each of which articulates a short seta. There is a long terminal seta on this article. The endopodite is subrectangular and reaches approximately to the end of the second article of the exopodite. It bears a short seta in an emargination at the middle of the medial margin and 2 long terminal setae. All long setae of the appendage are coarsely plumose.

The mandible (fig. 56, d) is biramous with bimerous protopodite, tetramerous exopodite and bimerous endopodite. The basal article of the protopodite bears no armature or ornamentation. The basipodite has a minute point at the middle of the medial margin. The 3 basal articles of the exopodite bear single setae at the distal medial corners. The rounded apical article has a pointed unarticulated terminal process and a terminal articulated seta. The basal article of the endopodite has a minute setule at the middle of the medial margin. The second article, broadening somewhat at the apex, has a minute setule in an emargination at about the middle of the medial margin, and two subequal long apical setae. All setae of the appendage are coarsely plumose.

Although our cultures were vigorous and we obtained many first and second copepodids, we did not make a complete study of the detailed changes in the nauplii. The naupliar development was very rapid, with about 30 hours elapsing from hatching to the first copepodid stage.

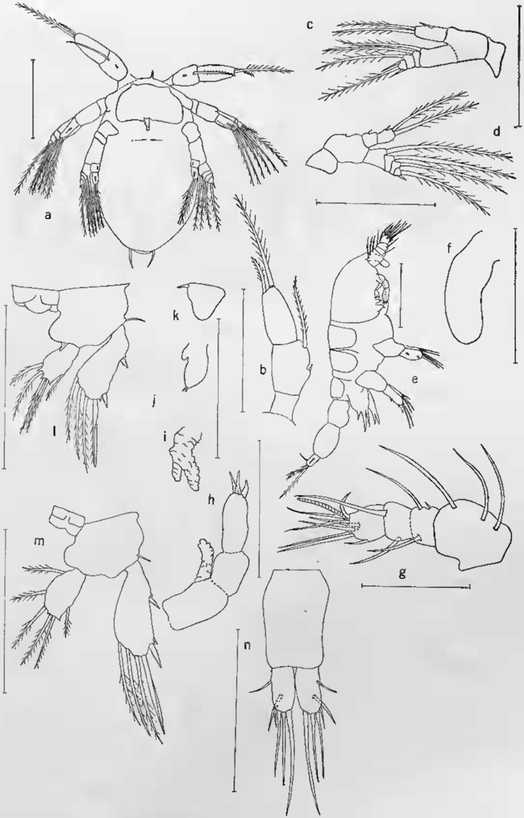

Fig. 56. *Enterocola fertilis* : first nauplius (a-d) ; first copepodid (e-n) : a, habitus, ventral ; b, antennule ; c, antenna ; d, mandible ; e, habitus, lateral ; f, rostrum ; g, antennule ; h, antenna ; i, mandibular remnant ; j, maxillule ; k, maxilla ; l, first leg ; m, second leg ; n, end of urosome and caudal rami, ventral. Scales for a, b, c, d, e, l, m, n = 0.1 mm ; for f, g, h, i, j, k = 0.05 mm.

Source : MNHN, Paris

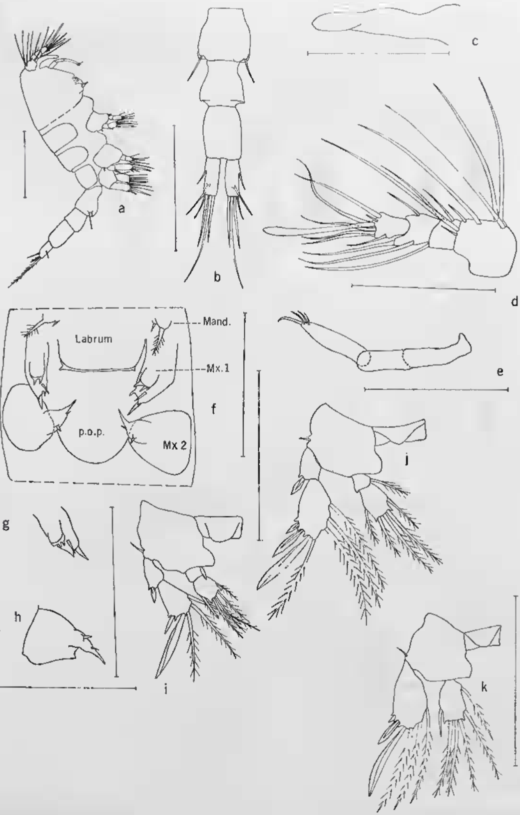

FIG. 57. — ***Enterocola fertilis*** : second copepodid : a, habitus, lateral ; b, urosome, ventral ; c, rostrum, lateral ; d, antennule ; e, antenna ; f, *en face* view of posterior cephalosome : mand. = madible, Mx1 = maxillule, Mx2 = maxilla, p.o.p. = postoral protuberance ; g, maxillule ; h, maxilla ; i, first leg ; j, second leg ; k, third leg. Scales for a, b, i, j, k = 0.1 mm ; other scales = 0.05 mm.

The body of the first copepodid (fig. 56, e) is composed of the cephalosome, metasome and urosome. The cephalosome includes the portion of the body anterior to the segment of the first legs. The metasome has 2 leg-bearing segments. The urosome is composed of 2 segments and the anal somite bearing the caudal rami. The first urosomal segment bears the rudimentary third legs.

There is a rostrum (fig. 56, f) which is long and bulbous, reaching beyond the bases of the antennae. The antennule (fig. 56, g) is obscurely tetramerous. The basal and terminal articles are set off by distinct articulations, but the second and third articles are delimited from each other only by a cuticular indentation. The armature is as follows : Article I — 3 setae ; II — 2 setae and 1 setule ; III — 2 setae ; IV — 7 setae, 1 vestigial seta, and 1 aesthete.

The antenna (fig. 56, h) is clearly biramous at the early copepodid stage, but very soon after the molt from the last nauplius, the internal tissue of the exopodite regresses and the cuticle crumples. The tissue within the protopodite and the endopodite does not regress, and by the end of the stage, the appendage assumes an obscurely trimerous form, with an attached remnant of the exopodite. The 2 basal articles bear no armature or ornamentation. The narrower apical article bears 3 flexible terminal setiform elements.

The mandible (fig. 48, i) is regressing from immediately after the completion of the molt. It consists of a crumpled sac with some indication of biramous condition. Within the crumpled sac there is developing a minute setigerous lobe which will be the only evidence of this appendage at the second copepodid stage.

