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THE PARASITES OF CEPHALOPODS: A REVIEW

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THE PARASITES OF CEPHALOPODS: A REVIEW

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Abstract

The literature and the status of our knowledge of the parasites of cephalopods are reviewed. Published and unpublished records of all hosts examined and parasites encountered are summarized in the text and a table. Of the approximately 650 species of cephalopods known, partial data on parasites are available for only about 150 species. Only two host species, *Octopus vulgaris* and *Sepia officinalis*, have been studied in detail and their total parasite loads documented. In addition to viruses, bacteria and fungi, three phyla of protists and six phyla of metazoans are recognized as symbionts of cephalopods. Several groups, such as the dicyemids, are known to be unique to the cephalopods. Many groups, especially the larval platyhelminths and nematodes, need to be properly associated with their corresponding adult forms. Viruses and fungi are potentially pathogenic to cephalopods and may be important in situations where cephalopods are reared, cultivated or maintained in captivity. Larval anisakid nematodes are a potential human health problem and should be monitored in areas where squids are eaten raw.

Introduction

In view of the important role which cephalopods play in the marine ecosystem and their increased commercial exploitation and consumption, a review of their parasites is both timely and relevant. In this paper I have attempted to bring together and briefly summarize the rather vast literature which deals with all the parasites of cephalopods. The task was not without some obstacles. Many references to parasites are buried in papers which otherwise deal with cephalopods and hence escape notice of parasitologists. Likewise, papers on parasites which list cephalopod hosts may be overlooked by teuthologists. Finally, many Russian and Japanese papers have been hard to track down and obtain and then usually required translation before the contents could be evaluated.

The text of the review is divided into sections by parasite group. In each I summarize the literature and briefly discuss the cephalopod hosts and their parasites. Location on or in the host is specified and information on prevalence and pathology is provided where known. The life cycle of the parasite is outlined and related when possible to the biology and feeding habits of the host. For obvious reasons I devote more space to discussions of parasites which have not been well reviewed. In all cases I provide the currently recognized name of the host cephalopod if it is different from the name used in the original publication. No attempt was made to resolve the many taxonomic problems that exist especially among the larval cestodes and nematodes. This would require more time than could be devoted and in many cases would require critical attention by an expert.

Historically, the first known reference to a cephalopod parasite was in a book by Redi (1684). During the ensuing decades as cephalopods attracted more attention there has been a dramatic increase in the number of phyla and the number of species of parasites recorded from these molluscs. Table 1 lists all the parasites currently known to be associated with cephalopods. In this Table are included all the published and unpublished records I could locate in order to present as complete as possible an overview of the diversity and distribution of parasites and the hosts examined. It can be seen that the total spectrum of organisms living symbiotically with cephalopods is as great as that found on or in most other marine organisms. With the exception of the dicyemid mesozoans and the apostome ciliates, which are unique in their occurrence in cephalopods, the parasite loads most closely parallel the loads in marine fishes.

In the older literature considerable confusion exists. The identifications of the parasites and sometimes even the hosts often are in doubt. In many cases the lack of adequate descriptions and figures makes it impossible to determine

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TABLE 1

Summary of all published and unpublished records of cephalopod genera examined for parasites and the parasitic groups encountered.

Parasite Group Host Genera	Viruses	Bacteria	Fungi	Sporozoans	Ciliates	Dicyemids	Monogeneans	Digeneans	Cestodes	Acanthocephalans	Nematodes	Polychaetes	Hirudineans	Branchiurans	Copepods	Isopods
NAUTILOIDEA																
Nautilus															●	
COLEOIDEA																
SEPIOIDEA																
Spirula		●			●											
Heteroteuthis		●			○				○							
Euprymna		●														
Rossia		●			○	●		●	●							
Rondeletiola		●				●										
Semirossia		●														
Sepietta		●			○	●										
Sepiola		●			●	●		●	●		●					
Sepiolina		●														
Sepia	●	●	●	●	●	●		●	●		●			●	●	●
Sepiella									●							
TEUTHOIDEA																
Alloteuthis					○		●	●	○		●				○	
Doryteuthis		●									●					
Loligo		●			●		●	●	●		●	●			●	●
Loliolopsis								●			○					
Lolliguncula					○			●			●					
Sepioteuthis						●										
Uroteuthis		●														
Abralia					○				○		○					
Abraliopsis					○			●	○		○					○
Enoploteuthis					○				○		○					
Pterygioteuthis					●			●	○		○					
Pyroteuthis					○											
Thelidioteuthis					○											
Octopoteuthis									○							
Kondakovia									●							
Moroteuthis					○				●		○					
Onychoteuthis					○						●					
Onykia																
Berryteuthis																
Gonatopsis					○											
Gonatus					○				●							
Lepidoteuthis					○				●		●					
Architeuthis									●							
Bathyteuthis																
Histioteuthis					○				○		●					
Ctenopteryx					○											
Dosidicus					○			●	●							
Hyaloteuthis								●								
Illex					●			●	●		●					

Host Genera / Parasite Group	Viruses	Bacteria	Fungi	Sporozoans	Ciliates	Dicyemids	Monogeneans	Digeneans	Cestodes	Acanthocephalans	Nematodes	Polychaetes	Hirudineans	Branchiurans	Copepods	Isopods
Martialia																
Nototodarus									●		●					
Ommastrephes					○			●	●	●	●				●	
Ornithoteuthis								●								
Symplectoteuthis					○			●	○		○					
Todarodes					●			●	●		●				●	
Todaropsis								●	●		●				●	
Thysanoteuthis								●								
Chiroteuthis					○			●	○		○					
Mastigoteuthis					○											
Bathothauma																
Cranchia																
Galiteuthis																
Helicocranchia																
Leachia																
Liocranchia									○							
Megalocranchia																
Phasmatopsis																
Sandalops																
Taonius																
VAMPYROMORPHA																
Vampyroteuthis					○				○		○					
OCTOPODA																
Chunioteuthis									●							
Grimpoteuthis						○										
Opisthoteuthis						○										
unid. cirrate															●	
Bolitaena					●											
Eledonella					○											
Japatella					○			●			○					
Bathypolypus						●										
Bentheledone						●										
Benthoctopus						●									●	
Eledone					○	●		●	●		●				●	
Graneledone						○										
Octopus	●		●	●	●	●		●	●				●		●	
Pareledone						●										
Pteroctopus					●				○							
Robsonella						●		●								
Scaeurgus					○	○			○							
Thaumeledone						○										
Ocythoe																
Argonauta								●								

● Published reports
○ Unpublished records (Hochberg)

whether the parasite was a ciliate, dicyemid, monogenean, digenean, cestode, nematode or even a part of the host. Only a very few groups of parasites have been reviewed critically in the last 50 years, namely: bacteria (Buchner, 1965); chromidinid ciliates (Chatton & Lwoff, 1935; Hochberg, 1971); dicyemid mesozoans (Nouvel, 1947, 1948; McConnaughey, 1949a, 1951); and the digenetic trematodes (Overstreet & Hochberg, 1975). The most recent reference which takes a broader perspective in reviewing both the crustaceans and helminths of cephalopods as a whole is Dollfus (1958). The present paper is the first review which treats all parasites.

Table 1 shows that with few exceptions the total picture for the parasites of cephalopods is inadequately known. To date only 63 genera and about 150 species of cephalopods have been examined for parasites. This represents fewer than half the known genera and fewer than a quarter of the approximately 650 species of cephalopods currently recognized. In only two cases have the total parasite loads been documented, namely, *Sepia officinalis* and *Octopus vulgaris*. Members of several genera of squids have been studied in some detail and these include *Loligo*, *Illex*, *Ommastrephes*, and *Todarodes*.

Almost without exception all large, mature cephalopods are infected with parasites. Viruses, bacteria, fungi, three phyla of protists and six phyla of metazoans have been recorded. Parasites have been recovered from almost all the tissues and organs of cephalopods. In general terms, however, they are most commonly located: (A) on the gills, (B) in the digestive tract, (C) in the 'kidneys' or excretory organs, and (D) in the musculature. The excretory organs are unusual in that they provide a uniquely suitable environment for the establishment and maintenance of parasites and as such have been exploited by a number of phylogenetically distinct groups (Hochberg, 1982a).

Particular attention has been focused on those parasites which may cause problems during culturing activities. At present only viruses and fungi have been implicated as potential pathogens. However, cephalopod mariculture is such a new field that we constantly need to be alert to the presence and effects of parasites in monoculture situations. In particular, we need to investigate infestations of sporozoans, monogeneans, and copepods.

As the search for additional fisheries resources expands, cephalopods are more commonly being marketed for human consumption. In Japan and other countries where cephalopods, especially squids, are eaten raw there is the very real possibility that larval nematodes will be transmitted to humans. Anisakaisis is currently recognized as an important medical problem which warrants further investigation. This is briefly discussed in the nematode section.

The role of cephalopods in the food web is only now beginning to be understood. One way ecological relationships have been elucidated is through examination of parasites. All the evidence at hand indicates that cephalopods play a similar and equal role to fishes in the transmission of parasites in the marine environment. Many species serve as primary hosts for protozoans, dicyemids, helminths, and crustaceans but more commonly cephalopods function as secondary or reservoir hosts for larval stages of digeneans, cestodes, and nematodes and thus play a vital role in the transfer of parasites through the food web to final hosts such as elasmobranchs, fishes and marine mammals.

Although built on the work of many others, this review is still only a beginning. We must continue to survey wild populations and monitor cultivated stocks of cephalopods for the presence of potential pathogens. But, we must also turn our attentions to the critical tasks of unraveling taxonomic problems, completing life cycles, evaluating the effects of parasites on the growth, reproduction and survival of cephalopods and clarifying the details of cephalopod/parasite interactions in the marine environment.

