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Ascidicolous copepods of Dillon Beach, California

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ASCIDICOLOUS COPEPODS
OF DILLON BEACH, CALIFORNIA

A Thesis
Presented to
The Faculty of the Department of Zoology
College of the Pacific

In Partial Fullfillment
of the Requirements for the Degree
Master of Arts

by
David Horace Montgomery
June 1956

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INTRODUCTION

Work on the copepods parasitizing ascidians has been relatively extensive in Europe, less so on the East Coast of the United States and negligible on the West Coast. Of this work, a major portion has been concerned with the solitary ascidians, while the colonial or compound forms have been largely neglected. The apparent lack of interest in copepods parasitizing compound ascidians may be attributed to the smallness of the animals, their associations with both zooids and the colonial matrix which makes dissection difficult, and the chaotic condition of their taxonomy. The writer has here attempted a compilation of basic knowledge concerning the ascidicolous copepods, and he has described species collected at Dillon Beach, California. Taxonomic confusion prevents identifications beyond those of families, but the writer hopes that the results of his efforts may stimulate additional studies on the much-neglected ascidicolous copepods of the Pacific Coast.

HISTORY OF RESEARCH ON ASCIDICOLOUS COPEPODS

Among the animals studied by man, one of the most fascinating groups is the class Copepoda. Free-living and parasitic, ranging from microscopic size to several inches in length, assuming great diversity of form and habitat, they offer a challenge to the student of zoology.

A major classification of the Copepoda segregates the animals into those of the free-living species and those that are parasitic, semi-parasitic or commensal with a variety of hosts or, in some cases, with a specific host. Copepods have been found in various associations with practically every known marine invertebrate, with many marine and freshwater fishes, and in some cases with such unlikely hosts as the lowly Porifera (Topsent, 1928).

Of the parasitic groups perhaps none assumes body shapes more dissimilar to their free-living relatives than do the ascidicolous copepods. They make their homes in the branchial sacs and stomachs of ascidian zooids; they burrow and move throughout the test of a colony; they riddle both the colony tests and zooids with their bodies and eggs until survival of the colony seems threatened, although no work has been done on the pathology of these infections.

Research on the ascidicolous copepods began with the work of Costa (1829) and Allman (1847). Thorell (1859, 1860), Claus (1864), Hesse (1864-78) and Bucholz (1869) made early contributions. Brady (1878) published a three-volume treatise on the free and semi-parasitic copepods of the British Isles which included portions on the ascidicolous copepods, and Kerschner (1879) followed this with a publication on the Notodelphyidae. The work of Canu (1890-92) marked the advent of more comprehensive work on the ascidicoles. Others in the same decade who did much to erect new taxonomic groups in the field were Aurivillius (1882-87), Giesbrecht (1882), Thompson (1888).

With the turn of the century scholars in France began a period of research that was to last until 1930. This investigation was headed by such men as Chatton (1909-24) at Laboratoire Arago working with Brément (1909) and Harant (1922). Their works were confined to the ascidicolous copepods and they did much toward clarifying the taxonomic position of many of the groups. Norman (1906), Brian (1905), Pesta (1909), Scott (1901-07) and Giesbrecht (1901) contributed findings. Probably the first comprehensive compilation of such research was attempted by Sars (1921). This work, monumental in scope, was published about the same time that Schellenberg (1921) published a like study of the Notodelphyidae, together with keys to the genera, at the Berlin museum.

Several genera were incorrectly assigned positions in the family, an error that only lately has been corrected. Wilson (1932) published a monograph on the copepods of the Woods Hole Region of Massachusetts. The 1940's brought to the fore the work of such men as Barnard (1948), Capart (1941), Gurney (1945), Heegaard (1947), Nicholls (1944), Pearse (1947) and Sewell (1949). Lang (1946-49) published articles which cleared away much of the "deadwood" and tried to consolidate the group. Work in the current decade is being carried on by Lang (in press), Gotto (1952-56), Grainger (1950), Illg (1951-55), Stock (1950-51), Lindberg (1952) and Deboutteville (in press) of the Laboratoire Arago, Chatton's successor.

Earlier works sometimes lacked accurate measurements and many times tended to place more emphasis on general outline and color than on exact descriptions and measurements. It is the morphological detail of appendages upon which copepod classification is now largely based.

TAXONOMY OF THE ASCIDICOLOUS COPEPODS

The taxonomic picture of the ascidicolous copepods remains confused and, in order to achieve some clarification, a review of taxonomic literature is here presented. Early reports merely lumped these copepods under a general heading of Ascidicolidae. Sometimes the designation was used in a broad sense to cover all ascidicolous copepods; sometimes it was used as a true family including all copepods without dorsal brood pouchs.

Thorell (1859) differentiated the Copepoda into three groups on the basis of mouth parts: Gnathostoma, those with true mandibles; Siphonostoma, those with sucking mouth parts; Poecilostoma, those with indefinite mandibular structures. Gnathostoma and Poecilostoma were further divided into four families, two of which were directly concerned with the ascidicoles. These families were: Calanidae, Cyclopidae, Notodelphyidae and Buprovidae. The family Notodelphyidae, concerned with ascidicolous copepods, was split into two sub-families: Notodelphyinae verae and Ascidicolinae. The genera listed under Notodelphyinae verae included Botachus Thorell, Doropygus NOB, Gunenotophorus Costa, Notodelphys Allman, and Notopterophorus Costa. Under the sub-family Ascidicolinae was a single genus, Ascidicola NOB.

Buproridae, also concerned with ascidicolous copepods, had but a single genus, Buprorus Thorell.

Canu (1892) believed that a major characteristic of the main divisions in the Copepoda should be the placement and number of the genital pores on the female. Using these as criteria, he divided the group into two primary divisions: Monoporodelphya, whose females had but a single, ventral, genital pore, and Diporodelphya, where the females possessed two ventral pores. The latter group was then divided into Ascidicolides, Cyclopides, Calanides and Harpacticides. Only one division, the Ascidicolides, is noteworthy here, and under this Canu listed the following genera: Aganthaner Canu, Aplostoma Canu, Bonnierilla Canu, Doroixys Kerschner, Doropygus, Enterocola van Beneden, Enteropsis Aurivillius, Gunenotophorus and Notodelphys.

Brady (1878) listed the families: Artotrogidae, Calanidae, Corycaeidae, Cyclopidae, Harpacticidae, Misophriidae, Notodelphyidae and Sapphrinidae. He further divided Notodelphyidae into the sub-families: Ascidicolinae, Doropyginae, and Notodelphyinae. The Doropyginae possessed the genera of Botachus, Doropygus and Notopterophorus. Ascidicola was listed under Ascidicolinae, while Notodelphyinae had one genus, Notodelphys.

Sars (1921) and Schellenberg (1921-22) independently

assembled compilations of previous publications. While Sars dealt with all the Crustaceae of Norway, Schellenberg's work was concerned exclusively with the notodelphids. Some overlapping of generic placement occurred, which might have been avoided had Sars' publication been printed earlier.

Sars made a major change in the then existing taxonomic structure. Giesbrecht (1882) had split the Copepoda into two sub-orders, Podoplea and Gymnoplea. Under the Podoplea he had listed a tribe Ampharthrandia, containing the families Notodelphyiada, and Monstrilloida. Sars believed that several morphological inconsistencies within the Ampharthrandia demanded the elevation of both the Notodelphyiada and the Monstrilloida to the ranks of sub-orders. He believed, furthermore, that ecological and life-history differences should be incorporated in taxonomic thinking.

Sars' scheme of classification established the Notodelphyiada and Monstrilloida as sub-orders. Under Notodelphyiada he listed six families, some old, some new. These were: Ascidicolidae, Botryllophilidae, Buproridae, Doropygidae, Enterocolidae and Notodelphyidae. Generic break-down is as follows: Aganthaner, Notodelphys under Notodelphyidae; Buprorus under Buproridae; Ascidicola under Ascidicolidae; Botryllophilidae included Botryllophilus Hesse, Pteropygus, Sars and Schizoproctus Aurivillius. Enterocolidae included Enterocola, Cryptopodus Hesse and Mycophilus Hesse, while

the largest group was that of Doropygidae, containing Botachus, Doropygus, Doropygopsis Sars, Doropygella Sars, Gunentophorus, Pachypygus Sars and Notopterophorus.