The maxillule (fig. 56, j) is unequally bilobed, with a more lateral large lobe bearing 2 apical setules perhaps representing the palp at least apically. A more basal, minute lobe extends medially with no articulation between the parts of the appendage.

The maxilla (fig. 56, k) consists of a low lobe with a single articulated apical spiniform projection. There is no maxilliped.

The first leg (fig. 56, l) is biramous with unimerous protopodite and rami. The lobed intercoxal lamella is subquadrate and well-developed. The protopodite has a small seta at the distal lateral corner near the articulation of the exopodite. There is a flattened spiniform projection, obscurely articulated on the distal medial margin at the articulation of the endopodite. The exopodite has 1 spine at the proximal lateral third, 1 spine at the distal lateral third, 1 terminal spine, 1 terminal seta, and 2 distal medial setae. The endopodite bears 1 lateral seta in an emargination at the distal third, 2 terminal setae, and 2 distal medial setae.

The second leg (fig. 56, m) has a unimerous protopodite and rami. The intercoxal lamella is subquadrate. A small seta articulates at the distal lateral corner of the protopodite. The exopodite bears 1 lateral spine at the proximal third, and 2 distal lateral spines, the more distal much longer, 1 terminal spine, 1 terminal seta, and 2 medial setae. The endopodite bears 1 distal lateral seta, 2 terminal setae, 2 distal medial setae and 1 proximal medial seta. The third legs are rudimentary, with the basal articulation with the body undeveloped. Each leg consists of 2 sacs which encapsulate the developing rami. The exopodal portion has 3 spinelike projections and the endopodal portion has 2 projections.

The caudal rami (fig. 56, n) are about 1/2 as long as the anal somite. There are 6 setae on each ramus, 1 at the proximal lateral third, 1 at the distal third on the dorsal surface, and 4 terminal. The medial terminal seta is the longest, approximately 3 times as long as the caudal ramus.

The second copepodid (fig. 57, a) has a body composed of the cephalosome, metasome of 3 leg-bearing segments, and urosome of 2 segments and the anal somite bearing the caudal rami (fig. 57, b).

There is a rostrum (fig. 57, c) very long and almost cylindrical. The antennule (fig. 57, d) is clearly 4-segmented. The armature is as follows : Article I — 5 long setae and 2 short setae ; II — 3 setae ; III — 3 setae ; IV — 7 setae, 1 aesthete.

The antenna (fig. 57, e) is uniramous and obscurely trimerous. Two basal articles, which are only obscurely articulated with each other, are unarmed and unornamented. The terminal article, which is the longest, has a terminal armature of a very narrow curved articulated hook and 3 small setae. Each of the articles is very much narrower than in the previous copepodid stage and there is no evidence of the exopodite.

The labrum (fig. 57, f) is well differentiated at this stage, but is completely unornamented. The madibular remnant (fig. 57, f) consists of a lobe with an apical seta and a subapical setule.

The maxillule (figs. 57, f, g) is a bilobed structure. In an *en face* view the more ventral lobe terminates in 2 spiniform processes. The more dorsal lobe, somewhat longer at this stage, also terminates in 2 spiniform processes, and there is an articulated setule on the ventral surface.

The maxilla (figs. 57, f, h) is subtriangular in outline with an expanded base and an apical lobe somewhat demarcated and tapering acutely apically as a hook-like process. The apical lobe bears 2 articulated elements, the more distal possibly the rudiment of the second hook-like process of later stages. There is a large hemispherical bulge of the cuticle between the bases of the maxillae ; we have termed it the postoral projection (fig. 57, f : p.o.p.).

The first leg (fig. 57, i) is biramous, with unimerous protopodite and bimerous rami. The subquadrate intercoxal lamella is well developed. There is a small seta on the distal lateral margin of the protopodite and a spine on the distal medial margin at the articulation of the endopodite. The basal article of the exopodite bears 1 spine at the distal lateral corner. The second article bears 1 spine at the distal lateral corner, a terminal spine, a terminal seta, and 2 medial setae. The basal article of the endopodite bears no armature. The distal article bears a seta at the middle of the lateral margin, 2 terminal setae and 2 distal medial setae. No new elements of armature have been added to either ramus.

The second leg (fig. 57, j) is biramous, with unimerous protopodite and bimerous rami. The intercoxal lamella is subquadrate. The protopodite bears a short seta at the distal lateral corner near the articulation of the exopodite. The basal article of the exopodite bears a distal lateral spine. The terminal article bears 2 distal lateral spines, 1 terminal spine, 1 terminal seta, and 3 medial setae. The basal article of the endopodite bears a distal medial seta. The terminal article bears 1 seta at the middle of the lateral margin, 3 terminal setae, and 1 distal medial seta. Only 1 seta has been added to the appendage, this to the medial margin of the terminal article of the exopodite.

The third legs (fig. 57, k) are articulated with the body for the first time. Each consists of unimerous protopodite and rami. A subquadrate intercoxal lamella is well developed. The protopodite bears a short seta at the distal lateral corner. The exopodite bears 2 distal lateral spines, 1 terminal spine, 1 terminal seta, and 2 medial setae. The endopodite bears a lateral seta at the distal third, 3 terminal setae, 1 distal medial seta, and 1 proximal medial seta.

The first segment of the urosome bears the rudimentary fourth legs. Each consists of a bilobed pad, with a single seta articulating on the more lateral lobe.

The caudal rami (fig. 57, b) are slightly shorter than the anal somite and each bears 6 setae. The lateral and dorsal setae are as in the first copepodid, the second medial seta of the 4 terminal is now the longest, a little more than twice as long as the ramus.

We have no material available of the third, fourth and fifth copepodid stages.

Development of *Enterocola laticeps*

(Figure 58)

We have been able to obtain only the first nauplius stage of this species. The first nauplius is a lecithotrophic larva, with basic characteristics of cyclopoids of non-feeding type (see Dudley, 1966).