I. VIRUSES AND TUMORS

Viruses and virus-like particles have been observed in several species of benthic cephalopods. Rungger and his coworkers (1971) described an iridovirus associated with lesions on the arms and mantle of *Octopus vulgaris*. Infected specimens were first discovered in culture tanks at the Stazione Zoologica in Naples, Italy. Naturally infected animals were later collected in the Bay of Naples where a prevalence of 8.4% was recorded for the population sampled. In initial stages, tiny edematous, nodular tumors appear in the muscle tissue of the arms. As the infection progresses the diameters of the lesions increase and nodules spread to other areas of the body. Death occurred 3-5 months after the appearance of visible tumors.

Devauchelle & Vago (1971) reported on a reovirid infecting the cells of the stomach epithelium of *Sepia officinalis*. Virus-like particles have been observed in sections of the renal appendages of several octopod species from New Zealand, Florida and California (Short & Hochberg, unpub.). This virus is found in the nuclei of the renal epithelial cells of the octopus and also in the nuclei of the somatic cells of the dicyemid parasites which attach to the renal appendages (Short & Hochberg, 1969).

A rare benign tumor in the mantle musculature of *Sepia officinalis* was described by Jullien and coworkers (Jullien, 1928b; Jullien & Jullien, 1951; and Jullien, *et al.*, 1951-52). A causitive agent was not identified but inflammations, lesions, and tumors could be induced experimentally by injection of a wide variety of chemical compounds (Jacquemain, *et al.*, 1947; Jullien, 1928a, c, 1940; Jullien *et al.*, 1951-52, 1953).

II. BACTERIA

The presence of symbiotic bacteria or bacteria-like inclusions in association with cephalopods has an extensive literature which has been summarized in the excellent reviews by Harvey (1952) and Buchner (1965). The majority of the papers investigate luminescent bacteria contained within specialized photogenic organs. A discussion of this topic is outside the scope of the present paper. With the exception of the report by Shibata (1953) of luminescent bacteria in the intestine of *Doryteuthis* (=*Loligo*) *bleekeri*, all the remaining publications deal with non-luminous bacteria found on the skin or in the accessory glands.

In most female sepioid and myopsid cephalopods a pair of glandular organs are located at the anterior end of the nidamental glands in close association with the ink sac. As early as 1918 Pierantoni discovered that these accessory glands (=accessory nidamental glands) do not play a true role in reproduction but instead are packed with dense concentrations of rod- and coccoid-shaped bacteria. At the onset of sexual maturation the accessory glands increase in size and become bright orange or red in color (see Richard, *et al.*, 1979). The color is due to carotenoid pigments contained within the bacteria which reside in the accessory glands. The change in color is accompanied by an increase in the number of bacteria present in the glands. Both events imply an intimate symbiotic relationship which is controlled by the host cephalopod.

Pigmented, non-luminescent bacteria recently have been isolated from the accessory glands of *Loligo pealei* (Bloodgood, 1977) and *Sepia officinalis* (Van den Branden, *et al.*, 1980; see also Decleir & Richard, 1972; Van den Branden, *et al.*, 1979). According to Bloodgood (1977) the bacteria form a stable dividing population that presumably benefits from its location within the tubular matrix of the accessory glands. What benefits accrue to the host cephalopods are not known but warrant investigation.

III. FUNGI

In several specimens of *Sepia officinalis* and *Octopus vulgaris* from the Mediterranean Raabe (1934) discovered filamentous fungal thalli penetrating throughout the renal appendages and causing considerable damage to the host tissue. Raabe placed this highly pathogenic fungus in the ascomycete genus '*Aspergillus*'. The systematic treatment of the ascomycetes is subject to considerable controversy, hence, until more material is available Raabe's identification cannot be verified or rejected. It would appear that this parasite is quite rare, since it has never been reported or mentioned again, in spite of the large numbers of cephalopods subsequently examined in the Mediterranean and elsewhere.

Recently, Polglase (1980) described a pathological condition in *Eledone cirrhosa* which she attributed to the presence of thraustochytrid and labyrinthulid fungi. These highly pathogenic lower fungi are associated with both plant and animal tissues but their roles have rarely been defined. McLean & Porter (1982) suggest that the thraustochytrids, which they consider to be saprobic normally, are merely secondary invaders of the lesions in *Eledone*. In any event, in *Eledone* the two fungi, either singly or in combination, produce ulcerations in the skin, followed by oedema of the body tissues and eventually death.

Originally observed in wild-caught animals, the pathogens rapidly became established in holding tanks in Scotland from which the disease could not be eliminated. The contagious nature of these fungi is such that no octopods could be maintained in a healthy state in contaminated tanks for long periods of time. Polglase's report indicated that captive animals which frequently display skin lesions should be examined carefully to determine if they are infected by contagious fungal pathogens.

IV. SARCOMASTIGOPHORA

Flagellates and amoebae have not been reported in association with cephalopods. However, Brocco (pers. comm.) discovered an unidentified species of dinoflagellate imbedded in the skin of *Octopus dofleini* collected in Washington. Micrographs of the alga in situ show a dissolution of the epidermal layers associated with lesions in the mantle. No further information is available on this parasite.

V. APICOMPLEXA (=SPOROZOA)

The protozoan genus *Aggregata* has a two host life cycle. Sexual stages occur in the digestive tracts of cephalopods and asexual stages infect the digestive tracts of crustaceans. When first reported by Lieberkuhn (1854) *Aggregata* was thought to be a gregarine. It was correctly interpreted as a coccidian by Schneider (1883) though for many years it was placed in the family Aggregatidae (see Pixell-Goodrich, 1914). Fine structure studies by Heller & Scholtyseck (1969a,b, 1970a,b) indicated affinities with *Eimeria* in the family Eimeriidae and this placement has been accepted by most modern protozoologists (see Grell, 1973; Levine *et al.*, 1980).

The best known cephalopod apicomplexan, *Aggregata eberthi*, infects *Sepia officinalis* and *Portunus depurator* in the Mediterranean, English Channel and North Sea (Dobell, 1925). The parasite probably occurs wherever the distributions of *Sepia* and *Portunus* overlap. Two species of *Aggregata* have been reported from *Octopus vulgaris* in the Mediterranean and also in the English Channel. *Aggregata octopiana* was described by Schneider (1875a,b) and *A. spinosa* by Moroff (1906a). The crustacean hosts for these two species are not known.

Moroff (1908) lists an additional nine species which are thought to be synonyms of the species listed above. A number of species have been described from crustaceans in Europe but as yet these forms have not been identified in specific cephalopod hosts. Among these, *Aggregata coelomica* lives in *Pinnotheres* (Leger, 1901); *A. vagans* in *Eupagarus* (Leger & Duboscq, 1903), *A. inachi* in *Inachus* (Smith, 1905) and *A. leandri* in *Leander*, *Solenocera* and *Acanthephyra* (Pixell-Goodrich, 1950; Theodorides, 1965). Several undescribed species are known to occur in *Octopus* species off California and the west coast of Mexico (Hochberg, unpub.), off Florida (McSweeney, pers. comm.) and in the Caribbean off the Virgin Islands (Hochberg & Couch, 1971). The reports by DeHorne (1930a,b) of *Aggregata* in the polychaete, *Nereis*, represent an obvious misidentification.

Aggregata selectively infects the non-cuticularized, nutrient uptake portions of the digestive tract of both cephalopod and crustacean hosts. In cephalopods the parasite is located within epithelial cells of the mucous membrane and in the submucosal connective tissue. As infective stages (merozoites) migrate through the epithelium of the caecum and intestine, the invaded cells die and degenerate. Periodically, necrotic portions of the gut lining are sloughed off and eliminated. In heavy infections the submucosal tissue of the cephalopod may be almost completely replaced by parasite cells. When *Aggregata* is present in large numbers the mechanical effects of compressing and deforming host tissue may prevent circulation and muscular activity in the gut wall. In *Sepia* the individual infected cells exhibit no apparent response to the presence of the parasite. However, in *Octopus*, the invaded cells may undergo enormous nuclear and cytoplasmic hypertrophy (Brumpt, 1910; Dobell, 1925; Wurmbach, 1935).

The live cycle of *Aggregata eberthi* is one of the classics in parasitology (see Figure 1). Originally outlined by Leger & Duboscq (1906-1908), the cycle later was studied in detail by Dobell (1914, 1925), Naville (1925) and by Bĕlăr (1926). Fine structure studies of a number of the stages in the life cycle have confirmed the observations of earlier workers (see Porchet-Hennere & Richard, 1969-1971; Porchet-Hennere & Vivier, 1970; Vivier, *et al.*, 1970).

The infection is initiated when *Sepia* feed on crabs such as *Portunus*. Ripe, infective stages (merozoites), which reside in the coelom of the crab, are released into the digestive tract of the cuttlefish upon ingestion of the intermediate host. The merozoites actively bore through the epithelial lining of the caecum and intestine of *Sepia* and enter connective tissue cells in the submucosa. Growth occurs as nutrients are taken up from lymph spaces within the connective tissue of the cephalopod host. During gamogony the merozoites are transformed into gamonts of two types. Each macrogamont gives rise to a single macrogamete and as these large cells develop the nucleus approaches the surface of the cell. Development of the microgamete proceeds until large numbers of biflagellated microgametes are produced. Eventually, motile, male gametes are released into the surrounding tissue and enter the macrogametes in the area where the nucleus touches the pellicle.