The above taxonomic arrangement is in marked contrast to that of Schellenberg, who established a single family, Notodelphyidae, containing the sub-families Notodelphyinae and Ascidicolinae. Schellenberg included under Notodelphyinae the genera: Bonnierilla, Botachus, Campopera Schellenberg, Doroixys, Doropygus, Gunentophorus, Lonchidiopsis van hoffen, Ophioseides Hesse, Paranotodelphys Schellenberg, Notodelphyopsis Schellenberg and Notopterophorus. The Ascidicolinae included Ascidicola, Aplostoma, Botryllophilus, Enterocola and Mycophilus.

Wilson (1932) followed Sars' scheme of classification but, when dealing with ascidicoles, included many genera not parasitic in ascidians. Under sub-order Notodelphyoidae he listed not only all the fore-going and many more parasitic in ascidians, but such aberrant genera as: Ive, parasitic in Balanoglossus; Lamippe, whose host was an alcyonarian; Nerocola, parasitic on annelids; Lomanticola, a nudibranch parasite.

Lang (1948) presented the latest and most logical division, at least to family. He agreed with Giesbrecht that the Copepoda should be divided into Podoplea and Gymnoplea

but thought that a third and fourth sub-orders were necessary. The Platycopiidae, for instance, were regarded as having branched off a main stem before Podoplea and Gymnoplea, and the family Misophriidae and its allies were unique in the possession of a heart. Lang felt that these distinctions demanded elevations of the families to order ranks.

Lang and Sars both utilized mouth parts as basic taxonomic criteria as originally proposed by Thorell. Since, however, complete agreement seemed impossible among investigators as to the interpretation of mouth parts, Lang distinguished between the Poecilostoma and Gnathostoma by the structure of the male antennule. He considered the occurrence of a non-prehensile antennule a primitive characteristic and so placed those animals with the Poecilostoma. The Gnathostoma possesses prehensile antennules, that is, antennules used for clasping. The Enterocolidae are thus placed with the Poecilostomes because of the reduced mouth parts and non-prehensile antennules of the male, indicating that they may have had a common root in the Poecilostoma. The following is a representation of Lang's classification concept.

COPEPODA

<u>Progymnoplea</u>	<u>Gymnoplea</u>	<u>Propodoplea</u>	<u>Podoplea</u>
Harpactoida			Cyclopoida
Cyclopoida gnathostoma		Cyclopoida siphonostoma	Cyclopoida poecilostoma

The sub-section Cyclopoida gnathostoma was then divided into two tribes. Cyclopoida gnathostoma cyclopinidiformes, free-living forms lacking a dorsal brood pouch, constituted one group and Cyclopoida gnathostoma notodelphyidiformes, those possessing a dorsal brood pouch, and parasitic on ascidians, the other. The Cyclopoida gnathostoma notodelphyidiformes were further split into sub-tribes: Notodelphyidimorpha, with a brood pouch and the fifth pair of legs placed ventrally; Ascidiocolidimorpha, without a brood pouch and with fifth legs dorsal or dorsolateral. The relationships of the Cyclopoida gnathostoma are presented below.

Cyclopoida gnathostoma
notodelphyidiformes

Cyclopoida gnathostoma
cyclopinidiformes

Notodelphyidimorpha

Ascidiocolidimorpha

Notodelphyidae

Ascidiocolidae

Doropygidae

Botryllophilidae

Buproridae

The Cyclopoida poecilostoma are divided into Cyclopoida poecilostoma lichomolgidiformes and Cyclopoida poecilostoma enterocolidiformes. The scheme regarding the Cyclopoida poecilostoma is shown as follows.

Cyclopoida poecilostoma
lichnomolgidiiformes



Lichnomolgidimorpha



Lichnomolgidae

Cyclopoida poecilostoma
enterocolidiformes



Enterocolidimorpha



Enterocolidae

The following is a list of genera encountered in the literature to date.

Agnathaner	Canu	1892
Ascidicola	Thorell	1859
Aplopodus	Hesse	1869
Adranesius	Hesse	1865
Amompsyllus	Sars	1921
Botachus	Thorell	1859
Bonnierilla	Canu	1891
Botryllophilus	Hesse	1864
Bremenia	Chatton & Brément	1915
Blakeanus	Wilson	1921
Buprurus	Thorell	1859
Campopera	Schellenberg	1921
Cryptopodus	Hesse	1865
Doroixys	Kerschner	1879
Doropygella	Sars	1921
Doropygopsis	Sars	1921
Doropygus	Thorell	1859
Dysgenopsyllus	Nicholls	1944
Enterocola	van Beneden	1860
Enterocolides	Chatton & Harant	1922
Enteropsis	Aurivillius	1885
Goniodelphys	Buchholtz	1869
Gumentophorus	Costa	1840
Haplosaccus	Chatton & Harant	1924
Haplostomides	Chatton & Harant	1924
Haplostomella	Chatton & Harant	1924
Haplostoma	Canu	1886
Hypogastrion	Wilson	1924
Hypnoticus	Wilson	1924
Lequerra	Chatton & Harant	1924
Lichnomolgides	Gotto	1954
Lichnomoligus	Thorell	1860
Linchidiopsis	Van hoffer	1917
Lygephilus	Hesse	1865
Mycophilus	Hesse	1865
Narcodina	Wilson	1924
Notodelphyopsis	Schellenberg	1921

Notodelphys	Allman	1847
Notopterophoroides	Schellenberg	1921
Notopterophorus	Costa	1829
Ooneides	Chatton & Brement	1915
Ophioseides	Hesse	1864
Pachynesthus	Hesse	1878
Pachypygus	Sars	1921
Paranotodelphys	Schellenberg	1921
Platythorax	Hesse	1866
Podolabis	Hesse	1864
Polyoon	Hesse	1878
Pseudonotodelphys	Gurney	1927
Pteropygus	Sars	1921
Schizoproctus	Aurivillius	1885
Scolecimorpha	Sars	1926
Tranestoma	Wilson	1924
Ustina	Illg	1951
Zanclopus	Calman	1908

Names of several genera in the above list are newly established to replace those rendered invalid by prior usage. They are: Hypnoticus (Hypnodes) (Hesse 1865) Wilson 1924, Hypogastrion (Gastrodes) (Hesse 1865) Wilson 1924, Narcodina (Narcodes) (Hesse 1865) Wilson 1924, and Tranestoma (Aplostoma) (Canu 1886) Wilson 1924.

KEY TO THE FAMILIES OF ASCIDICOLOUS COPEPODS

1. Antennules of male not always prehensile; commensals; dorsal brood sac or 5th pair of legs placed dorsally or dorsolaterally.....2
1. Antennules of male always prehensile; free-living; no dorsal brood sac, 5th pair of legs ventral.
.....Cyclopoida gnathostoma cyclopoidiniformes.
2. Dorsal brood sac; 5th pair of legs ventral.....3
2. Lacking dorsal brood sac; external ovisacs; 5th pair of legs dorsal or laterodorsal.....4
3. Head usually well defined; antennae short, stout, joints reduced in number; 4 anterior pairs of legs poorly developed; 5th pair of legs rudimentary.....6
3. Head not well defined, fused with 1st thoracic segment; antennae moderate size, many setaceous joints; antennule prehensile, ending in strong claw, smaller than antenna; body cyclopoid; tail 5-segmented; 4 anterior pairs of legs cyclopoid, adapted for swimming; 5th leg very small, biarticulate.....NOTODELPHYIDAE
4. 1 or 2 free ovisacs on dorsal surface of abdomen; tail of 4 or varying number of segments; antennae short, thick; 4 anterior pairs of legs very reduced.....5
4. Antennae very small; antennules not prehensile, bi-articulate; body shape vermiform, faintly segmented; tail poorly developed; 4 anterior pairs of legs imperfectly developed, rami rudimentary; 5th pair of legs 2 short, lateral lappets, when present; caudal rami small, simple, bladelike.....ENTEROCOLIDAE
5. Antennules not prehensile; body shape segmented, anterior and posterior sections sharply delimited; 4 anterior pair of legs more or less reduced; 5th pair of legs modified support for ovisac; caudal rami end in strong, claw-like spines.....BOTRYLLOPHILIDAE