The antennule (fig. 58, a) is uniramous and functionally trimerous. The basal article lacks armature and ornamentation, and, since in similar forms, it coalesces with the head in later development, it may be only a mechanically differentiated sclerotized ring. The much larger second article bears a single seta, long and well developed, inserted on the ventral face at the distal margin. Proximal to this on the ventral margin is a minute setule, inserted in an indentation at the distal fifth. At the distal third there is a minute pointed projection which may be homologous to such a setule. Three rows of spinules are about equally spaced on the distal half of the medial surface. The terminal article is somewhat longer than the preceding and tapers slightly distally to a truncate apex. On the apical

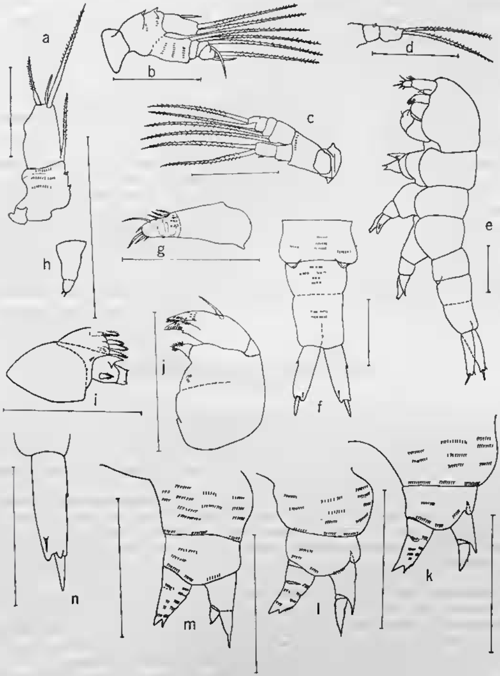

Fig. 58. — *Enterocola laticeps* : first nauplius (a-d) ; third copepodid (e-n) : a, antennule ; b, antenna ; c, mandible ; d, endopodite of mandible ; e, habitus, lateral ; f, urosome, ventral ; g, antennule ; h, antenna ; i, maxillule ; j, maxilla ; k, first leg ; l, second leg ; m, third leg ; n, caudal ramus. Scales for a, b, c, d = 0.05 mm ; other scales = 0.1 mm.

margin there is a long ventral seta, accompanied by a short aesthete and somewhat removed from these a dorsal seta, about half as long as the ventral seta. All long setae of the appendage are coarsely plumose.

The antenna (fig. 58, b) is biramous with an obscurely bimerous protopodite, an obscurely tetramerous exopodite and a unimerous endopodite. The basal article of the protopodite lacks armature and ornamentation. The second article has 2 rows of spinules on the surface and 2 pointed projections on the medial margin distal to the midpoint. The basal article of the exopodite is rather poorly articulated with the protopodite and is slightly longer than the combined lengths of the remaining 3 segments. It bears a long seta at its distal medial corner and 3 rows of spinules on the surface. The second and third articles are wider than long and each bears a long seta at the distal medial corner. The terminal article is rounded, with an emargination on its medial face ; a short seta is inserted in this. Apically there are a long seta and a much shorter seta. The endopodite is subrectangular and reaches only slightly beyond the distal end of the basal article of the exopodite. It bears a setule in an emargination at the middle of the medial margin and 2 long terminal setae. All long setae of the appendage bear coarse hairs.

The mandible (fig. 58, c) is biramous, with an obscurely bimerous protopodite, obscurely trimerous exopodite and bimerous endopodite. The basal article of the protopodite has no armature or ornamentation. The second article has a single row of spinules. The basal article of the exopodite is only faintly set off from the protopodite and its length about equals the combined lengths of the other 2 article. The first and second articles each bear a single seta at the distal medial corner. The terminal article is rounded with an emargination at the middle of the margin, in which is set a single long seta. There is a single long apical seta. The endopodite (fig. 58, d) is long, subrectangular, reaching to the end of the second segment of the exopodite. The basal article has a minute setule at the middle of the medial margin. The second article has a minute setule at the middle of the medial margin and 2 long setae on the truncate apex. All long setae of the appendage bear coarse hairs.

Third Copepodid of *Enterocola laticeps*
(Figures 58, e-n)

From material taken from the host ascidian we have a specimen that we assign with some misgiving to the third copepodid stage. The overall size and the advanced development of the 3 pairs of legs present would suggest a later stage. The segmentation of the urosome, the lack of setae on the endopodite of the legs, and the fact that the species is a large one are indications that this could be the third stage.

The habitus (fig. 58, e) is cruciform, the animal having assumed a pattern of considerable conformity to the adult structure. The overall length is 0.66 mm, measured from the apex of the head to the end of a caudal ramus. The body divisions are cephalosome, bearing 4 pairs of appendages ; a metasome, of 3 demarcated segments, each bearing a salient pair of legs ; and the obscurely 3-segmented urosome (fig. 58, f), bearing rudiments of fourth legs on the first segment and terminal caudal rami.

The antennule (fig. 58, g) is unimerous, but a pattern of sclerotization suggests 4 ingredient articles. There are no basal setae, and distally 11 setae are rather regularly distributed.

The antenna (fig. 58, h) is obscurely bimerous, the basal portion below a weakly suggested subdivision much larger than the terminal portion. There are 2 minute setules on the apex.

The labrum was not discerned in the dissection. The mandible is absent.

The maxillule (fig. 58, i) is bilobed, with unsegmented base and lobes. The base extends in a medial lobe, forming a basal piece which is rather heavily sclerotized. The minor lobe is produced into two subequal processes. One process terminates acutely, the other is larger, truncate with acute terminal corners. On the face there is a spinulose seta. The lobe of the basal piece is obscurely articulated. It is bilobed terminally, 1 lobe bearing 2 short setae, the other with 3 setae. There is an additional very short seta at the middle of the ventral margin. A few spinules are found on the surface.

The maxilla (fig. 58, j) is bimerous and, although resembling the appendage of the adult, is not quite so modified and suggests the anatomical composition somewhat more strongly. The basal article is long and bears a thumb-like, spinulose, articulated endite distally. The terminal article is produeed medially as 2 strong, pointed, spinulose processes, each with a proximal serrated margin. There is a seta, with an expanded base, inserted on the distal margin.

The 3 pairs of legs all have bimerous protopodites, obscurely articulated on the body and are biramous. In the first leg (fig. 58, k) the endopodite is unimerous, approximately as long as the exopodite. It terminates in 2 small, subequal, acute processes. The exopodite is bimerous, with the basal article produced distally as a stout process. The distal article is subconical. The lateral margin bears 2 minute, equispaced spinules.

The second leg (fig. 58, l) has an obscurely bimerous endopodite, slightly shorter than the exopodite. It terminates in 2 small, acute processes, one about twice as long as the other. The exopodite resembles that of the first leg, except that the terminal article is slightly longer and lacks lateral spinules.