Following fertilization the zygote undergoes a reduction division which subsequently triggers a burst of mitotic activity. During sporogony the cytoplasm of the sporont is progressively divided up and a large number of sporoblast produced. When finally enveloped by a gelatinous coat the sporoblasts, which now fill the oocyst, are termed spores or sporocysts. In *Aggregata eberthi*, following two additional divisions, each sporocyst contains three sporozoites measuring 8-9 μm.

Mature sporocysts rupture out of the oocyst and are eliminated with the feces. Often entire portions of necrotic gut lining containing intact oocysts are sloughed off and discharged to the exterior. The infection can be experimentally transmitted to crabs by feeding them ripe spores contained in either detrital material contaminated with cuttlefish feces or scraps of cuttlefish intestine. Within a few hours after ingestion, the infective sporozoites are released and move actively about in the lumen of the crab gut. Within 24 hours they will penetrate the epithelial lining of the midgut and migrate into the lymphoid tissues of the submucosa. Here they round up and enlarge into meronts. When growth is completed an asexual phase of reproduction begins. During merogony the nucleus divides many times producing a large number of daughter nuclei which come to lie near the surface of the highly convoluted cytoplasm. After the merozoites are released, there is no further development until the crab is eaten by the cuttlefish and the cycle starts over again.

VI. CILIOPHORA

With the exception of the dicyemids, ciliates are the most frequently encountered parasites of cephalopods. At least five families are parasitic in the renal organs, in the digestive glands and on the gills of cuttlefishes, squids and octopuses. However, only a few published studies deal with these unusual forms and many new findings await analysis.

The genus *Chromidina* is restricted to a small group of vermiform ciliates which attach to the appendages within the renal or renal-pancreatic coela of cephalopods. Only three species have been described, though a total of 23 species of cephalopods in 20 genera currently are known to harbor chromidinids (Hochberg, 1982a). In the Mediterranean and English Channel, *C. coronata* occurs in *Octopus vulgaris*, *Sepiola rondeleti*, *Illex coindetti*, *Eledone cirrhosa* and *Scaeurgus unicirrhus*. A second species, *C. elegans*, lives in *Sepia elegans*, *S. orbignyana* and *Illex coindetti*. For details see Chatton &

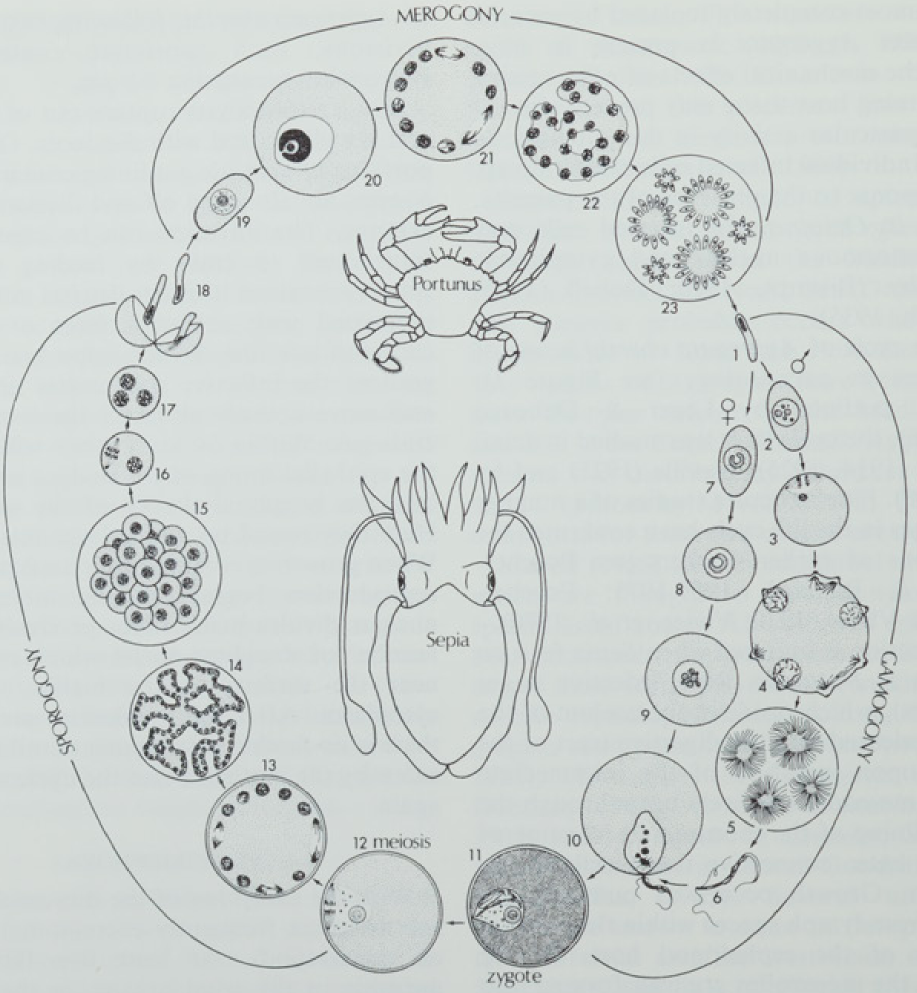

Figure 1. Life cycle of the eimeriid apicomplexan, *Aggregata.* (after Dobell, 1925 and Grell, 1973).
1. merozoite
2-5. microgamont development
6. microgamete
7-9. macrogamont development
10. macrogamete at time of fertilization
11. zygote
12-14. sporont development
15. oocyst with developing sporocysts
16-17. sporocyst development
18. sporocyst (spore) with 3 sporozoites
19-23. meront development

Lwoff (1928, 1931, 1935); Collin (1941b, 1915); Dobell (1909); Foettinger (1888a,b); Gonder (1905); Hochberg (1971); and Nouvel (1935a,b,c, 1937, 1945). A third species, reported from *Pterygioteuthis giardi* in the Gulf of California, Mexico, is treated by Hochberg (1971).

Ciliates, attributed to *Chromidina elegans*, have been reported from *Todarodes sagittatus* and *Octopus salutii* in the Mediterranean (Nouvel, 1945; Hochberg, 1971); from *Loligo* sp. off Russia (Wermel, 1928); and from *Spirula spirula* in the Atlantic Ocean (Clarke, 1970; Jepps, 1915). This material has not been critically examined and compared to the type species and hence the true designations are not known. In the North Pacific Ocean a wide variety of schooling epi- and mesopelagic cephalopods are infected. Of these oceanic cephalopods, *Chromidina* infects species of the following genera: *Heteroteuthis*, *Abralia*, *Abraliopsis*, *Pterygioteuthis*, *Ctenopteryx*, *Mastigoteuthis*, *Histioteuthis*, *Dosidicus*, *Symplectoteuthis* and *Japatella*. Several undescribed species are involved (Hochberg, in prep.).

Characteristically only truly pelagic squids and octopods are infected. Infection of benthic or epibenthic hosts occasionally has been reported but in all of these cases the ciliates were found only in octopods which have planktonic larvae (i.e., *Octopus salutii*, *O. vulgaris*, *Scaeurgus unicirrhus*, and *Eledone cirrhosa*) or in sepioids whose young feed in surface waters (i.e., *Sepia elegans*, *S. orbigiana* and *Sepiola rondeleti*).

As elucidated by Hochberg (1971, see also 1982a) *Chromidina* has a two-host life cycle (see Figure 2). Like the better known foettingerids, it undergoes a complex polymorphic cycle involving an ordered sequence of distinct phases. Young squids pick up ciliates when they associate with or feed on swarms of pelagic crustaceans, such as euphausiids. At present the method of entry into the host is not known. Within the cephalopod, the stages of the cycle are considerably modified and condensed, compared with the small, ovoid, and less specialized foettingerids (see Bradbury, 1966; Chatton & Lwoff, 1935). In *Chromidina*, the vegetative and divisional phases are combined into long, thin tropho-tomonts. These vermiform individuals attach to the renal appendages by means of a thigmotactic anterior end. The remainder of the body, which is actively involved with nutrient uptake and division, hangs free in the fluid-filled coelomic space. Reproduction takes place by unequal, transverse fission or budding at the posterior end of the body.

Two distinct budding patterns are observed, monotomy and palintomy. In young hosts, the ciliates all produce large, single buds, termed apotomites, which resemble the parents. When detached they are transformed directly into second generation tropho-tomonts. By means of this initial budding process the number of ciliates is continually increased within the renal sacs until eventually the renal habitat is saturated with ciliates. The second divisional phase, palintomy, is probably triggered by chemical factors related to the density of parasites or maturation of the host. During palintomy, a multiple fission process takes place which produces long chains of 8, 12, or 24 small buds. Tiny, ovoid dispersal stages, termed tomites, eventually are formed which bear little resemblance to the parent tropho-tomonts. The tomites conjugate immediately after detachment from the parent, and then exit through the renal pores to the exterior with the passage of urine.

Once in the sea, the ciliates swim about until they contact a euphausiid or other appropriate crustacean host. The tomites then encyst on the mouth parts and setaceous appendages of the new host. During this phoretic stage, the ciliates undergo several growth phases. Euphausiids are known to molt every few days. As in other apostome cycles, it is presumed that the ciliates encyst with each molt, feed, grow, and then recyst on another host crustacean (see Bradbury & Trager, 1967; Trager, 1957). Eventually they attain a size which is capable of infecting a cephalopod, and the cycle begins again.