5. Antennules slender, prehensile; body shape slender, vermiform; anterior and posterior sections not delimited; 5th pair of legs modified into large lamellae covering genital area; caudal rami simple, lacking claw.....ASCIDICOLIDAE
6. Antennules prehensile, ending in claw; body shape curved ventrally, compressed, sharp delimiting of anterior and posterior sections; tail 4-segmented; caudal rami with few or lacking setae, may have hooks.....DOROPYGIDAE
6. Antennules not prehensile, armed with simple spines; body shape short, stout, unsegmented, merely head and trunk; tail not distinguishable or absent; caudal rami absent or rudimentary.....BUPRORIDAE

METHODS AND PROCEDURE

Collection Data

Collection of specimens was concentrated during the period from July 30 through August 25, 1955. Since the latter date collections have been made at least once a month to the present time. All collections were taken in Marin County, California. The majority of wave-cast specimens were found on the beach at the area known to Pacific Marine Station students as Second Sled Road (Plate 5). Other loose specimens were recovered from the beach below Perch Rock and the water near Pelican Point. Attached forms were taken from the area around Castle Rock, Bodega Jetty, Perch Rock and the wharf pilings at Marshall's and Villicich's harbors (Table I). Solitary ascidians such as Styela montereyensis were taken from the Castle Rock area. Ascidia ceratodes and Ciona intestinalis were dredged from Tomales Bay. No enterocolids or notodelphyids were found in solitary forms, but two female botryllophilids were encountered.

The initial collection was of one Amaroucium californicum colony encrusted on a stipe of Fucus sp. Subsequent collections were made along the beach where the supply was

plentiful even during high tides. The collections covered a number of ascidian genera (Table 1). However, it was felt that data procured in such a manner might be invalid because of the possibility of abnormal infections acquired while drifting or in a partially necrotic state. Consequently, collections were made both of attached and drifting forms of the same species. Comparisons revealed identical parasitic conditions.

Enterocolid parasites were found during the entire collection period. Their numbers increased during late August and early September, and then declined sharply in October though the numbers of ascidians collected remained the same. During the latter part of August, however, infections had so increased that it was possible to examine a colony in the field with a 10x hand lens and perceive parasites under the transparent test.

The notodelphyids were first encountered August 20, 1955. Miss Jane Westfall, of the University of California at Berkeley, brought in a wave-cast specimen of Amaroucium solidum. It was very heavily parasitized with notodelphyids in all stages of development. Thereafter until early October

notodelphyids were encountered in large numbers. The first collection in November and subsequent collections, however, failed to reveal any infections.

Collection of the unidentified parasite was begun August 18, 1955 (Plate 4, fig 3). Heretofore the writer may have mistaken these copepods for the nutrient masses encountered in the ascidian, Syncoinum par-fustis. The parasites were very much in evidence until early October when the incidence of infection took a sharp drop (Table 2). None was found after November.

Laboratory Techniques

One of the major problems faced in the laboratory was the extraction of zooids from colony masses without damage either to the fragile zooid or the smaller parasite within. Light (1954) advised the use of forceps to pull gently the zooids from the test. This was tried, found to work well for zooids without a post-abdomen, but was inadequate for the removal of Amaroucium spp. zooids, where the post-abdomen makes up two-thirds of the total body length (Plate 6). Furthermore, the wave-cast specimens were partially disintegrated and the pulling only served to break many zooids. In some ascidians (e.g. Polyclinum planum) with a tough test, the method was useless.

A second method was the squeezing of the entire colony in a bowl of sea water. It was found that permitting the colonies to remain in areated aquaria for two to three hours before squeezing hastened the liberation process. The change from the natural habitat to the confines of the aquarium seemed to loosen the test surrounding the individual zooids. The time required for loosening, however, varied with different species. Amaroucium spp. were easily extracted after a half-hour, while the test of Polyclinum spp. and Cystodytes lobatus resisted any sort of action up to twenty-four hours.

After comparison of the above methods a mass-removal technique was evolved. The specimens were placed in aquaria and allowed to remain for from one to eight hours. After the colonial test had loosened sufficiently, the specimen was washed in filtered sea water and gently squeezed into a bowl containing filtered sea water. Filtered sea water was used to eliminate chances of other non-ascidicolous copepods being misassociated with a given species of ascidian.

Pressure was exerted on the colony from all sides, and the zooids literally "popped" from the colony test. Damage to some zooids was unavoidable but, with practice, the writer was able to lower the incidence of injury. The colony was checked from time to time with a hand lens. As many as fifty small culture dishes containing filtered sea water were

placed on a table. After the mass of liberated zooids and parasites was allowed to settle, four or five drops of the material were placed in each of the culture dishes. The unavoidable mashing of ascidian testes and the attendant release of sperm, the breaking down of the colonial matrix and the fragmentation of some of the zooids necessitated limiting the amount placed in each dish. Dilution of the mass with sea water provided the observer with a clear view of zooids, copepods, mites, amphipods and other organisms present.

In some colonies, where the parasites could be seen with the hand lens or naked eye, thin slices were made, both parallel and perpendicular to the long axis of the colony. These sections were then examined under transmitted and reflected lights. The contrast of the relatively opaque body mass of the parasite with the transparent zooids facilitated detection and removal. Parasites could then be easily removed with a probe. Although some parasites were damaged by the slicing, the method proved invaluable for cursory examination of the colony and observation of parasites within the canals.

Parasites found free in the water were placed apart from those still within the colony or zooid, so that the patterns of behavior could be observed. The animals were also segregated according to: (1) family, (2) possession of att-

ached egg capsules, (3) stage of development and (4) sex.

Attempts were made to rear the nauplii of all groups, but without success. Either laboratory conditions were inimical to normal development or some environmental factor was lacking. Nauplii seldom lived longer than twenty-four hours and no molts were observed.

Most preserved specimens were fixed in Bouin's with sea water. According to Dr. Illg, Miss Patricia Dudley, University of Washington reports that Bouin's is very good for sectioning but recommends short fixation of one to a few hours, before transference to alcohol. For killing and fixing any small crustacean Gray (1954) states, "it is however much easier to identify specimens if their appendages are properly spread out, and the writer kills crustaceans either with weak alcohol or chloroform, a few drops of which are sprinkled on the surface of the water. After dropping to the bottom they will be found to be flexible, and may then be arranged more or less in the order required, and 95% alcohol cautiously dropped on them until they have stiffened into position. Such specimens may then be transferred to a tube of 95% alcohol where they will retain the required shape until needed for mounting." Illg reports excellent results with the above method, and further cautions against xylol, toluol, and other dealcoholizers which render material destined for dissection too brittle for manipulation.

COMPOUND AND SOLITARY ASCIDIANS

Vane Name (1945) divides the ascidians morphologically into two groups: the solitary and compound ascidians. The colonial or compound forms reproduce both sexually and by budding. The solitary or simple forms, which are usually much larger than the individuals of a colony, normally do not bud.

Solitary ascidians are typically sac-like organisms, ranging from less than an inch to two or three inches in diameter and covered with a tough protective tunic usually referred to as the test. The inner organs are completely surrounded by a membranous tissue or mantle, which makes possible the removal of the entire body from its test. Within the sac-like body is a spacious cavity, very delicate in appearance, which is the pharyngeal or respiratory portion of the gut. It is termed the branchial sac. On the ventral aspect of the branchial sac is found the endostyle, a ciliated structure that moves the food posteriorly into the esophagus. The stomach, intestine and rectum form a U-shaped tube terminating in the atrium. Two openings in the test permit the flow of water into the pharynx and out of the atrium. These openings are termed the oral or branchial ap-

erture and the atrial aperture, respectively. The branchial aperture marks the anterior end of the body, while the atrial indicates the dorsal side.