The third leg (fig. 58, m) has an obscurely bimerous endopodite, about 3/4 as long as the exopodite. It terminates in 2 small, subequal, acute processes. The exopodite is bimerous, the terminal article reduced to about half the length of the basal article. The basal article has a stout, long, setiform process at the lateral distal corner, about twice as big as the distal article. The protopodites and endopodites of all the legs have rows of ornamentating spinules.

The fourth leg is a simple lobe on the posterior lateral margin of the first urosomal segment (fig. 58, f).

The caudal ramus (fig. 58, n) is flattened, subrectangular in outline, slightly longer than the anal somite. There are 3 terminal lobes and an apical seta, which is about 1/3 as long as the ramus. There is a short dorsal medial seta at about the distal fifth and a minute knob-like, articulated element on the lateral margin just proximal to the middle. Rows of fine spinules are found on the surfaces of the urosomal segments and the caudal ramus.

The absence of setae on the endopodites of the legs, although well-developed ones occur on the adult, furnish the strongest indication to us that this is a third copepodid.

Developmental Stages of *Enteropsis capitulatus*
(Figure 59)

The first nauplius is a lecithotrophic larva, with basic characteristics of cyclopoids of non-feeding type (Dudley, 1966). We have found 5 naupliar stages and the usual 6 copepodids can be assumed to occur from our sampling. It appears, however, that the mid-gut is well-formed when the nauplius hatches. Yellow yolk is contained within the gut and large globules of purplish-red yolk are associated with the mid-gut wall. It would seem that both the stomodaeum and proctodaeum are patent at this stage. There is a very large red eye. There is no other significant pigmentation, except some yellow globules.

The antennule (fig. 59, a) is uniramous, and functionally trimerous. The basal scleritic ring lacks armature and ornamentation. The second article bears a single long seta at the distal margin on the ventral face. Proximal to this on the ventral margin are 2 minute setules, set at the distal third and fifth. Three rows of spinules are equally spaced on the medial surface. The terminal article is about 1/3 longer than the second and shows little taper, but is rounded apically. On the apex there is a long ventral seta, accompanied by a short aesthete and a dorsal seta about 1/3 as long. The latter seta bears coarse hairs. Two rows of spinules, one at the proximal third and one the distal third ornament the medial surface.

The antenna (fig. 59, b) is biramous, with obscurely bimerous protopodite, obscurely tetramerous exopodite, and unimerous endopodite. The basal article of the protopodite lacks armature and ornamentation. The second article has rows of spinules on the surface and shows a coalescence with the basal article of the exopodite. On the latter there is a seta which represents the corresponding article at the distal medial corner. The remaining articles of the exopodite are poorly articulated with each other, indentations indicating the ingredient elements. The second and third articles each has a long seta at the distal medial corner. The terminal article is rounded and has a short medial seta and a long terminal seta. The endopodite is subrectangular and reaches to the end of the second

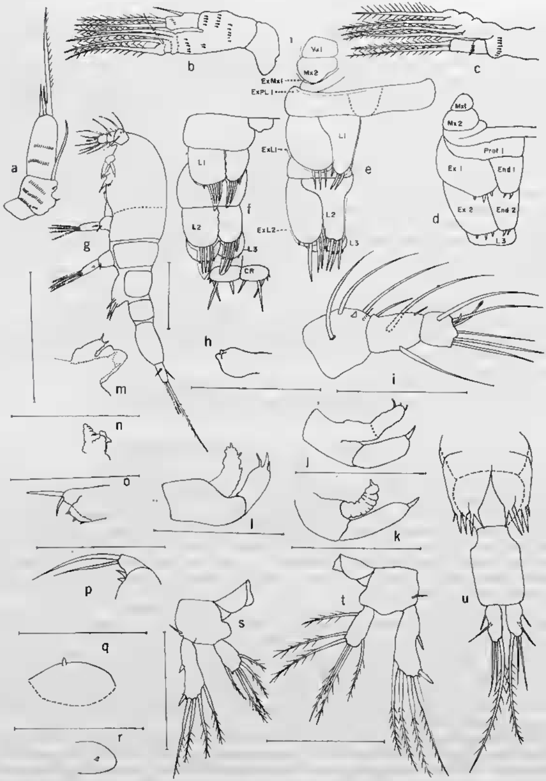

Fig. 59. — *Enteropsis capitulatus* : first nauplius (a-d) ; fourth nauplius (e) ; fifth nauplius (f) ; first copepodid (l, n, p, r) ; *E. roscoffensis* : first copepodid (g-k, m, o, q, s-u) : a, antennule ; b, antenna ; c, mandible ; d, subcuticular postmandibular appendages ; e, subcuticular postmandibular appendages and exuvial lines ; f, subcuticular postmandibular appendages and exuvial structure ; g, habitus, lateral ; h, rostrum, lateral ; i, antennule ; j, antenna ; k, antenna, late stage of first copepodid ; l, antenna, late first copepodid ; m, mandible, early ; n, mandible, late first copepodid ; o, maxillule ; p, maxillule ; q, maxilla ; r, maxilla ; s, first leg ; t, second leg ; u, urosome and third legs. Legend : CR = caudal ramus ; ExL1 = exuvial indication of leg 1 ; ExL2 = exuvial indication of leg 2 ; ExMx1 = exuvial indication of maxillule and maxilla ; Ex^{P}L1 = exuvial indication of protopodite of leg 1 ; L1 = leg 1 ; L2 = leg 2 ; L3 = leg 3 ; Mx1 = maxillule ; Mx2 = maxilla. Scales for g, s, t = 0.1 mm ; other scales = 0.05 mm.

article of the exopodite. It bears a seta in an emargination at the middle of the medial margin and 2 long terminal setae. All long setae of the appendage are coarsely plumose.

The mandible (fig. 59, c) is biramous, with obscurely bimerous protopodite, unimerous exopodite and bimerous endopodite. The basal article has a single row of spinules on the surface. This article is fused with the exopodite. The latter, although unimerous has some indentations, possibly indicating a basic tetramerous condition. The ramus bears 3 long medial setae and 1 long terminal seta. The endopodite is subrectangular and elongate, reaching to about the middle of the exopodite. The basal article has a minute setule at the distal medial corner and a row of spinules. The second article has a minute setule at the middle of the medial margin and 2 long setae on the truncate apex. All long setae of the appendage bear coarse hairs.