The maximum length of vermiform stages in the cephalopod renal organs ranges from 400 to 2 000 μm depending on the species. Two basic body shapes occur. *Chromidina coronata* has an inflated anterior end and a conspicuous crown of elongate cilia whereas in *C. elegans*, the anterior end is not swollen and the ciliary crown is lacking. In other ways the species are almost identical. The infraciliature of the tropho-tomonts consists of a tight dextral helix, continuous without breaks from the anterior to the posterior pole. Typically 12-14 kineties are present. The macronucleus is an open network of chromatin found throughout the entire body. A tiny spindle-shaped macronucleus is located in the posterior end of the body in the region of the future fission plane. The appearance of trichocysts in the posterior region of the body signals the onset of division. Unlike the foettingeriids, full grown vegetative stages do not encyst prior to division. Mouth, rosette and contractile vacuole, typically found in the foettingeriids, are absent in the stages within the cephalopod host. During palintomy the

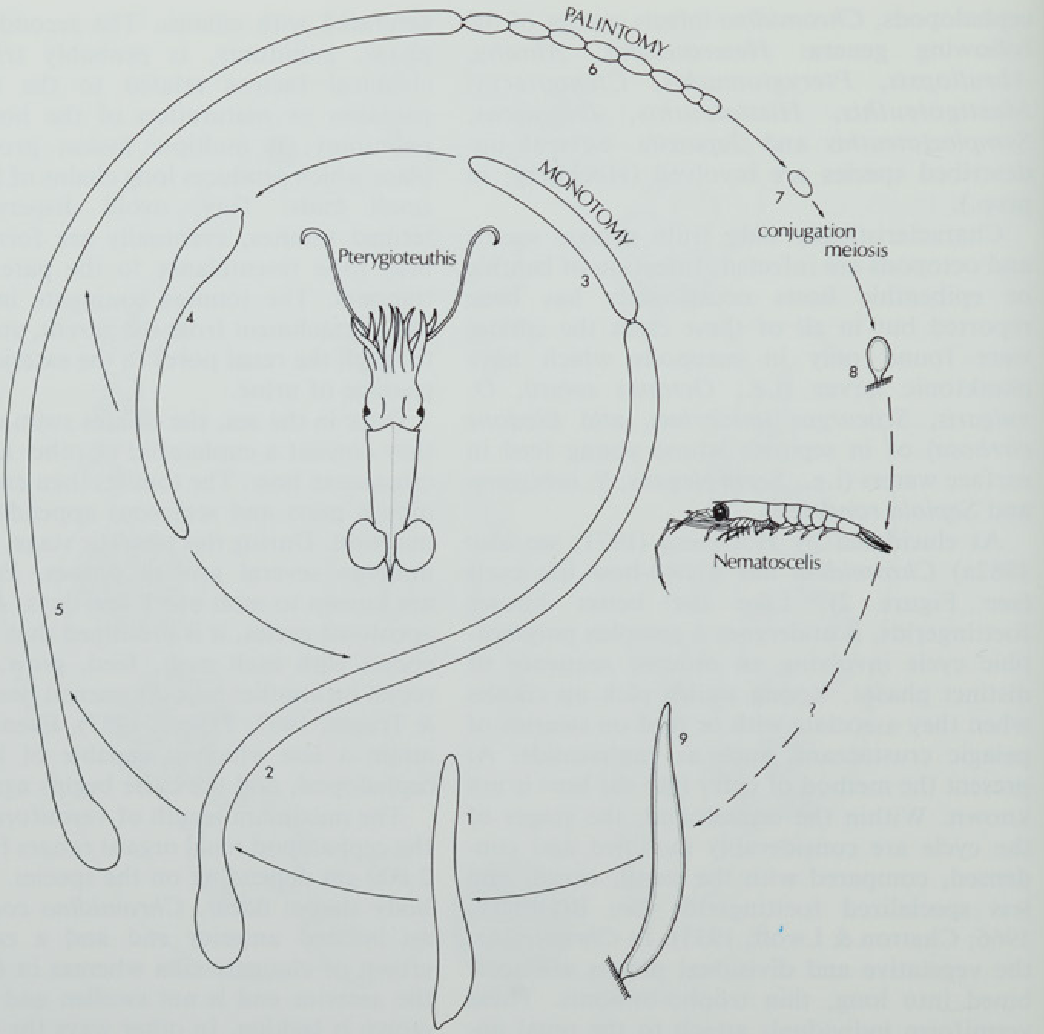

Figure 2. Life cycle of the apostome ciliate, *Chromidina*.
1. protropho-tomont
2. 1° tropho-tomont
3. production of apotomite via single fission
4. apotomite
5. 2° tropho-tomont
6. production of tomites via multiple fission
7. tomite detached from parent
8. 1° phoront
9. 2° phoront

kineties are shortened and straightened with each successive division. The oral field and contractile vacuole develop after detachment from the parent. The appearance of the nuclei also alters markedly during palintomy, as shown by Chatton & Lwoff (1935) and Hochberg (1971). Fully developed tomites range in size from 15 to 30 μm. They are pyriform in shape with a convex dorsal surface and a flat or slightly concave ventral surface. Hovasse (pers. comm.) observed conjugation immediately following release of the tomites.

Occasionally hypertrophonts, measuring up to 5 000 μm, are found. Described by Collin (1914b, 1915) these degenerative individuals appear to have penetrated the epithelium of the reno-pancreatic appendages and entered the blood spaces within. Here they increase rapidly in size, probably because of high osmotic pressures. The nuclei undergo caryolysis and the cilia are lost.

Small, ovoid infusorians infecting the midgut and digestive glands of cephalopods are placed in the related genus, *Opalinopsis*. Two species have been described from the Mediterranean and the English Channel. *Opalinopsis sepiolae* is reported from *Sepia rondeleti*, *Sepia elegans* and *S. officinalis* (see Collin, 1941b, 1915; Dobell, 1909; Foettinger, 1881a,b; Gonder, 1905). I have observed what is probably the same species in *Sepiola atlantica*, *Sepietta oweniana*, and *Rossia macrosoma*. *Opalinopsis octopi* has been obtained from *Pteroctopus tetracirrhus* and *Octopus macropus* at Naples and Banyuls (Foettinger, 1881a,b; Hochberg, 1971). Collin (1914a) described a third species of *Opalinopsis* from the heteropod mollusc, *Carinaria mediterranea*, collected at Villefranche. This later species has not been studied since first described and should be reexamined. Collin (1914a) promised a review of the genus *Opalinopsis* but it was never forthcoming. Recently, I have found several undescribed species of *Opalinopsis* in *Heteroteuthis*, *Histioteuthis* and *Japatella* off Hawaii and Baja California, Mexico (Hochberg, 1982b).

The life cycle of the opalinopsids is incompletely known. In the cephalopod host, tropho-tomonts of *Opalinopsis* move freely through the digestive gland and the digestive gland appendages ('liver', 'pancreas', and 'hepatopancreas' of previous authors). Division is equatorial and monotomic. Long chains of buds are not produced nor is sexuality known. Stages outside the cephalopod are not known.

The taxonomic position of *Opalinopsis* and *Chromidina* has been subject to considerable debate. In the past both genera were most often treated together. An affinity between these two genera of highly specialized cephalopod parasites and the apostome ciliates was first proposed by Chatton & Lwoff (1926). Their ideas regarding this relationship were later expanded (1928, 1930), and in 1931 they reported stages in the life cycle of *Chromidina* that were very similar to the foettingeriids. In reviewing the systematic literature (Hochberg, 1971) I pointed out the distinctness of the two genera and placed each in its own family. I also reaffirmed placement of the chromidinids in the Order Apostomatida. The opalinopsids, on the other hand, are regarded as perhaps outside the defined limits of the apostomes (Chatton & Lwoff, 1935; Hochberg, 1971, 1982b).

VII. DICYEMIDA

The dicyemid mesozoans are a small and puzzling group without definite affinities in the animal kingdom. They exhibit an impressive array of truly unique characters which hold a special curiosity for zoologists. They were first described by Krohn (1839). Later, Erdl (1843) observed that they produced two kinds of embryos but it was not until 1849 that von Kölliker gave them the generic name, *Dicyema*, to denote this alteration of stages. Beneden (1876) believed that these simple, cell constant organisms linked the protozoans and the metazoans and hence he proposed the name, Mesozoa. The dicyemids, along with the orthonectids, have long been considered a Class within the Phylum Mesozoa (see reviews by Czihak, 1958; Dodson, 1956; Grassé, 1961; Hyman, 1940, 1959; McConnaughey, 1963, 1968; Mendes, 1940; and Stunkard, 1954). The orthonectids parasitize a number of marine invertebrate phyla: Platyhelminthes (turbellarians); nemerteans; annelids (polychaetes); molluscs (gastropods, bivalves, but *not* cephalopods); echinoderms (ophiuroids); and chordates (ascidians). In light of dissimilar internal features and the lack of homologies in stages of life cycles, it is best to treat these two assemblages as separate phyla and to use the term 'Mesozoa' to refer to their grade of organization only.

The dicyemids are the most common and characteristic parasites of the excretory organs of cephalopod molluscs. These minute, vermiform organisms attach principally to the renal appendages while the remainder of their worm-like bodies float in the fluid-filled renal coelom. In decapods they are found additionally in the reno-pancreatic coelom attached to the digestive duct appendages and very rarely are located in the pericardium attached to the branchial heart appendages. They live and reproduce in these organs doing no apparent harm to the host.