The colonial forms consist of many individuals, called zooids, clustered together in a common mass. They are imbedded in a matrix, secreted by the individuals, with the atrial apertures of individuals opening in common cloacal cavities or canals which run through the colony test, connecting with large surface openings, the common cloacal apertures. The morphology of the individual zooid is essentially the same as that of the solitary ascidian, with the difference that the body mass is divided into distinct regions: the thorax, abdomen, and in the Syncoidae, the post-abdomen, which is a long tube containing the gonads and part of the circulatory system (Plate 6). The heart of the ascidian, tubular in form, is situated in the posterior portion of the body and is able to reverse the direction of the blood flow, so that blood vessels serve as both arteries and veins. In the Syncoidae the heart is situated at the very tip of the post-abdomen.

FREE-LIVING AND PARASITIC COPEPODS

In a comparison of free-living and parasitic copepods, one is impressed by the degeneration of the appendages. The swimming appendages are more or less reduced to stumps which may be incapable of locomotive function. The spines are reduced in number and size. The thoracic appendages are especially abberent. The body segments are enlarged, in some species. The progressive change, especially in the ascidicolous copepods, is from a swimming mode of locomotion toward a feebly crawling one. Indeed, some forms seem to be immobile. This is especially true in the female specimens, which spend most of their life cycles within the host, absorbing food particles from the steady stream of water. It might be significant that the size of the individual ascidian can be correlated with the locomotor function of the female's appendages. Members of the Doropygidae and the Botrylliphilidae inhabit the larger, solitary ascidians, while the Enterocolidae frequent the zooids and test of the compound forms. The thoracic appendages on the Botrylliphilidae seem almost normal when compared with those of Cyclops, (Plate 7) while the same structures in the Enterocolidae seem capable only of crawling.

The shapes of the body segments seem to follow an intraphyletic change from the condition in Cyclops to that of the Enterocolidae and then to that of the notodelphyids and the doropygids where some thoracic segments are expanded to form a dorsal brood pouch not found in the other ascidicolous copepods. (Plate 3, fig 3).

The apparent degeneration of the swimming appendages of the Enterocolidae when compared with those of Doropygidae may be correlated with the habits of the Doropygidae, which are able to move about freely in the fairly large branchial sac of the solitary ascidians, while the enterocolids inhabit the narrow cloacal canals and viscera of the compound species. Long, armed appendages would be a liability in this situation. In some notodelphyids the swimming appendages are reduced to mere flaps of tissue, seemingly incapable of any locomotion. (Plate 3, fig 2).

DESCRIPTION OF PARASITES

Enterocolid #1. (Plate 1)

Body length 1.9 mm., width 0.38 mm. Body color milky white with brown intestine and red oviducts. Nauplii bright red with red eyespots. Metasome four-segmented dorsally. (Fig 1.). Urosome with bluntly lobed caudal rami, armed with one lateral seta and one spine each, curved posteriorly (Fig 3). First to fourth legs bear median, biramous lobes 0.053 mm. long, united with a curved digitiform ramus 0.07 mm. long armed with two claws, one apical, one proximally anterior (Fig 4). Fifth legs located dorsolaterally near fourth pair, rounded lobes bearing apical seta. Antennules 0.07 mm. long, short, thick, bearing several setae. Antennae 0.03 mm. long, three-jointed, with short apical spine (Fig 5). Paired oviducts lateral and parallel to median intestine. External ovisacs 0.6 mm. long attached laterally, posterior to fifth leg (Fig 2).

This animal, like others of the same group, occupied the canals throughout the colony test. When dissected out and placed in a culture dish, the animal was capable of some forward movement on an uneven surface, but locomotion was greatly retarded.

Several animals were dissected out of colonies and placed near or on the exhalent openings. When placed over two centimeters away from an exhalent opening they made clawing motions and finally collapsed on the surface of the test. Otherwise they entered the opening at once and progressed into the center of the test, towing the egg cases behind them. They seemed to have no difficulty passing through the canals, even though at times the egg capsules, quite firmly attached to the genital segment, were longer than the animal itself. In some cases, however, a slight pressure on the test of the colony was enough to sever the animal from the egg capsules. This action was only observed where the developing nauplii had reached a stage where the eyespot, internal structures and appendages were visible. Egg capsules in early stages of development were retained in spite of pressure. Nauplii were observed hatching both in culture dishes and within the test. When hatched in the test, nauplii immediately moved off through the canals.

Animals were also found in the zooids. Here they occupied any of several places: post-abdomen, branchial sac, intestine and atrium. They were found in all stages of development including fully mature parasites with egg capsules. In such cases the parasite and egg cases filled the entire post-abdomen. Specimens developing in the branchial sac projected egg cases out of the atrial aperture, while those

inhabiting the atrium projected them from the atrial opening.

The majority of specimens were found in the tip of the post-abdomen. This region, near the heart, was probably a rich source of nourishment. Forty-seven females, when subjected to a strong beam of light, clawed their ways out of the post-abdomens or branchial sacs. Specimens kept in the dark did not exhibit such a negative phototropism. This aversion to light was not as pronounced in the other enterocolids, but females still clawed their way out of the zooid. They sometimes took the egg cases with them, and sometimes detached the cases, moved to the posterior end of the abdomen and clawed their way out.

This action of rupturing the zooid's body to gain exit was observed repeatedly. Emerging Enterocolid #1 seemed to be accelerated by the strong light, but the other enterocolids reacted indifferently. Over one hundred zooids were found with mature egg capsules in the post-abdomen or branchial cavity. These eggs were observed hatching within the zooid, and the nauplii left the host through the atrial and oral apertures. Hatching was observed within the post-abdomen, and the nauplii left the host zooid and moved off through the canals. No males were encountered.

Enterocolid #2. (Plate 2)

Body 2.24 mm. long, 0.43 mm. wide, curved dorsally, vermiform in appearance (Fig 1). Color opaque white with reddish spots throughout median area. Oviducts purple; nauplii lavender with red eye-spots. Metasome unsegmented dorsally, urosome not defined (Fig 1). Caudal rami 0.07 mm. long, digitiform, bearing two long, apical spines (Fig 4). First leg closely applied to mouth parts, 0.07 mm. long, one-jointed, biramous with very short anterior claw and bluntly pointed posterior lobe (Fig 3). Second to fifth legs biramous, anterior rami 0.006 mm. long, clawlike; posterior rami 0.01 mm. long, rounded lobe united with median, biramous lobed laminae 0.02 mm. long. (Fig 2). Oviducts dorsal and parallel to median intestine.

This form, like enterocolid #1, was encountered in the cloacal canals and zooids. A few animals were encountered in the atrium and branchial cavity. The size of the mature animal was, in most cases, smaller than the diameter of the canals, and locomotion was limited to the action of the legs. Locomotion was not as rapid as in #1. This animal was found most frequently in the post-abdomen in developmental stages, mature individuals occupying the canals. Attachment of the external egg capsules was rather tenuous. Females were observed clawing their way out of zooids, indifferent to light.

Aside from these characteristics, they resembled enterocolid #1 in movement and habits. No males were encountered.

Notodelphyid. (Plate 3)

Body somewhat compressed laterally, curving ventrally; 2.58 mm. long, 1.25 mm. thick (Fig 1). Color pattern varied; some with brown intestine speckled with gold, lime green oviducts and bright green nauplii with red eyespots; others with bright purple intestine, yellow oviducts and nauplii. Other portions of body always milky white. Metasome unsegmented dorsally, forming a brood pouch for eggs (Fig 3). Urosome three-segmented, with two caudal rami. Caudal rami 0.15 mm. long, low, rounded lobes, armed with very short hook or spine. (Fig 3). First three pairs of legs 0.9 mm. long, V-shaped, flabby in appearance, covered with setae (Fig 2). Fourth pair also V-shaped, one-third smaller. Fifth leg minute or absent. Oviducts extend full length of body, lateral and parallel to median intestine. Egg size progressively larger toward posterior end, with eggs emerging into brood pouch. Large unidentified red sphere in anal region.

Female notodelphyids were found inhabiting the cloacal canals and zooids of the three local species of Amaroucium. The animals were found in three definite locations throughout the colony: in cavities on the surface, in the common cloacal canals deep in the test, and in the post abdomen of

of the individual zooids. The mature forms were found only in the surface cavities, the immature specimens within the canals, and early developmental stages in the zooids.