Even at this first stage, the subcuticular indications of the postmandibular appendages are well-formed (fig. 59, d). The maxillule (Mx1) and the maxilla (Mx2) are simple lobes ; there is no maxilliped ; legs 1 and 2 (L1 and L2) have indications of the protopodite and rami, the exopodites with 3 pointed terminal projections and the endopodites with 2. The third leg (L3) is a simple lobe, with a slightly undulate posterior margin. The second and third nauplii apparently do not differ much from the condition described for the first nauplius. The legs and the gut are much the same. In the exuviae of these latter second and third stages lines are present for maxilla 1, maxilla 2, leg 1 and leg 2. In the fourth nauplius the reddish-purple yolk has disappeared and is replaced by smaller globules of yellowish-orange. In this nauplius the postmandibular appendages show some additions (fig. 59, e). The maxillules (Mx1) and maxillae (Mx2) are much the same as before, in legs 1 and 2 (L1 and L2) the exopodites and the endopodites have each added 1 terminal projection. All such elements have elongated. The third legs (L3) show some posterior division into rami and the endopodite has 3 small pointed projections. Lines on exuviae indicate the margins of the maxillule (ExMx1) and the maxilla and indicate the margins of the exopodites and endopodites of legs 1 and 2 (ExL1 ; ExL2) and the endopodite of leg 3.

In the fifth nauplius (fig. 59, f) the condition of the exuvia, although changed some what from the fourth, does not express the entire complement of developed subcuticular appendage rudiments. The mouthparts are the same. The subcuticular pads of the first and second legs (L1, L2) have very well-developed protopodites and intercoxal lamellae. An additional terminal process has been added to the endopodite. The third legs (L3) have added 3 terminal projections to the apex of the exopodite in each. On the exuvia exopodites are indicated each by a line and a sac which encapsulates 3 or 4 internal elements. The endopodites are indicated each by a line and 2 pointed sacs, one much larger than the other. The larger sac encapsulates 3 internal elements and the smaller 1. The caudal rami (CR) are well indicated, with each a rectangular lobe with 2 lateral and 3 terminal setae. One of the terminal setae on each ramus was already present in the first nauplius.

The naupliar development in this species is very rapid, taking approximately 33 hours. In the culture studied, hatching was observed at 10 a.m. on one day and by 10 a.m. the day following, most nauplii were molting to the fifth stage and by 7 p.m. the first copepodid was seen.

In none of the naupliar stages was any evidence of the maxilliped found.

In this species we have been able to study the first 3 copepodids, which were obtained by rearing the nauplii. There were large numers of first copepodids, many second copepodids, but a single third copepodid. The first copepodids were molting to second copepodids after about 24 hours. We did not determine the duration of the second copepodid stage. Although the only other stage available to us of this species is the adult, we feel we have been able to piece together the representative life history for the genus *Enteropsis* by adding in the fourth and fifth copepodids from *E. superbus*. Comparative material, serving to corroborate our interpretations, is available to us also in the first and second copepodids of *E. roscoffensis* which we were able to obtain through culturing methods. We will describe the copepodids in the order of the successive stages, referring to each the available comparative material.

In the first copepodid the body (fig. 59, g) is composed of the cephalosome, metasome and urosome. The overall length is .434 mm (*E. capitulatus*) or .392 mm (*E. roscoffensis*). By analogy with the later developmental stages we consider the cephalosome to include the portion of the body anterior to the segment of the first legs, although there is not an actual articulation so far. The remainder of the body is well articulated. The metasome has 2 leg-bearing segments, these legs functional. The urosome consists of the segment bearing the rudimentary third legs, one legless segment and the anal somite, with its terminal caudal rami.

There is a rostrum (fig. 59, h), bulbous in lateral outline, with several terminal protuberance. The antennule (fig. 59, i) is 3-segmented, the terminal 2 articles about half as wide as the basal at its greatest width. The armature is a follows : Article I — 3 setae, 1 setule, 1 spine ; II — 3 setae, 1 setule ; III — 5 setae, 1 vestigial seta, 1 aesthete.

The antenna (figs. 59, j-l) at the early first copepodid stage is clearly biramous (fig. 59, j) but very soon the internal tissue of the exopodite regresses and the cuticle crumples (figs. 59, k, l). The result is a uniramous appendage of 2 articles. The basal article, representing the protopodite, has no armature or ornamentation. The terminal article, the endopodite, in *E. roscoffensis* (figs, 59, j, k) has one terminal seta, which is slightly hooked. In *E. capitulatus* (fig. 59, l) the endopodite has 2 terminal hooked setae, one about twice as long as the other, and what appears to be a regressing seta.

The mandible (figs. 59, m, n) at the early first copepodid stage is biramous (*E. roscoffensis* [fig. 59, m]) but very soon the tissue in both rami regresses. It would appear, however, that some part of the exopodite will be retained, at least at the next stage. After the regression all that remains is a crumpled cuticular sac (*E. capitulatus* [fig. 59, n]).

The maxillule (figs. 59, o, p) in *E. roscoffensis* consists of a bilobed structure. The ventral, more proximal lobe bears 3 short spinose articulated processes. The distal lobe, more medially placed, bears 2 terminal setae, 1 twice as long as the other. Neither lobe is articulated. In *E. capitulatus* (fig. 59, p) the appendage is similar in outline, but the ventral lobe appears to bear only 2 unarticulated processes. The other lobe has 2 setae, but these are much longer and one is about 3/4 as long as the other.

The maxilla (figs. 59, q, r) is a small domed projection, bearing an eccentrically placed setule ; this is larger in *E. roscoffensis* (fig. 59, q) than in *E. capitulatus* (fig. 59, r). There is no maxilliped.

The first leg (fig. 59, s) is biramous, with unimerous protopodite and rami. The intercoxal lamella is subquadrate and well developed. The protopodite has a small seta at the distal lateral corner, near the articulations with the exopodite. The latter, flattened and about twice as long as the endopodite, has 1 spine at the middle of the lateral margin, 1 spine at the distal lateral corner, 2 setiform elements terminally and two setae distally on the medial margin. The endopodite has 1 lateral seta, 2 terminal setae distally on the medial setae. The lateral terminal setiform element of the exopodite would usually be replaced by a spine.

The second leg (fig. 59, t) is biramous, with unimerous protopodite and rami. The intercoxal lamella is subquadrate. The armature of the protopodite and the exopodite is as in the first leg. The endopodite is about 2/3 as long as the exopodite, has 1 distal lateral seta, 2 terminal setae, 2 distal medial setae and 1 proximal medial seta.