A total of 59 species of cephalopods, representing 18 genera, are currently known to host dicyemids (see Table 1). They occur in sepioids, especially cuttlefishes and sepiolids, and also in octopods in both cirrate and incirrate groups. Among the teuthoids, only *Sepioteuthis*, an epibenthic loliginid, has been reported to be infected. Each cephalopod host species harbors either a single species of dicyemid or a complex of species that are most often distinct at the generic level. As examples: *Octopus rubescens* hosts *Dicyema balamuthi*, *Dicyemennea adscita* and *Conocyema adminicula* (Hochberg, 1971; McConnaughey, 1949a); *O. tehuelchus* harbors *Dicyema australis*, *Dicyema platycephalum* and *Conocyema marplatensis* (Penchazadeh, 1968, 1969, Penchazadeh & Christiansen, 1970); *Benthoctopus magellanicus* is infected with *Dicyema benthoctopi* and *Dicyemennea littlei* (Hochberg & Short, 1970); and *Sepia officinalis* may concurrently host *Dicyemennea gracile*, *Pseudodicyema truncatum* and *Microcyema vespa* (Nouvel, 1947).

Dicyemids parasitize only benthic or epibenthic cephalopods although the distribution is by no means universal. In temperate and polar waters adult, benthic cephalopods generally are 100% infected. In subtropical waters the prevalence of infection varies but is always less than 100%. In the tropics and off oceanic Islands no cephalopods have been reported to be infected. The reasons behind these distribution patterns are not known.

Initial infections normally occur in very young animals, either immediately following hatching, as in cephalopods with demersal juveniles, or following settlement to the bottom, as in those host species with planktonic larval stages. In all the cephalopods I have examined I have never encountered dicyemids in neritic or oceanic species. McConnaughey (1959) reported a species of *Dicyemennea* in *Loligo opalescens* and Aldrich (1964) reported a single dicyemid in a single specimen of *Illex illecebrosus*. Both *Loligo* and *Illex* are neritic genera and hence these reports are probably in error. Thousands of specimens of *Illex* and *Loligo* have been examined by many investigators and none have been infected with dicyemids.

Nouvel (1947) and McConnaughey (1949a) reviewed the dicyemids and hosts known until then. Since that time a number of species have been described from a variety of geographical localities: East coast of Russia (Bogolepova, 1957; Bogolepova-Dobrokhotova, 1960, 1962); France (Nouvel, 1961); Florida and the Gulf of Mexico (McConnaughey & Kritzler, 1952; Couch & Short, 1964; Short, 1961, 1962, 1964); West coast of North America (McConnaughey, 1949b, 1957, 1959, 1960; Hoffman, 1965); Argentina (Penchaszadeh, 1968, 1969; Penchaszadeh & Christiansen, 1970); New Zealand and the Antarctic (Hochberg & Short, 1970; Short, 1971; Short & Hochberg, 1969, 1970; Short & Powell, 1969).

To date 65 species of dicyemids have been described. If we add to this the undescribed species in several collections and the number of potential host species still to be examined, it is possible to project a total of about 200 species in the phylum. Seven genera are currently recognized and placed in two families—DICYEMIDAE: *Dicyema* (32 species), *Dicyemennea* (25), *Dicyemodeca* (2), *Pleodicyema* (1), and *Pseudicyema* (1); CONOCYEMIDAE: *Conocyema* (4 species), and *Microcyema* (1).

Genera are determined by the number and orientation of cells in each tier of the calotte, the presence or absence of abortive axial cells and the presence or absence of syncytial stages. Species are characterized by the size of the adult stages, the number of cells comprising the body, the shape of the calotte, the anterior extension of the axial cell, the presence or absence of verruciform cells and the structure of the infusiform larvae. Recent description of new species from a number of new host genera has greatly expanded our ideas about the morphological characteristics of the phylum as well as helped to define the limits of geographic distribution and host specificity.

Close examination of the dicyemids reveals a simple structure. In the adult vermiform stages, called nematogens and rhombogens, a single internal, axial cell runs almost the entire length of the body (Figure 3). The total length of the vermiform stages ranges from 500 to 10 000 μm, depending on the species. Reproductive products are relegated to the interior of the axial cell of the parent, which functions as a nurse or follicular cell providing both protection and nourishment for the germ cells and developing embryos. The axial cell is surrounded by a jacket of 20 to 40 large ciliated cells, called somatic or peripheral cells, The number of cells in the jacket is species specific. The head or anterior end is modified into a calotte, by which the parasite attaches to the host renal tissue.The calotte is covered by short stiff thigmotactic cilia which interdigitate with the brush border of the renal epithelial cells. The actual shape of the calotte varies a great deal depending on the species. There is no trace of a differentiated digestive, circulatory, nervous, respiratory, glandular or excretory system. No muscles, sensory receptors, or skeletal elements are present. In fact, nothing comparable to organs, tissues or glands is observed.

The infusiform, or dispersal stage, is morphologically the most complex stage in the life cycle, and yet, it is remarkably similar from species to species. It has been described in detail by Nouvel (1933a, 1948, 1961) and Short & Damian (1966). Mature larvae are ovoid. All species are ciliated posteriorly and most have two large refringent bodies anteriorly. They range in length from 25 to 50 μm and have a total of either 37 or 39 cells. Internally there is an urn cavity filled with four large cells each containing a smaller germinal cell. A relatively large nucleus and the intracellular location of these small cells indicates that they are probably germinal cells which give rise to the next generation. Recent fine structure studies by Bresciani & Fenchel (1965, 1967); Ridley (1968, 1969); and Matsubara & Dudley (1967a,b) have helped to clarify and resolve many observations on both the vermiform and infusiform stages in the life cycle.

The life cycle (Figure 3) has been a subject of controversy and, in spite of extensive study, it is still incompletely known (see papers by Gersch, 1938a,b, 1941a,b; Hartmann, 1904, 1906, 1925; Hochberg, 1982a; Koeppen, 1892; Lameere, 1905-1923; McConnaughey, 1951; Nouvel, 1947, 1948; Stunkard, 1937, 1954; Wheeler, 1899; Whitman, 1883). In its simplest expression it consists of an alteration of essentially isomorphic, parent generations. The embryos of all known stages develop within the axial cell of the parent until they are released through rupture of the parent's body wall. Cleavage is determinant, and a definite cell number is attained early in development. Subsequent growth is by cell enlargement.

The mode of entry into the host and the initiation of the infection is not known. Lapan & Morowitz (1972) proposed that germinal cells from the urn of the infusiform could directly infect the circulatory system of the host and from there penetrate into the kidneys. However, they did not present evidence or experimental data to support their contention. The earliest known stage observed in juvenile cephalopods is termed a stem nematogen. This stage differs from the typical adult vermiform stages principally in having two or three axial cells instead of the usual one. Subsequently, however, these stem nematogens produce vermiform embryos which have only one axial cell (see Figure 3).

The stage of the dicyemid cycle appears to depend on the maturity of the host. Immature hosts harbor populations of nematogens, all of which contain elongate vermiform embryos in their axial cells. The embryos develop asexually from gametes (axoblasts) and resemble the parent nematogens by the time they are released. Constant proliferation of daughter nematogens eventually results in an enormous population of dicyemids which fills the renal organs of the cephalopod host.

In older hosts the adult vermiform stage is called a rhombogen. In the axial cell of this parent stage the vermiform embryos are replaced by gamete-producing infusorigens and infusoriform larvae. Long a subject of controversy the hermaphroditic infusorigen has been described as either an individual or a gonad. The infusorigen consists of a nearly spherical axial cell which contains all the developmental stages leading to mature spermatozoa, and a jacket composed of oogonia and oocytes. Amoeboid spermatozoa emerge from the axial cell and penetrate peripherally

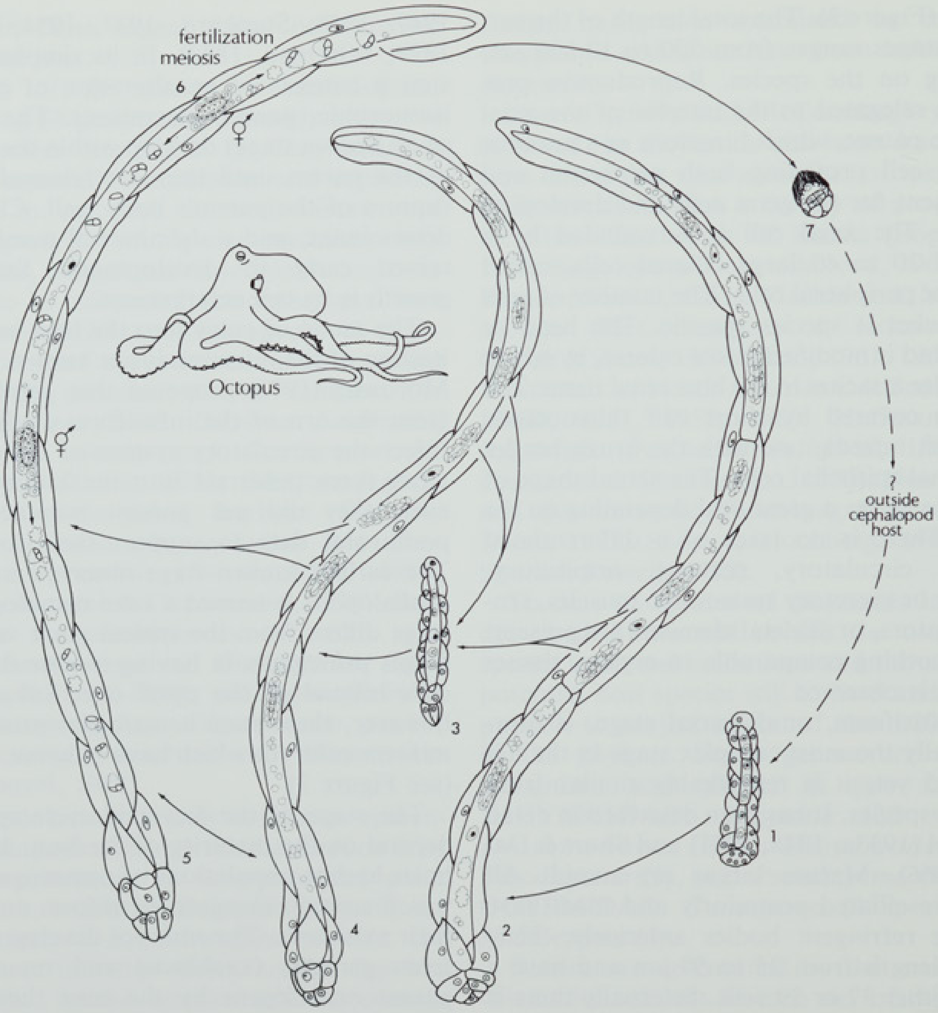

Figure 3. Life cycle of the dicyemid mesozoan, *Dicyemennea.*
1. larval stem nematogen
2. stem nematogen
3. vermiform embryo
4. nematogen
5. rhombogen
6. infusorigen
7. infusoriform released from parent