The mature specimens were covered by a thin sheet of the test and were easily removed. The animals did not seem to have any particular orientation to the host as regards the canal opening into the surface cavity. The only motion observed was a slow flexion of the body and peristaltic motions of the gut.

The immature specimens were closely surrounded by the walls of the common cloacal canals. Due to the lack of setae or spines, it is difficult to understand how these animals can dig their own canals, although they may possess enzymes that simplify the task. Feeble movement through the canals seems to be accomplished by pressure of the body and rudimentary appendages against the walls of the canal. It was noted that the immature specimens were more active than the surface-inhabiting forms. They did not seem to be able to crawl along the flat surface of a culture dish, but the movements of body flexion were more vigorous and rapid than in the mature animals. Organs in the juvenile specimens were developing, the oviducts appearing as thin green lines. The gut was the only large, conspicuous organ in the body.

Developmental stages above that of the nauplius were found in the zooids. Specimens were found in all segments of the post-abdomen. In direct contrast with the enterocolids, these animals were not found in the branchial sac or stomach. The characteristic dorsal brood pouch identified these developmental forms as belonging to the notodelphyids. Movement in these smaller animals was very rapid due, apparently, to rapid flexion of the body.

Reproductive processes in the female were especially noteworthy. The eggs emerged from the oviducts into the dorsal brood pouch. Development of the nauplius within the egg continued until the eyespot, internal structures and appendages began to appear. The brood sac contained, on an average, fifty to seventy-five eggs at a time. Upon completion of internal development the nauplii ruptured the thin membrane of the egg and moved freely about in the brood sac. As far as could be observed, the nauplii behaved as do all typical nauplii. Locomotion was in an anterior to posterior direction, along the interior, ventral surface. Within a period of not less than four hours, observed in over thirty such patterns of behavior, the nauplii clustered at the posterior end of the sac. During this activity the animal had continued to slow, methodical flexion of its body. This flexion, first ventrally, then dorsally, became more rapid. The urosome, at the height of the ventral flexion, showed a tendency to bend sharply in a dorsal direction.

When a majority of the nauplii had gathered in the posterior portion of the sac, flexion became very rapid and finally, with a convulsive jerk the urosome was folded sharply up against the ventral surface of the body. A pore appeared at the junction of the metasome and urosome and the hatched nauplii were ejected. They were ejected in groups of five, ten and twenty at a time until almost all the hatched nauplii had been released. Several hatched nauplii that were in the anterior end of the sac at the time of release moved immediately to the pore when release occurred. The animal then straightened its body and resumed flexion. The number of unhatched nauplii ejected with the hatched ones was small. Development of these nauplii continued, and another release was observed seven hours later.

This curious process was viewed with some scepticism at first, for it was thought that, perhaps, the transition from natural habitat to laboratory conditions might have upset the delicate mechanisms of hatching and release. However, the following facts shed some light on the validity of the interpretation. In over thirty specimens possessing mature nauplii in the brood sac, hatching was observed within a period of from three to seven hours after removal from the ascidian. Eight specimens went through the same process while still within the surface cavity, the nauplii being released

into the cavity and immediately scuttling out of sight into the common cloacal passages. Moreover, specimens were examined in the field and the nauplii could be seen dashing back and forth in the sac. The release of the young was always followed by a period of slow body flexion before the next release. Gray (1933) observed numbers of Mycophilus rosovula laying eggs in groups of two and three. The eggs were unhatched. This method of egg-laying and release of young from a brood pouch is markedly atypical of the majority of copepods which bear external ovisacs.

It is significant that this species of notodelphyid, unlike the enterocolids, apparently prefers to deposit young in the surface cavities, rather than lay eggs in the zooid. A reason for this seems evident. The nauplii, upon release immediately enter the cloacal canals, apparently in search of a host zooid. While nauplii of other copepods mature within the zooids and then lay eggs within its body, this notodelphyid attains such size that it would rupture the zooid before it (the parasite) came to maturity. No males were encountered.

Unidentified Copepod: (Plate 4.)

One parasite not identified to family was a white, amorphous form 2.56 mm. long, usually associated with Amaroucium spp. (Fig 3), devoid of identifiable structures. The

entire mass was irregularly ovoid in form, with many projecting lobes. The body mass was more or less filled with developing eggs. Paired egg capsules were attached to one end of the animal. This animal was found in all sizes, from a small white mass without egg capsules, to the fully formed animal with paired egg cases (Fig 2). After the egg capsules attained full size the size of the animal seemed to decrease.

The animal occupied a position across the stomach of the zooid, projecting into the atrium, although a few animals were found in the atrium proper. Each was covered with a thin fold of tunic, easily dissected out, except for the point of attachment to the egg capsule (Fig 1). At this point dissection was impossible. The egg cases projected into the atrium, and thence into the branchial sac; when fully developed they filled the branchial cavity. Hatched, the nauplii emerged from the branchial aperture.

This animal was found in great numbers during the middle of August, 1955. It became so widespread among Amaroucium spp. that the surface of the colony seemed to be speckled with white. No males were encountered.

DISCUSSION

The life history of an ascidicolous copepod is a difficult thing to demonstrate. The absence of males, failure to rear nauplii and absence of several stages in the life history cloud the picture.

Calman (1908) believed that enterocolid nauplii actively swam from one host to another in dissemination of infections. Development was believed to occur within the zooid and, when sexually mature, the female left the zooid, mated and returned to a host zooid. The eggs were presumed to be either left in capsules in the branchial cavity of the ascidian until hatched or abandoned in the cloacal canals.

The writer encountered enterocolids free in the canals, in the branchial sac of zooids, the stomach and post-abdomen. Hatching was observed in all cases. The nauplii, without exception, seemed unable to swim except for short, abortive jerks through the water, but were able to scuttle over the surface of the colony to an excurrent opening. There they would descend into the common cloacal canals, presumably to seek out a host zooid. Developmental stages between nauplius and immature individuals were not found.

Enterocolid females were observed tearing their way through the walls of the post-abdomen, with and without egg capsules. Such action may be the result of laboratory conditions, or it may be a normal procedure. Many zooids were encountered with egg cases within the post-abdomen and branchial sac; yet no females were present. Either the female tore her way out and the zooid regenerated the tissue, or she forced her way through the atrial aperture, leaving the eggs behind. Enterocolid females were observed towing egg cases through the colony canals, yet developmental stages were found only within the zooid.

Calman's idea of a free-swimming nauplius stage may be accepted, at least tentatively, but the act of the female leaving the zooid for fertilization is uncertain. Perhaps the male enters the zooid. This is not as incredible as it may seem, in view of the spiniferous appendages of the male. A few males were encountered, thrust head-first into the atrial aperture of the zooids.

The notodelphyids present a less uncertain life history. The nauplius seeks a host zooid and development proceeds. At a certain stage, apparently limited by size, the female leaves the host zooid and proceeds to a surface cavity of the colony through the cloacal canals. Hatched nauplii seek out the cloacal canals and disappear into the colony. These processes

were observed by the writer although no male notodelphids were encountered.

Another question is the degree of parasitism or commensalism exhibited by these animals. Brady (1878) believed they are not true parasites because they have no suckorial apparatus, move freely about within the host and do not attach themselves to the host tissue. Sars (1921) thought that they were more like commensals since they did not feed on the host's juices but on the particles of food brought in by the currents of water. Calman (1908) observed that zooids containing parasites had well developed gonads, indicating that no "parasitic castration" of the host had occurred.

The writer observed zooids similar to those seen by Calman. In all cases the gonads were not atrophied, and seemed fully functional. None of the species examined was attached to the host's tissue. Unless evidence showing injury to the host is revealed, it is doubtful that these animals are true parasites.

SUMMARY

Specimens of parasitic copepods were collected from both compound and solitary ascidians in the area of Dillon Beach, California. Descriptions and line drawings were made of several species, and a key to the families of ascidicolous copepods was constructed. Tables were prepared of the occurrence, location and incidence of infection of these copepods. The history of research on ascidicolous copepods was reviewed, as was the taxonomic structure of the group. Discussion was limited to possible schemes of life histories and the placement of these animals in parasitic or commensal relationships.