The third legs (fig. 59, u) are non-functional, whith the basal articulation with the body undeveloped. Each leg consists of 2 sacs which encapsulate the developing rami. The endopodal portion has 2 terminal spine-like projections projections ; the exopodal portion has 2 spine-like projections and an articulated seta. The projections encapsulate developing setae and spines. The second urosomal segment and the anal somite have no ornamentation. Each caudal ramus is about 1/2 as long as the anal somite. There are 5 setae on each caudal ramus, 1 at the proximal lateral third, 1 at the middle of the dorsal surface and 3 terminal. The medial terminal seta is the longest and bears long coarse hairs. All the ~~other~~ setae are without hairs.

The second copepodid of *E. roscoffensis* (fig. 60) and *E. capitulatus* has a body composed of cephalosome, somewhat more clearly delimited from the metasome than in the first copepodid, a metasome of 3 leg-bearing segments and urosome of 2 segments and the anal somite with its terminal caudal rami. The overall length is .392 mm in *E. roscoffensis.*

The rostrum (fig. 60, h) is long, basally articulated, the antennule (fig. 60, b) is 4-segmented. The armature is as follows : Article I — 5 setae, 2 spines ; II — 2 setae, 1 setule ; III — 3 setae ; IV — 7 setae, perhaps including an unrecognizable aesthete.

The antenna (figs. 60, c, d) is uniramous and unimerous. There are 2 faint lines on the surface at the proximal third and distal third, but no actual articulations. The medial basal part of the appendage has an indentation approximately at the position formerly occupied by the exopodite. There is a single row of spinules on the surface of the appendage at the base of an apical elongate spinose process.

The labrum (fig. 60, e) is a semicircular lobe, ornamented distally with fine hairs, and 2 setiform processes project near the lateral extremes.

The mandibular remnant (figs. 60, f, h) consists of a minute, cylindrical lobe, with 5 or 6 tiny setae radiating from the tip. This lobe is inserted between the antenna and the maxillule, very close to the base of the maxillule (fig. 60, h).

The maxillule (figs. 60, g-i) consists of a bilobed structure. The ventral more proximal lobe, somewhat smaller proportionately than in the first copepodid, in some specimens is weakly articulated at the base, in others is unarticulated (fig. 60, i). This lobe terminates in 2 spinose processes and there is an additional third process laterally inserted on the lobe. The longer, more medial lobe is somewhat fingershaped and bears 2 long terminal setae, 1 of these about 1 and 1/4 to 2 times longer than the other.

The maxilla (figs. 52, j, k) is a low lobe with a single ventral spiniform, unarticulated projection. A patch of spinules ornaments the lobe at the base of the projection. There is no maxilliped.

The first leg (fig. 60, 1) is biramous, with bimerous protopodite and rami. The subquadrate intercoxal lamella is well developed. The coxopodite has neither armature nor ornamentation. The basipodite has a small seta at the lateral margin and 2 rows of spinules at the surface near the articulation of the endopodite. The exopodite has 1 spine at the distal lateral corner of the basal article. The second article has a spine at he distal lateral corner, 1 terminal spine and 1 terminal seta and 2 distal medial setae. The spines are very flat, with broad serrated marginal flanges. The basal article of the endopodite has no armature but has a row of spinules on its distal margin. The second segment has 1 lateral seta, 2 terminal setae and 2 distal medial setae. This is the same complement of armature as found in the first copepodid. In the later period of this stage one can see the developing rami of the third copepodid under the cuticle (fig. 60, m).

The second leg (fig. 60, n) is biramous, with bimerous protopodite and rami. The intercoxal lamella is subquadrate. The armature, segmentation and ornamentation are exactly as in the first leg except that there is an additional seta on the medial distal corner of the basal article of the endopodite.

In the late second copepodid one can see the leg of the third copepodid developing under the cuticle (fig. 60, o).

The third leg (fig. 60, p) now metasomal and functional at this stage, is biramous, with bimerous protopodite and unimerous rami. The intercoxal lamella is subquadrate, well developed. The coxopodite has no armature or ornamentation. The basipodite has a short seta on the lateral margin. The exopodite has 1 minute spinule at the middle of the lateral margin, a distal lateral spine, 1 terminal spine and 1 terminal seta and 2 distal medial setae. The spines are greatly flattened and have broad serrate flanges marginally. The endopodite has 1 distal lateral seta, 2 terminal setae, 2 distal medial setae and 1 proximal medial seta. In the late second copepodid one can see the leg of the third copepodid developing under the cuticle (fig. 60, q).

The first segment of the urosome bears the rudimentary fourth legs (fig. 60, r). Each consists of a bilobed pad, with a single seta articulating on the face of the medial lobe. The second urosomal segment has no armature or ornamentation. The unornamented anal somite bears only the caudal rami. Each ramus is about 2/3 as long as the anal somite (fig. 60, s). There are 5 setae, 1 at the proximal lateral third, 1 at the distal third of the dorsal surface and 2 setae, and 1 setule terminally. The medial terminal seta is the longest. The 2 long terminal setae and the lateral seta bear coarse hair.

The remaining setae are unornamented.

The third copepodid of *E. capitulatus* (fig. 61, a) shows a drastic change of body configuration,

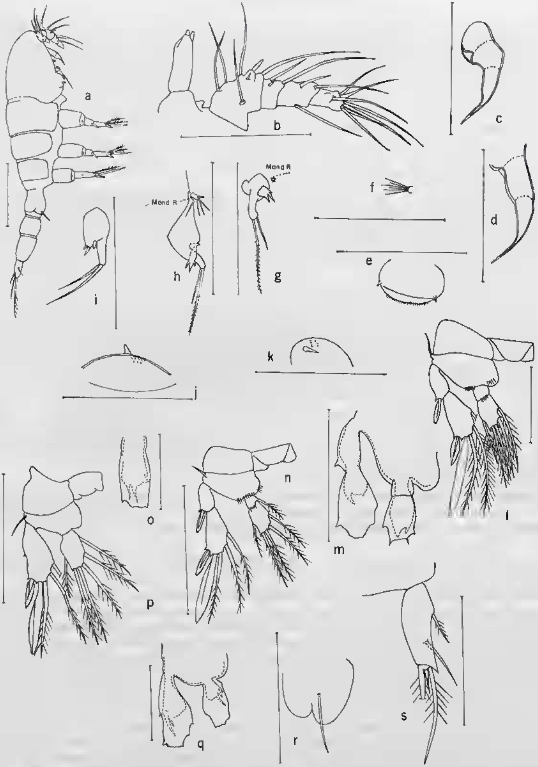

Fig. 60. — ***Enteropsis roscoffensis*** **from *Styela* : second copepodid ; a, habitus, lateral ; b, rostrum and antennule ; c, antenna ; d, antenna ; e, labrum ; f, mandibular remnant ; g, mandibular remnant and maxillule ; h, mandibular remnant and maxillule ; i, maxillule ; j, maxilla ; k, maxilla ; l, first leg ; m, outline of rami of first leg of late second copepodid, showing developing leg of third copepodid ; n, second leg ; o, outline of endopodite of late second copepodid showing developing endopodite of second leg of third cope podid ; p, third leg ; q, outline of rami of leg of late second copepodid showing developing leg of third copepodid ; r, fourth leg : s, caudal ramus. Scales for a, n, p = 0.1 mm ; other scales = 0.05 mm.**