located oocytes (Austin, 1964; Short & Damian, 1967). The resulting zygotes develop into ovoid embryos which, when full grown, are termed infusoriform larvae. After breaking out of the parent body, the infusoriforms escape from the renal environment with the passage of the urine. The fate of this dispersal stage and the phase(s) of the cycle which occur(s) outside the cephalopod host are still a mystery. Several authors have suggested that the infusoriform larvae or their released germinal cells must infect a secondary benthic host since they are not attracted to young cephalopods (see Nouvel, 1947; McConnaughey, 1951; Stunkard, 1954). On the other hand, Lapan & Morowitz (1975) recovered dicyemids in the renal organs of *Sepia* reared from eggs in isolated aquaria and exposed only to infusoriform larvae. This indicates that an intermediate host may not be necessary.

Twice during the course of an infection the parasites undergo a change of phase. The initial infective phase is brief, and when the stem nematogens are spent they disappear and are replaced by nematogens. As the cycle progresses all nematogens are eventually transformed into rhombogens during which stage gametic reproduction takes place. In octopods, the transition from nematogens to rhombogens is prolonged and a mixture of stages is often found (Hochberg, 1971), whereas, in cuttlefishes a rapid metamorphosis is completed at the time of sexual maturation of the host (Nouvel, 1933b). Because the shift in phase is particularly evident in adult cephalopods, most authors have suggested that the hormonal flux associated with host maturation acts as a trigger. However, at the time of transition the renal organs are maximally crowded with parasites. Lapan & Morowitz (1975) demonstrated that population pressure or crowding may be the key factor which initiates the shift from the nematogen to rhombogen phase.

Both dicyemid mesozoans and chromidinid ciliates live in the excretory organs of cephalopods. Concurrent infections rarely occur since the hosts of these two parasites are normally spatially isolated. *Chromidina* typically infects oceanic cephalopods which never contact the bottom, whereas, the dicyemids are known from exclusively benthic or epibenthic hosts. The exploitation of the 'kidneys' of cephalopods by these two unusual vermiform parasites, therefore, is facilitated and maintained by the habits of the hosts and the spatial separation of the infective stages. In the absence of competition, adaptation to the selective pressures within the excretory environment has favored convergence of both form and reproductive strategy. In addition to the sizes and shapes of all stages being nearly similar, both parasites exhibit a diphasic life cycle which is remarkably well adapted to the requirements of their endoparasitic existence (Hochberg, 1982a).

VIII. PLATYHELMINTHES

A. Monogenea

Several monogeneans have been described from cephalopods. These forms are reviewed or figured by Bychowsky (1961), Dollfus (1958), Palombi (1949) and Sproston (1946).

Delle Chiaje (1822) recorded *Polystoma loliginum* from *Loligo vulgaris* in the vicinity of Naples, Italy. In 1841, he related that Krohn had discovered a similar monogenean in the vena cava of *Sepia officinalis*. Later, Diesing (1850) described *Solenocotyle chiajei*, which is now considered to be a synonym of *P. loliginum*. The existence of this species is the center of considerable controversy, as described by Dollfus (1913). This unusual endoparasitic worm is reported to infect the large blood vessels of at least two cephalopod hosts as mentioned above.

Two species of the genus *Isancistrum* have been found on adult *Alloteuthis subulata* (in older literature referred to as *Loligo media*) captured in the English Channel off France and England. Beauchamp (1912) originally described *I. loliginis*, which is now known to occur in small numbers (hundreds) in the mantle cavity and attached to the ends of the gill lamellae in the squid host (Sprehn, 1933; Llewellyn, 1974; see also Anon., 1976). A second, undescribed species lives in very large numbers (thousands) on the arms and tentacles of *Alloteuthis* (Llewellyn, 1974, 1979). These tiny, transparent parasites are viviparous gyrodactylids, which lack a free swimming larval stage. Llewellyn demonstrated that they invade new hosts by direct transfer during copulation. His studies also indicated the presence of overlapping generations of squid, which is an essential condition for survival and perpetuation of these two monogeneans.

Immature specimens of a third genus of monogenean were collected at Woods Hole, Massachusetts on an unidentified squid (probably either *Loligo* or *Illex*). This worm was originally assigned to the genus *Erpocotyle* by Price (1942). Though transferred to the genus *Squalonchocotyle* by Sproston (1946), Yamaguti (1963) later reassigned the original genus name. Until more material is available the exact generic placement and the specific name remain in doubt.

As more cephalopods, especially loliginids, are critically examined for parasites monogeneans may be shown to be common.

B. Digenea

Until recently cephalopods attracted little attention as potential hosts for digenetic trematodes. However, reviews by Overstreet & Hochberg (1975) and Gayevskaya (1977b) point out that almost 20 species of digeneans have been recovered from a total of nearly 30 species of cephalopod hosts (see Table 1). Cephalopods are parasitized by either larval stages (metacercaria) or adults and, hence, act as second intermediate, paratenic or final hosts but never first intermediate hosts.

The most characteristic and quantitatively the most important group of digeneans which infect squids are the larval didymozoids. Several distinct species are recognized that differ in body dimensions and the presence or absence of a thick walled stomach. In the majority of cases it has not been possible to associate these metacercarial stages with specific identified adult worms, hence, most are collectively lumped under the names '*Monilicaecum*' and '*Torticaecum*'. For a list of hosts and parasites see: Belyaeva (1979); Dollfus (1971); Fields & Gauley (1972); Gayevskaya (1976, 1977a,b); Gayevskaya & Nigmatulin (1975, 1976b, 1977, 1978); Hochberg (1969a); Overstreet & Hochberg (1975); Naydenova & Zuev (1978); Reimer (1974); and Yamaguti (1942).

Didymozoid metacercaria are localized in cysts adjacent to major blood vessels in the external wall of the stomach and caecum of most hosts. In certain tropical regions the prevalence of infection in oceanic squids may reach 100%, especially in the enoploteuthids and ommastrephids. Often hundreds or even thousands of worms may occur in a given host individual. Prevalence and parasitic load increase with an increase in the size of the host and with variations in diet. Maximum infections occur in squids which are intensively feeding on planktonic crustaceans and on small planktivorous fishes (Gayevskaya & Nigmatulin, 1977; Hochberg, 1969a). Gayevskaya (1976) proposed that infection may be initiated by free floating cystophorous cercariae which enter the mantle cavity and are 'fired' into the tissue of the host.

The life cycle of the didymozoids is thought to involve four hosts, but this has not been confirmed experimentally. The first intermediate stage probably occurs in pelagic molluscs, such as heteropods and thecosomes. The second intermediate or metacercarial stage occurs in crustaceans, such as copepods (Madhavi, 1968; Reimer, *et al.*, 1971). A third intermediate stage may occur in planktivorous fishes and squids. Hochberg (1969a) observed excysting metacercariae in squid stomachs filled with crustacean parts. Adult didymozoids occur in final hosts such as the large predatory tunas and billfishes.

Two genera of metacercariae are known from octopods, *Elytrophallus* from *Japatella heathi* and *Stephanostomum* from *Octopus briareus*. The latter is noteworthy because it is one of only a few digeneans known to infect its cephalopod host by active cercarial invasion rather than through ingestion of the metacercaria.

A number of immature, progenetic, and even a few sexually mature, adult digeneans have been reported. Two derogenids, *Derogenes varicus* and *Gonocerecella sepiocola* occur in *Sepia officinalis* (Overstreet & Hochberg, 1975; Reimer, 1974, 1975). The worms found in *Sepia* by Gros (1847) and Vaullegeard (1896) were probably *D. varicus*. *Gonocercella sepiocola* is not well known but *D. varicus* is considered by some to be the most widely distributed of all animals. It occurs world wide and has been reported from a great diversity of fishes and invertebrate hosts. Kφie (1979) reviewed the life cycle and redescribed several of its stages. Redia and cystophorous cercariae develop within the first intermediate host, which are gastropods of the genus *Natica*. When released the free swimming cercariae enter copepods and develop into metacercaria. When the copepods are ingested by larger crustaceans and chaetognaths the metacercaria may mature into adult worms, though usually *Sepia* and a variety of fishes are regarded as normal final hosts to the adult stage. Immature and even egg bearing progenetic worms may be transferred from one fish to another fish or to a cuttlefish.