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EXPLANATION OF PLATES

Abbreviations

A.	Attachment area of egg capsule.
Ba.	Branchial aperture.
Bc.	Branchial cavity.
Bp.	Brood pouch.
Ec.	Egg capsule of parasite.
Es.	Esophagus.
Int.	Intestine.
La.	Lateral appendage.
N.	Nauplius.
Ov.	Oviduct.
P.	Parasite.
St.	Stomach.
U.	Urosome.

Plate 1.

1. Enterocolid #1, mature female, lateral view, 35x.
2. Ovigerous female, dorsal view, 17.5x.
3. Caudal rami, dorsal view, 215x.
4. Second leg, lateral view, 215x.
5. Head, dorsal view, 50x.

Plate 2.

1. Enterocolid #2, female, ventral view, 17.5x.
2. Second leg, lateral view, 215x.
3. First leg, lateral view, 215x.
4. Caudal rami, lateral view, 215x.

Plate 3.

1. Notodelphyid, female, lateral view, 17.5x.
2. Second pair of legs, lateral view, 50x.
3. Caudal section of ovigerous female, lateral view, 17.5x.

Plate 4.

1. Point of attachment, unidentified parasite, 50x.
2. Zooid of Amaroucium solidum with parasite, 15x.
3. Unidentified parasite, 30x.

Plate 5.

Collection area, Dillon Beach, California.

Plate 6.

Diagram of generalized compound ascidian with post-abdomen.

Plate 7.

Diagram of generalized cyclopoid copepod.

Drawings of parasites were made with the aid of a camera lucida and reduced one-half.

TABLE I
DISTRIBUTION OF PARASITES

<u>Parasite</u>	<u>Host</u>	<u>Location</u>
Enterocolid #1	<u>Amaroucium solidum</u>	Pelican Point Tomaes Point 2nd Sled Road Bodega Jetty
" "	<u>A. californicum</u>	2nd Sled Road Tomaes Point Pelican Point
Enterocolid #2	<u>A. solidum</u>	2nd Sled Road
" "	<u>Distaplia</u> , sp.	Bodega Jetty 2nd Sled Road Vilisitch's
" "	<u>Eudistoma ritteri</u>	Bodega Jetty
" "	<u>Sigillinaria</u> <u>Aequali-siphonis</u>	1st Sled Road
Notodelphyid	<u>A. californicum</u>	Pelican Point 2nd Sled Road
" "	<u>A. solidum</u>	2nd Sled Road
Botryllophilid	<u>Ascidia ceratodes</u>	Dredged, Tomaes Bay
Unidentified copepod	<u>S. pulchra</u>	Tomaes Point
"	<u>A. californicum</u>	2nd Sled Road
"	<u>A. solidum</u>	2nd Sled Road

Note: All parasites were collected from June 26, 1955 to October 1, 1955.

TABLE II

INCIDENCE AND SITES OF INFECTION

<u>Number of Parasites</u>	<u>Number of hosts (colonies)</u>	<u>Position in Host.</u>
<u>Enterocolid # 1</u>	<u>Amaroucium spp.</u>	Cloacal canals Zooid post-abdomen Zooid intestine Branchial sac Atrium
253	11	
	<u>Distaplia spp.</u>	Zooid post-abdomen Atrium Branchial sac
3	1	
	<u>Sigillinaria sp.</u>	Cloacal canals Zooid post-abdomen Branchial sac
6	1	
	<u>Eudistoma sp.</u>	Branchial sac
3	1	
<u>Enterocolid # 2</u>	<u>Amaroucium spp.</u>	Cloacal canals Zooid post-abdomen Atrium
66	8	
	<u>Distaplia spp.</u>	Zooid post-abdomen Branchial sac
42	4	
	<u>Eudistoma sp.</u>	Cloacal canals
1	1	
<u>Notodelphyid</u>	<u>Amaroucium spp.</u>	Surface cavities Cloacal canals Zooid post-abdomen
59	8	
<u>Unidentified</u>	<u>Amaroucium spp.</u>	Atrium Stomach area
64	4	
	<u>Sigillinaria sp.</u>	Stomach area
4	1	