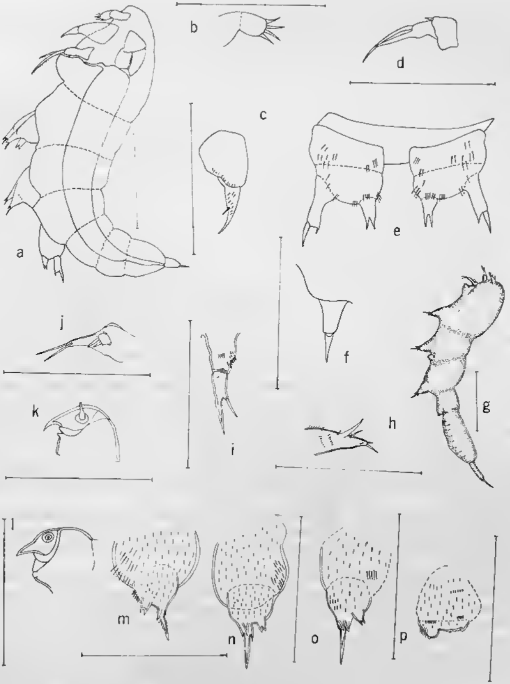

Fig. 61. — *Enteropsis capitulatus* : third copepodid (a-f) ; *Enteropsis superbus* : fourth copepodid (g-p) : a, habit, lateral ; b, antennule ; c, antenna ; d, base and distal process of maxillule ; e, first leg ; f, caudal ramus ; g, habitus, lateral ; h, antennule ; i, antenna ; j, maxillule ; k, maxilla ; l, maxilla ; m, first leg ; n, second leg ; o, third leg ; p, rudiment of fourth leg. Scale for g = 0.2 mm ; other scales = 0.1 mm.

no longer typically cyclopoid, but approaching the definitive eruciform habitus. There are still only 3 pairs of legs well-formed. The segmentation is now much obscured, with indentations rather than articulations spaced along the body. Because we had only a single specimen we could not make out all the appendages. We describe what we could discern satisfactorily.

The antennule (fig. 61, b) is obscurely bimerous, with 4 terminal setae.

The antenna (fig. 61, c) is bimerous, with the much larger basal article ornamented with a row of spinules. The terminal article tapers to a sharp point, evidently due to a coalescence of a terminal seta. There is a subterminal setule, and a general ornamentation of spinules.

Only one lobe of the maxillule was made out (fig. 61, d). This is set on a base and ends in a setiform process and an accompanying articulated seta.

The first leg (fig. 61, e) is biramous, with obscurely bimerous protopodite and unimerous rami. The articulations of the rami with the protopodite are also obscure. The articles of the protopodite have no armature but there is a general covering of spinules. The exopodite has 1 terminal, articulated seta and a medial terminal spiniform projection. The endopodite ends in 2 spiniform projections. There is no ornamentation on the rami. The present form of the appendage was apparent within the cuticle of the previous copepodid stage when we observed this specimen in life (fig. 60, m).

The second and third legs are relatively similar to the first but probably have additional processes, as seen within the cuticle of the preceding stage (figs. 60, o, q).

There are clear indications of 3 urosomal components, 2 segments and the anal somite bearing the caudal rami. Each caudal ramus (fig. 61, f) consists of a truncate cone, with a single articulated spiniform projection continuing its taper.

We cannot support our concept of the life history within the genus by a continuous sequence of stages molted one into the next, but by comparison with related notodelphyids and from the anatomical graduations we are relatively sure the copepodids collected from the host represent the penultimate and the antepenultimate stages. As cyclopoids they should thus be the female fourth and fifth copepodids.

As in the third copepodid of *E. capitulatus* the body of the female fourth copepodid of *E. superbus* is eruciform (fig. 61, g), with the segmentation obscured. The overall length is 0.80 mm. There are still only 3 pairs of legs developed, with indications of the fourth. The composition of the urosome remains 2 segments and the anal somite. There is a general body covering of fine hairs and the ventral surface of the urosome is covered with broken rows of spinules.

The antennule (fig. 61, h) is unimerous. There are 4 conspicuous setae and several setules, the exact number obscured by the spinulose ornamentation.

The antenna (fig. 61, i) is bimerous, heavily sclerotized. The basal article is ornamented with patches of spinules. The distal article tapers to a spiniform process. At the base of this there is an articulated setule.

There is no mandible. The maxillule (fig. 61, j) is bilobed. A small subquadrangular lobe is well articulated basally and bears 2 terminal setae. The main portion of the appendage is extended as a long, finger-formed lobe, obscurely articulated on the base. It bears 2 subequal terminal articulated setae.

The maxilla (figs. 61, k, l) is bimerous and heavily sclerotized. It has assumed essentially the definitive form for the genus at this stage. The basal article has no armature or ornamentation but there is a triangular projection at the distal medial margin. The terminal article forms a complicated articulation with the base. It is so arranged as to direct a pointed beak-like process medially. Set in a subcircular unsclerotized space on the ventral face is a stout seta. There is no maxilliped.

The first three legs are similar (figs. 61, m-o). Each of these legs is biramous, with poorly articulated protopodites, of obscurely indicated components, and with the rami coalesced with the base. The protopodite portion is ornamented with a general covering of hairs and rows of spinules. The endopodite is a very short lobe ending in 2 spiniform projections. The exopodite ends in 1 major spiniform projection surrounded basally by several shorter spiniform projections.

The fourth legs are represented only by a pair of lobes (fig. 61, p). The caudal rami are not actually articulated on the anal somite and they diverge markedly (fig. 62, a). They are proportionately long at this stage, each approximately equal in length to that portion of the urosome corresponding to the anal somite. At a slight demarcation each continues as an equally long spiniform process. The rami are covered with hairs and the spiniform projection has a short lateral spinuliform ornamentation along the proximal half of its length.