In New Zealand, the allocreadiid, *Plagioporus maorum* commonly infects *Octopus maorum* and occasionally occurs in *Robsonella* *australis* (Allison, 1966; Short & Powell, 1968). Typically 40% or more of these octopods are infected. The renal sacs and adjacent areas often contain 30 or more worms. The presence of sexually mature, adult worms indicate that these octopods can be regarded as final hosts and not merely intermediate hosts.

Most reports of trematodes in cephalopods are discoveries of single hemiurids, accacoelids and hirudinellids. Typically, the prevalence of infection is low. As a result, cephalopods are not thought to play an important role in the life cycle of most digeneans. In most cases, cephalopods probably function simply as paratenic hosts which acquire infections when they eat the same intermediate hosts normally consumed in large numbers by teleosts which serve as the final hosts. As examples, in the Atlantic, Gayevskaya (1977a) found *Hirundinella ventricosa* in fewer than 1% of the *Ommastrephes pteropus* examined, and in Mississippi, Overstreet & Hochberg (1975) reported *Lecithochirium microstomum* in only 10% of the *Lolliguncula brevis* examined. Thus, these 'accidental' occurrences are due to ecological similarities between cephalopods and fishes in the pelagic environment.

C. Cestoda

Adult cestodes have never been reported from cephalopods. However, a diversity of larval and post-larval stages repeatedly have been described from decapods and octopods. This diversity indicates that cephalopods are important as second intermediate or paratenic hosts for cestodes which mature in elasmobranchs and fishes, and are transferred from host to host through the food chain.

Two orders of cestodes are represented in cephalopods, namely the Tetraphyllidea and the Trypanorhynchidea. Adults in both groups parasitize the digestive tracts of sharks, skates, and rays. Life cycles have not been completed for either of these two orders although several possible patterns have been postulated. At least two and sometimes three intermediate hosts and as many morphological forms of the parasite are involved (Euzet, 1979; Mudry & Dailey, 1971; Overstreet, 1983). In general terms, eggs, each containing a ciliated larval stage, are discharged from the vertebrate definitive host with the feces. Once in the sea the eggs are ingested by crustaceans, especially copepods and euphausiids. In the first intermediate host the oncospheres (= hexacanths) penetrate the intestine and undergo metamorphosis in the hemocoel to form procercoids. When the copepods are ingested by large teleost fishes, like sciaenids, the procercoids develop into solid-bodied post-larvae or plerocercoids. Recent evidence suggests that, at least in the tetraphyllideans, small planktivorous fishes, such as the anchovy, serve as additional obligatory intermediate hosts between the crustacean and fish hosts (Overstreet, 1983). Cephalopods are thought to pick up post-larval stages by feeding on either crustaceans or small fishes. The cycle is completed when predaceous elasmobranchs feed on prey containing infective post-larvae.

Trypanorhynch post-larvae are not directly comparable to tetraphyllidean plerocercoids and hence some authors, such as Dollfus (1942), have proposed the term plerocercus for the equivalent life cycle stage. The term metacestode is used by many authors to refer to all post-larval stages between oncosphere and adult. Therefore, in the above discussions it would replace the words procercoid, pleurocercoid, and plerocercus.

In tetraphyllidean cestodes the scolex characteristically bears four large leaf-like flaps or bothridia. Plerocercoids of the genus *Phyllobothrium* occur free or attached in the stomach, caecum and rectum of host cephalopods. Though the genus was reviewed by Williams (1968), the species reported from cephalopods are not well known and the genus still needs extensive study. *Phyllobothrium loliginis* is the most common species encountered in cephalopods. Originally described by Leidy (1887) from *Illex illecebrosus*, this cestode has been reported in a number of species of loliginids (*Loligo*) and ommastrephids (*Illex*, *Todarodes*, *Todaropsis*) on both sides of the North Atlantic. Linton (1922b) and later Stunkard (1977) indicated that the species *P. tumidum* may be identical to *P. loliginis* in which case all host records may be referred to the one cestode species. (See also

Dollfus, 1936, 1958; Euzet, 1959; Guiart, 1933; Linton, 1922b; Squires, 1957; Stevensen, 1933; Stunkard, 1977).

In France, *Sepia officinalis* is infected by *Phyllobothrium lactua* (Dollfus, 1958). Two species originally placed in the genus *Orygmatobothrium* are now considered to belong to the genus *Phyllobothrium*. In the Mediterranean *Todarodes sagittatus* is infected with *P. dohrnii* and in the Baltic Sea *Eledone moschata* harbors *P. pusillus* (see Dollfus, 1936; Siebold, 1850). Specimens, referred to *Phyllobothrium*, but not identified to species, have been recovered from a wide diversity of hosts in addition to those listed above (see Brown & Threlfall, 1968a; Dollfus, 1958, 1964; Gayevskaya, 1977, 1977a, 1978; Gayevskaya & Nigmatulin, 1975, 1978; MacGinitie & MacGinitie, 1968; Naydenova & Zuev, 1978; Threlfall, 1970).

Representatives of the genus *Dinobothrium* have been reported from a few species of squids in the Mediterranean and on both sides of the Atlantic Ocean. Stunkard (1977) found *D. septaria* embedded in the digestive tract of *Loligo pealei*. *Illex, Todaropsis* and *Sepia* harbor either *D. plicitum* or an as yet undesignated species of *Dinobothrium* (see Brown & Threlfall, 1968a; Dollfus, 1936, 1958, 1964; Gayevskaya & Nigmatulin, 1975, 1978; Squires, 1957). Stunkard (1977) indicated the strong possibility that *D. septaria* and *D. plicitum* are conspecific. Evidence suggests that squids, especially the ommastrephids, may be obligate and not paratenic intermediate hosts for the dinobothrids which mature in large, oceanic selacians such as *Cetorhinus* and *Carcharodon*.

The genus *Pelichnibothrium* is represented by two species, though some workers (Yamaguti, 1959) consider the genus to be monotypic. Originally described from California by Riser (1949, 1956) *P. speciosum* and *P. caudatum* occur in *Dosidicus gigas* and *Loligo opalescens* respectively. *Pelichnibothrium speciosum* has also been recovered off Japan in *Loligo* (Yamaguti, 1934), off Newfoundland in *Illex illecebrosus* (Brown & Threlfall, 1968a), and off Argentina in *I. argentinus* (Threlfall, 1970). Adult worms have been recovered from the Blue Shark, *Prionace glauca*, the Opah, *Lampris regia*, and the Bluefin Tuna, *Thunnis thynnis* (see Yamaguti, 1934). Larval stages have been recently reported from the euphausiid, *Thysanoessa longipes* off Japan (Shimazu, 1975).

Loligo vulgaris is known to harbor two larval cestodes. *Diplobothrium pruvoti*, described by Guiart (1933) and later reclassified by Dollfus (1936) and placed in the genus *Scyphophyllidium*. According to Dollfus (1958) the true identity of the second species, originally named *Bothriocephalus loliginis* by Delle Chiaje (1829), is still an enigma.

The genus '*Scolex*' is a heterogenous assemblage in which tetraphyllidean plerocercoids of uncertain affinity are placed. Several distinct types of '*Scolex*' larvae have been described from some 30 species of decapods and octopods but most cannot be assigned to a specific genus or species (Dollfus, 1964). Wagener's '*Scolex bothriis bilocularis*' was found in *Loligo pealei* by Stunkard (1977) and tentatively identified as *Ceratobothrium xanthocephalum*. Adults infect the spiral valve of sharks such as *Galeocerdo*, *Lamna* and *Isurus*. The name '*S. pleuronectis*' represents a complex of species the members of which probably belong to either the genus *Phyllobothrium* or *Acanthobothrium* (Cake, 1976). Depending on the number of suckers in the bothridia, subspecific types have been designated as '*unilocularis*, *bilocularis*, *trilocularis* or *quadrilocularis*'. Other unidentified tetrephyllidean larvae are refered to by the name '*S. polymorphus*' or simply '*Scolex* sp.'. The literature in this area is confused and since descriptions of various larval forms are often inadequate, I have not made an attempt to identify specific hosts. However, even if the literature was consistent and complete descriptions were provided in the majority of cases, it would not be possible to identify the cestodes and relate them to specific cephalopod hosts. In all cases life history studies are critically needed. For additional information see Brown & Threllfall (1968a); Cake (1976); Dollfus (1923b; 1958, 1964); Euzet (1959); Gayevskaya & Nigmatulin (1975, 1978); Naydenova & Zuev (1978) and Stunkard (1977).

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possess four tentacles armed with hooks and thus are easily identified. Larval stages are typically embedded in tough, fibrous cysts in the walls of the stomach and caecum of cephalopod hosts. Cephalopods appear to function merely as paratenic hosts, acquiring larval trypanorhynchs by feeding directly on euphausiids and other crustaceans or on teleost fishes, which also commonly serve as hosts. Trypanorhynchs mature only in the intestine of elasmobranch fishes.

The widely distributed genus *Nybelinia* is the most commonly encountered trypanorhynch in cephalopods. *Nybelinia lingualis* has been reported from a diversity of hosts in the Mediterranean, Atlantic and Indian Oceans, namely: *Sepia officinalis*, *Loligo vulgaris*, *Ommastrephes bartrami*, *O. pteropus*, *Symplectoteuthis oualaniensis*, *Eledone moschata*, and *Octopus vulgaris* (see Belyaeva, 1979; Cuenot, 1927; Dollfus, 1929, 1936, 1958, 1964: Gayevskaya, 1976; Gayevskaya & Nigmatulin, 1976b; Naydenova & Zuev, 1978; Pinter, 1930). *Loligo pealei* harbors both *N. bisulcata* and *N. yamagutii*. The latter species is also found in *Ommastrephes pteropus* and *Illex coindetti* (see Gayevskaya, 1977a; Gayevskaya & Nigmatulin, 1975, 1978; Stunkard, 1977). Off Japan, the prevalence of *N. surmenicola* in *Todarodes pacificus* may reach 22% (Dollfus, 1929, 1930, 1942; Kurochin, 1972; Yamaguti, 1934).