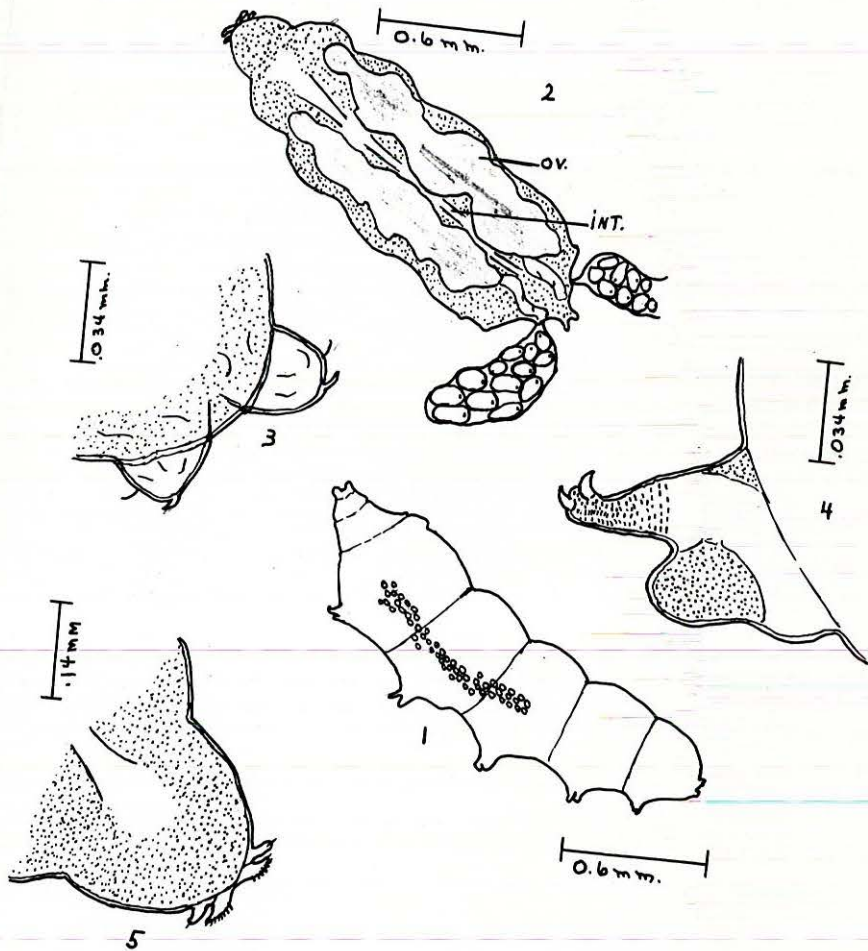


Plate 1
Enterocolid # 1

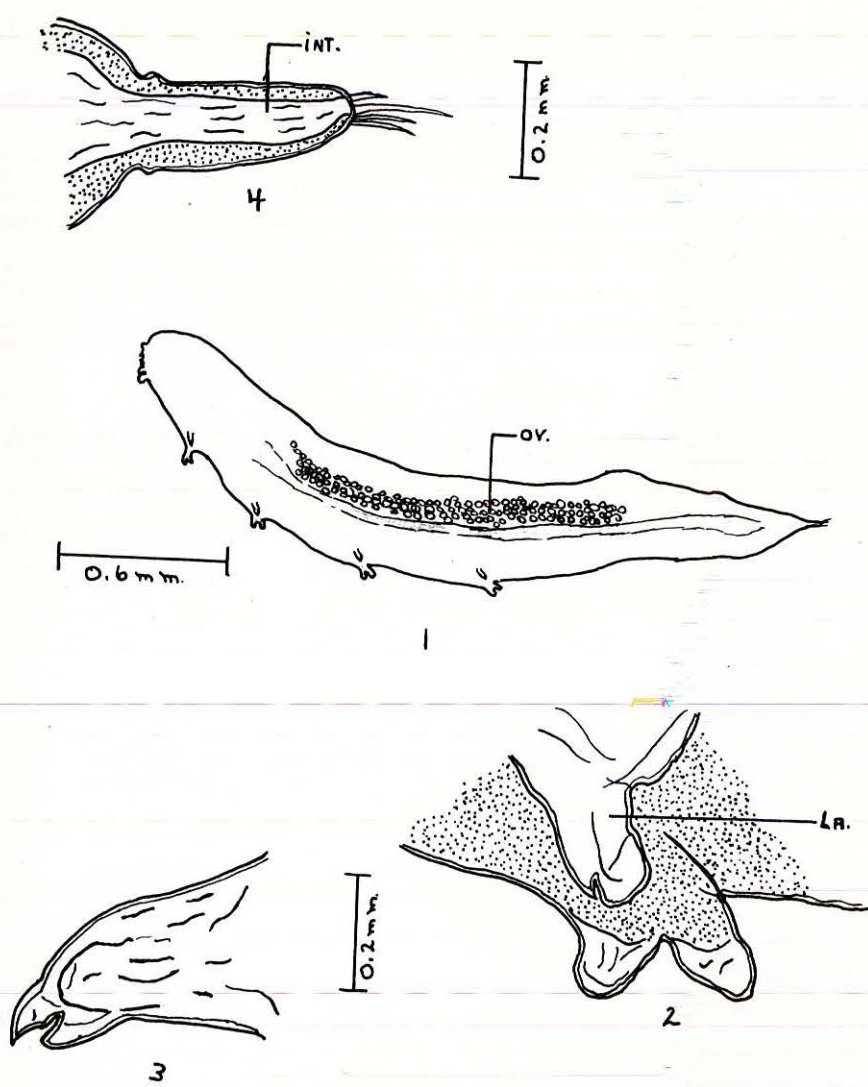


Plate 2
Enterocolid # 2

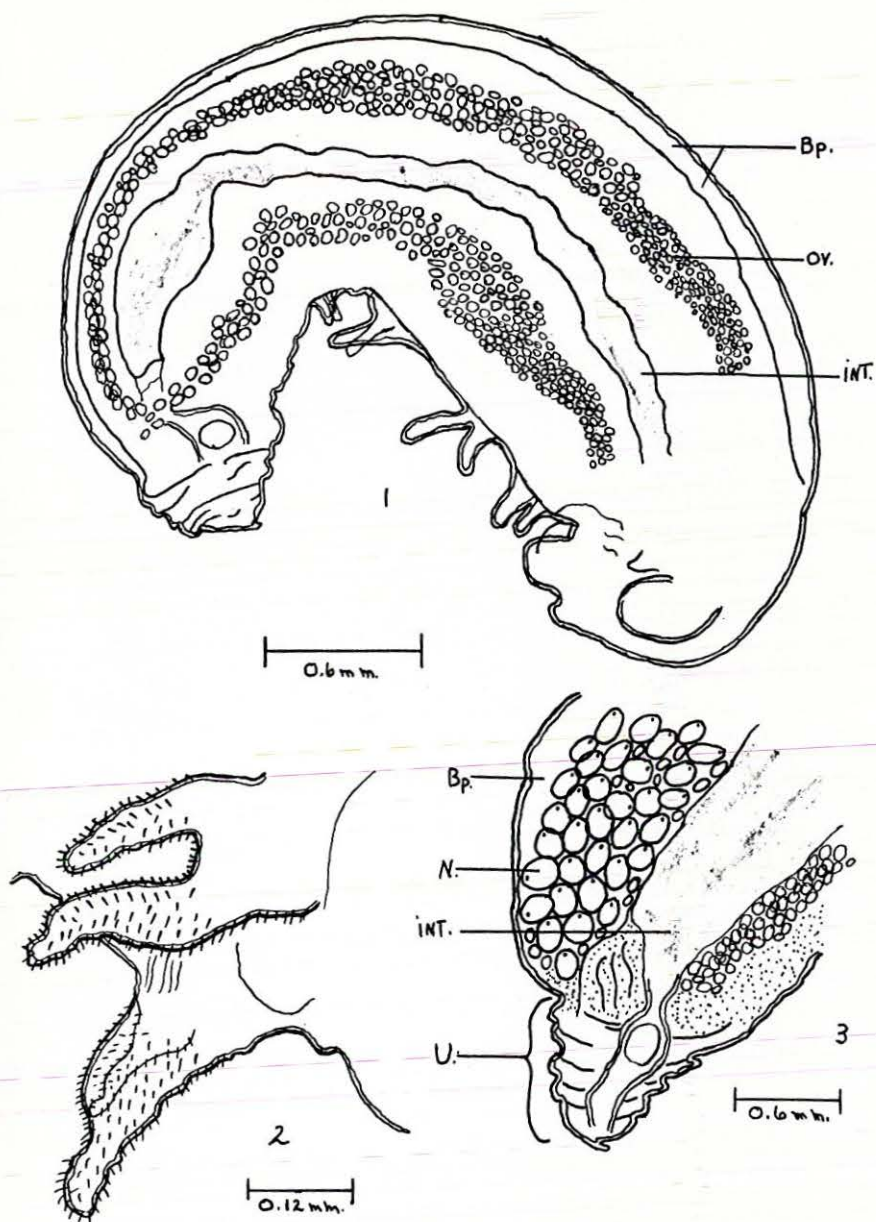


Plate 3
Notodelphyid

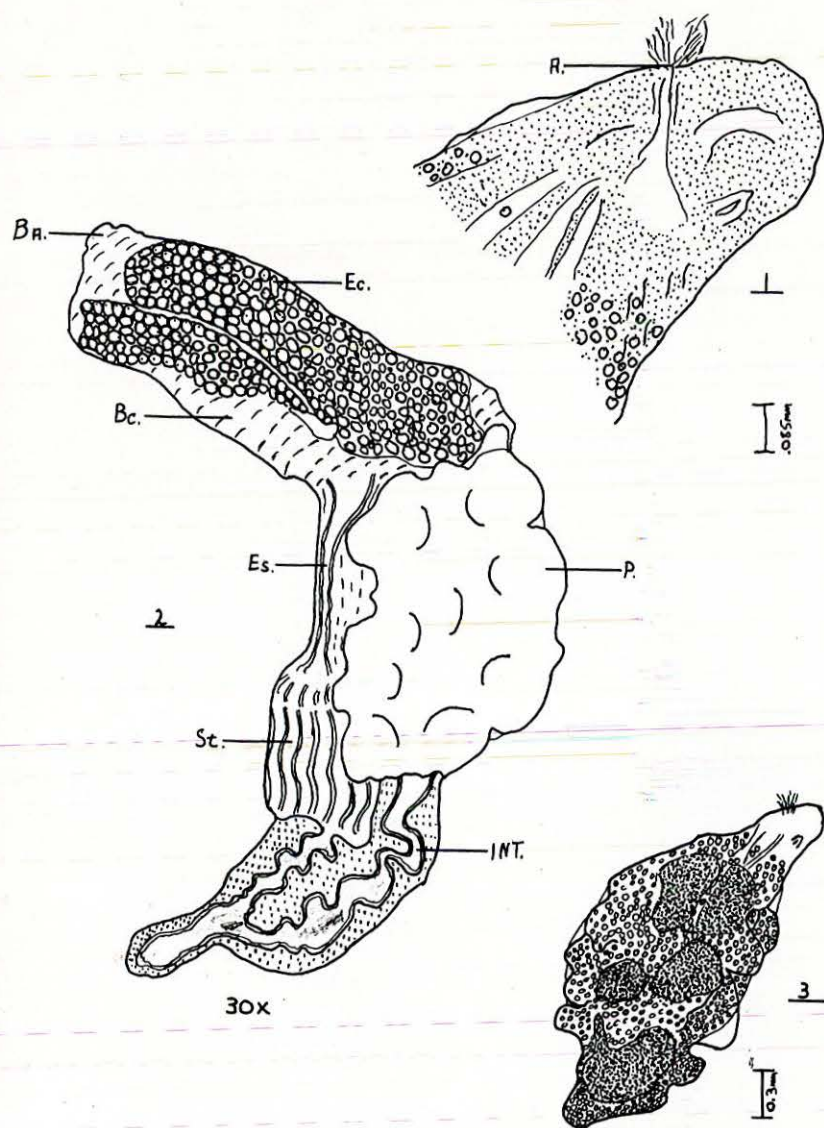


Plate 4
Unidentified Copepod

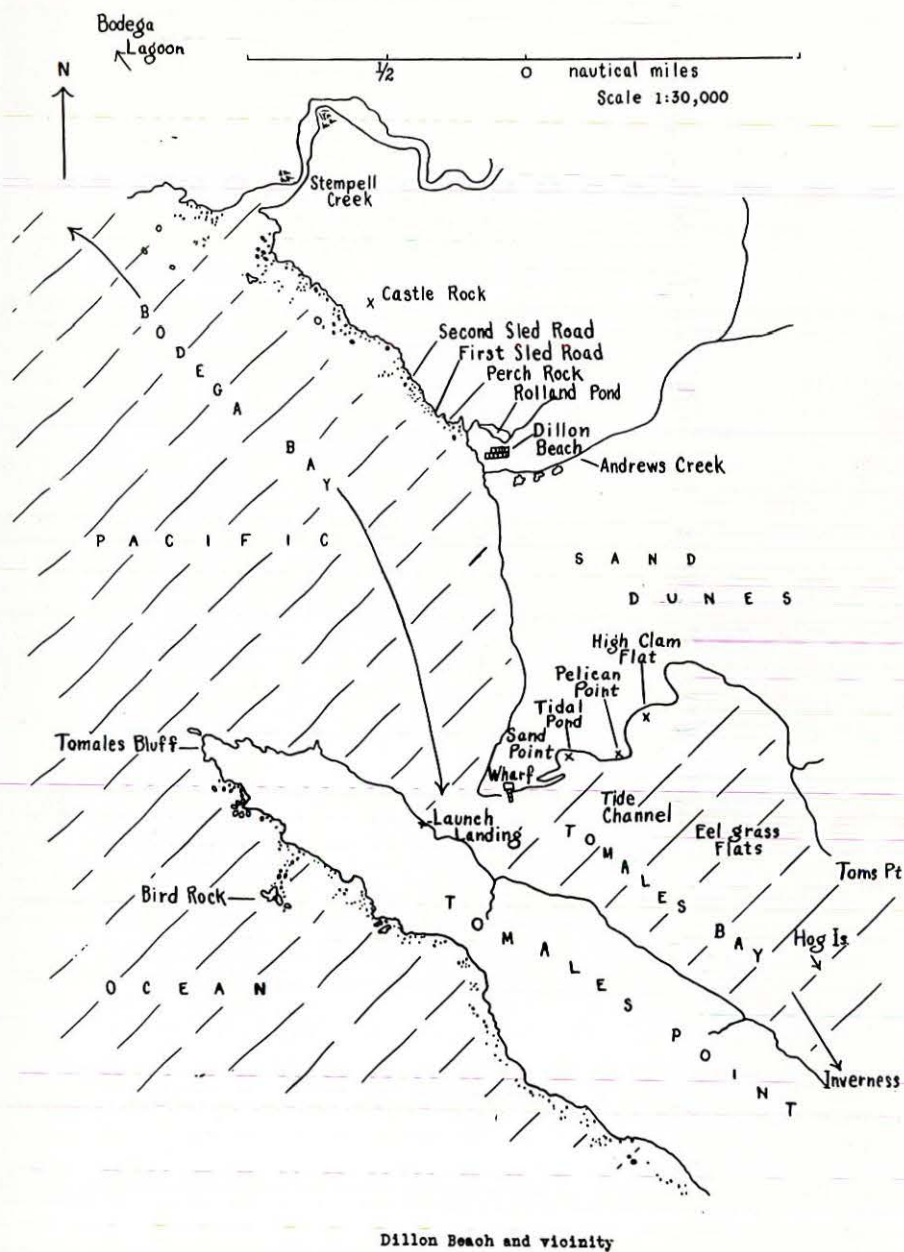


Plate 5
Collection Area

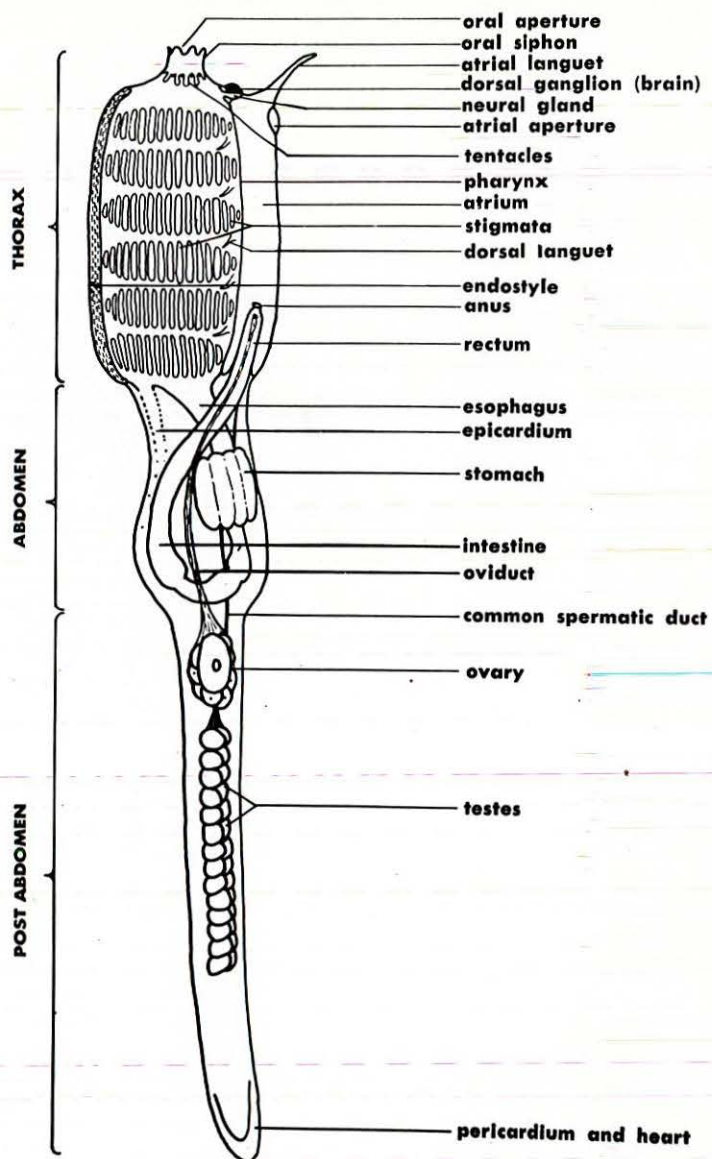
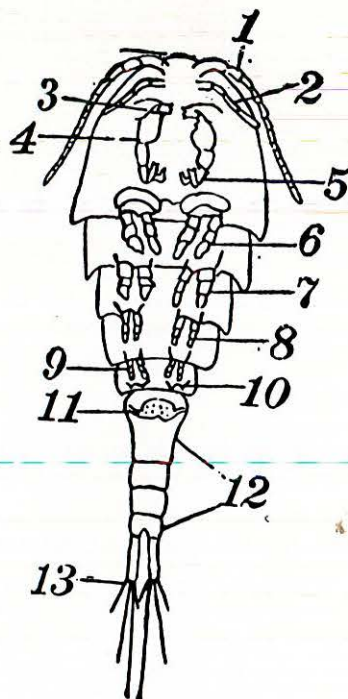


Diagram of generalized compound
ascidian zooid with a postabdomen.

Plate 6

Generalized Zooid



—Diagram of
Cyclops (altered from
Süssw. F. Deut.). 1, first
antenna; 2, second an-
tenna; 3, mandibles; 4,
first maxilla; 5, maxilliped;
6, 7, 8, 9, the first four
pairs of thoracic legs, each
leg being composed of a
basal piece, the protopod,
and two terminal pieces.
the exopod and endopod;
10, the fifth pair of
thoracic legs; 11, recepta-
culum seminis, in the first
abdominal segment; 12,
abdomen; 13, furca.

Plate 7
Free-living Copepod

The explanation of plates gives 15 X and the plate gives 30 X as the magnafication of this zooid.

I doubt both because 30 X would make the zooid thorax and abdomen about 4 mm long where as 15 X would make this measurement about 8 mm. Both are above the size limits of this species and further this is an immature zooid because of the lack of a post-abdomen which makes the measurements that much more over the size of Anaroucium solidum.

R.C. Haugsten