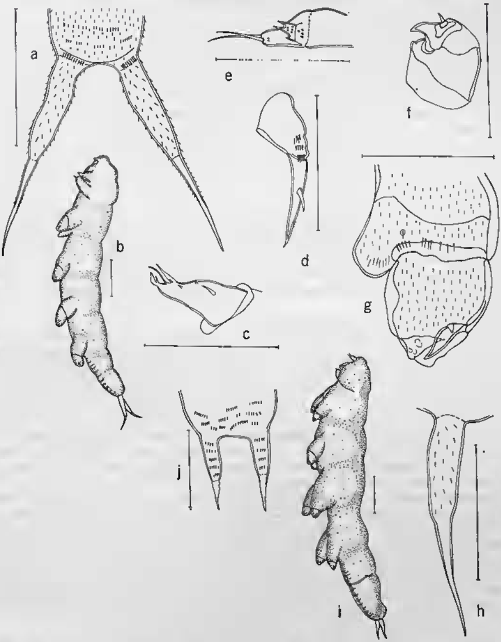

FIG. 62. — *Enteropsis superbus* : fourth copepodid (a) ; female fifth copepodid (b-h) ; immature adult female (i-j) : a, caudal rami ; b, habitus, lateral ; c, antennule ; d, antenna ; e, maxillule ; f, maxilla ; g, first leg ; h, caudal rami ; i, habitus, lateral ; j, caudal rami. Scales for b, i = 0.2 mm ; other scales = 0.1 mm.

No males were discovered by us, but it is very probable that *Haligryps aculeatus* Aurivillius is the male fourth copepodid of *Enteropsis sphinx*, as discussed above under that species.

The eruciform body of the female fifth copepodid of *E. superbus* (fig. 62, b) strongly resembles the adult. The overall length is 1.54 mm. There are 4 pairs of legs. The composition of the urosome appears to be 1 segment and the anal somite with its caudal rami. There is a general body covering of fine hairs and the ventral surface of the urosome is ornamented with broken rows of spinules.

The antennule (fig. 62, c) is unimerous. There are 5 setae and 2 obvious setules. There is no ornamentation.

The antenna (fig. 62, d) is bimerous, heavily sclerotized. It is as strongly developed as in the adult and has not changed in composition from the preceding copepodid.

There is no mandible.

The labrum is a simple, sclerotized lobe. The maxillule (fig. 62, e) is bilobed. The longer lobe has a clear articulation on only one surface, the shorter is clearly articulated. The latter is flattened and terminates in 3 unarticulated, flattened processes, each triangular in outline. Two of these are subequal, the third is much shorter. Spinules ornament the ventral surface. The longer lobe is slightly tapered, truncate, and bears 2 articulated, subequal, terminal setae. There are 2 subapical spinules.

The maxilla (fig. 62, f) is like that of the fourth copepodid and the adult. There is no maxilliped.

The four pairs of legs (first leg, fig. 62, g) are much alike and just as in the adult. Each leg is uniramous, bimerous. There is a general covering of fine hairs. The proximal article has heavy sclerotizations. On the anterior surface there is a single short setule emerging from a pit in the sclerotization and a row of spinules ornaments the distal margin. The distal article has a complicated apex. There is an apical medial tuberculated lobe, possibly a remnant of the endopodite. Beside this is a socket which received an articulated, heavily sclerotized terminal spine. The latter is possibly a remnant of the exopodite.

There is no sign of fifth or sixth leg at this stage.

The caudal rami are not articulated on the anal somite and they do not diverge as markedly as in the preceding copepodid stage. They are still relatively long, each just slightly shorter than that portion of the urosome corresponding to the anal somite. Beyond a slight demarcation at mid-length each ramus continues as a tapered spiniform process. Each ramus is rather sparsely coated with fine hairs.

The smallest adult of *E. superbus* obtained was 1.5 mm long, (fig. 62, i) almost the same size as the fifth copepodid. Its general body aspect and the appendages are exactly those of the larger specimens. Because of its smaller size, the caudal rami appear more salient than in large females (fig. 62, j). Since the largest specimen found measured 8.2 mm, it is apparent that a great increase in size can take place in this stadium without molting.

Developmental stages of a species of *Botryllophilus* were dealt with in a study of development of notodelphyids (Dudley, 1966). The first nauplius has the following features. The antennule is trimerous, the basal article is unarmed, the second has only 1 ventral seta, the terminal article has 2 apical setae and an aesthete. The antenna consists of a bimerous protopodite, unimerous endopodite and tetramerous exopodite. The protopodite has no setae. The endopodite has 1 medial seta and 2 terminal setae. Each of the 3 basal articles of the exopodite has 1 seta and the terminal article has 3 setae. The mandible consists of a bimerous protopodite, bimerous endopodite and tetramerous exopodite. The protopodite has no setae. The endopodite is about 2/3 as long as the exopodite and bears 2 setules and 2 setae. Each article of the exopodite bears a single seta.

The copepodid of *Botryllophilus* features the emergence of the maxilliped of the adult and all the other head appendages are present (Dudley, 1966, p. 160). The characters of these appendages form highly distinctive features of the lineage of *Botryllophilus* and close relatives among the ascidicolid copepods.

Canu's description and figures of features of the nauplius and the copepodids of "*Aplostoma*" *brevicauda* Canu (1892, p. 88-90) have been confirmed (Dudley, 1966, p. 157, 160). In the first nauplius the antennule is trimerous, the basal article unarmed, the second with 2 setae, the terminal article with 2 apical setae. There is no terminal aesthete. The antenna has a bimerous protopodite, unimerous endopodite and tetramerous exopodite. The protopodite lacks setae. The endopodite has 1 medial setule, 2 terminal setae. Each of the 3 basal articles of the exopodite has 1 seta, the terminal article has 3 setae. The mandible has a bimerous protopodite, bimerous endopodite and tetramerous exopodite. The protopodite lacks setae. The endopodite has 1 setule and 2 setae. The endopodite is about 2/3 as long as the exopodite. Each of the articles of the exopodite bears 1 seta.

In the copepodid the haplostomin also shows the well developed maxilliped characteristic of *Botryllophilus*. However, other of the mouthparts may show great reduction. The features of development and the developing and adult appendages have been worked out by Ooishi (to be published). Ooishi & Illg (1977) invoked these developmental features to interpret the anatomies in the haplostomin genera. Added to the information on *Botryllophilus* from the work of Dudley (1966) and the details compiled above, we have the basis for our interpretation of the anatomical details of the appendages in the ascidicolid subfamilies.

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