A number of undetermined or undescribed species of *Nybelinia* have been reported from *Sepiella*, *Lepidoteuthis*, *Moroteuthis*, *Illex*, *Notodarus*, *Ommastrephes*, *Symplectoteuthis* and *Gonatus* (see Belyaeva, 1979; Brown & Threlfall, 1968a; Clarke & Maul, 1962; Gayevskaya, 1977a; Gayevskaya & Nigmatulin, 1978; Hochberg, unpub.; Riser, 1949; Smith *et al.*, 1981; Yamaguti, 1934). Off Hawaii, I have commonly encountered two forms of *Nybelinia* in pelagic squids (Hochberg, unpub.). The first type is typically embedded in the digestive tracts of *Abralia*, *Abraliopsis*, *Enoploteuthis*, *Octopoteuthis*, *Histioteuthis*, *Symplectoteuthis*, and *Liocranchia*. The second type is found embedded either in the digestive gland or in the ventral mantle musculature of the sepiolid, *Heteroteuthis*. The older literature mentions *Amphistoma loliginis* and *Fasciola barbata* (=*F. loliginis*) from *Loligo vulgaris*. In both cases these worms are probably *N. lingualis* (see Dollfus, 1942, 1958).

A diversity of other genera of trypanorhynchs are known from cephalopods. Stunkard (1977) provisionally identified *Lacistorhynchus tenue* and *Otobothrium crenacolle* from *Loligo pealei*. *Tentacularia coryphaenae* has been recovered from a number of species of *Illex*, *Ommastrephes*, *Symplectoteuthis*, and *Todarodes* and from the finned octopod, *Chunioteuthis* (see Belyaeva, 1979; Dollfus, 1967; Gayevskaya, 1976, 1977a; Gayevskaya & Nigmatulin, 1976b, 1978; Naydenova & Zuev, 1978; Threlfall, *et al.*, 1971). Van Beneden (1870) mentioned finding a post-larva of *Christianelle minuta* in *Sepia officinalis*, though Dollfus (1958) doubts the validity of this earlier identification. *Dibothriorhynchus todari*, originally described by Delle Chiaje (1829, 1841) from *Todarodes sagittatus* was transferred to the genus *Hepatoxylon* by Yamaguti (1959). A second species of *Hepatoxylon*, *H. trichiuri*, has been reported from *Ommastrephes pteropus* in the Atlantic and from a specimen of *Architeuthis dux* stranded in Newfoundland (Gayevskaya, 1977a; Pippy & Aldrich, 1969).

Octopods generally harbor a distinct assemblage of trypanorhynch genera. Riser (1949, in Dollfus, 1964) identified a specimen of *Eutetrarhynchus* from *Octopus bimaculatus* in California. In France and Italy, *O. vulgaris* harbor both *Tetrabothriorhynchus octopodiae* and *Tetrarhynchus megabothrium* (see Diesing, 1850; Mingazzini, 1904; Redi, 1684; Vaullegeard, 1899). According to Dollfus (1958), this latter worm may represent a species of *Nybelinia*. Adam (1938) figured a *Nybelinia* from an unidentified octopus taken off the Andaman Islands in the Indian Ocean.

IX. ACANTHOCEPHALA

Two species of acanthocephalans have been reported from cephalopods. The presence of acanthocephalans in cephalopods is unusual since adults of this entirely parasitic phylum typically infect only vertebrate hosts. Gayevskaya (1977a) described and figured *Neorhadinorhynchus atlanticus* from the stomachs of *Om-*

mastrephes pteropus captured in the south Atlantic. Similar forms have also been recovered from the same host in the central and north Atlantic (Hochberg, unpub.; Naydenova & Zuev, 1978). Since these small (8-12 mm) rhadinorhynchids attain sexual maturity in cephalopods, Gayevskaya proposed that *O. pteropus* may function as a final host in this case and not simply a paratenic or transfer host. In the developmental cycle of acanthocephalans, stages normally infective to fishes are found in crustaceans and hence could also be ingested by squids.

Gayevskaya (1977a) and later Naydenova & Zuev (1978) referred to a second species, which also is found in *O. pteropus*, but which was located in the mantle cavity. Sufficient material was not available for identification of these large worms. Biological and ecological information relating to both parasites is not available.

X. NEMATODA

Larval nematodes are commonly encountered in many species of cuttlefishes, squids and octopuses. However, little information is available other than records of presence or absence. The abundant literature is complicated by a variety of unresolved taxonomic and nomenclatural problems (Smith & Wootten, 1978). In fact, the larval nematodes of marine animals, both fishes and invertebrates, are in need of critical review.

In the older cephalopod/parasite literature several species are briefly mentioned or figured. For the most part these worms are inadequately described and hence, a modern taxonomic designation cannot be applied. However, it is of interest to list these worms because the hosts are known and future investigators may some day be able to re-examine the host cephalopods and fit the pieces of the puzzle together.

Ascaris todari was reported to occur in *Ommastrephes bartrami* and *Todarodes sagittatus* in Naples (Delle Chiaje, 1829; Schuurmans-Stekhoven, 1935). A second species, *A. moschata*, was described by Stossich (1897; see Dollfus, 1958) from *Eledone moschata*, also from Italy. *Filaria loliginis* was described by Delle Chiaje (1829) from *Loligo vulgaris* captured in the vicinity of Naples. Schuurmans-Stekhoven (1935) indicated that the same nematode was found by Grümpe in the mantle cavity and ovaries of *Alloteuthis subulata* in Helgoland. Wülker (1930) presumed this worm to be a larval ascaridoid. Dujardin (1845) mentioned the presence of *F. piscium* in *Sepia officinalis*. This is probably the same nematode that Gros (1847) observed encysted in the stomach lining of *Sepia* (see Dollfus, 1958).

The majority of the nematodes that have been identified are ascaridoids. Five genera are reported to occur in cephalopods: *Porrocaecum* (Family Ascaridae); *Anisakis*, *Contracaecum*, *Terranova*, and *Hysterothylacium* (= *Thynnascaris*) (Family Anisakidae). Species in groups other than ascaridoids have been observed in cephalopods, but not commonly and they have not been reported. The only non-ascaridoid nematode reported from a cephalopod was an unidentified philometroid taken from the coelomic washings of *Loligo opalescens* in California (Dailey, 1969).

Although nematode genera are relatively easy to distinguish only a few species have been positively determined. In the Atlantic *Todarodes angolensis* and *Illex coindeti* only occasionally harbor *Porrocaecum* (Type I) larvae, whereas, a high percentage of *Ommastrephes bartrami* and *O. pteropus* were infected with *Porrocaecum* in both the North and South Atlantic (see Gayevskaya, 1974, 1976, 1977a; Gayevskaya & Nigmatulin, 1975, 1976a,b, 1978; Naydenova & Zuev, 1978). Belyaeva (1979) found *Porrocaecum* (Type I) larvae in *O. bartrami* in the Indian Ocean. 75-95% of the ommastrephids examined had small (3-5 mm), transparent larvae (Type I) encysted in connective tissue capsules on the external walls of the stomach, while 30-50% had larger worms (20-30 mm) encysted in the internal wall of the mantle. These worms are considered to be the same species, and they are characteristic of oceanic hosts.

In Norway, Berland (1961) was the first to note the presence of *Anisakis simplex*, encysted in the ventricle of *Todarodes sagittatus* (see Pippy & Banning, 1975). Throughout Japan, third stage larval anisakids of two distinct species have been commonly recovered by a number of investigators from *T. pacificus* and more rarely from *Doryteuthis bleekeri* (Kagei, 1970; Kato, *et al.*, 1968; Kobayashi, *et al.*, 1966; Koga, *et al.*, 1968; Kosugi, *et al.*, 1969; Koyama, *et al.*, 1969; Kurochin, 1972; Oishi, *et al.*, 1969; Okumura, 1967; Orihara, *et al.*, 1968; Oshima, 1972). A number of other species of cephalopods have been examined in the Orient and all have been found to be negative. Type I larvae are probably *A. simplex* and Type II larvae are currently recognised as *A. physeteris*. The majority of these worms occurred in circular cysts in the secretory portions of the visceral organs, and in the lining of the mantle cavity, although many also were found in the mantle musculature. When *Todarodes* makes a northward migration along the coast of Japan in spring and summer, the prevalence of infection is low, generally less than 10%. As the squid migrate southward during the fall and winter, following their stay in the waters off Hokkaido, the prevalence of nematodes rises to over 70% (Oshima, 1972). Their diet at this time is principally euphausiids which are known to harbor larval anisakids (Oshima, *et al.*, 1969; Shimazu & Oshima, 1972; Smith, 1971). Off New Zealand, *A. simplex* larvae have been found in a complex of *Notodarus* species (Smith, *et al.*, 1981).

Anisakis larvae have been observed by Clarke & Maul (1962) in a specimen of *Lepidoteuthis grimaldi* captured in the Atlantic and by Threlfall (1970) in *Illex argentinus* off Mar del Plata, Argentina. Belyaeva (1979) recovered *Anisakis* (Type I) larvae in *Symplectoteuthis* and *Ommastrephes* in the Indian Ocean. Gayevskaya & Nigmatulin (1975) reported *Anisakis* (Type I) larvae in *Todaropsis eblane* and *Todarodes angolensis* off southwest Africa and *O. pteropus* in several areas of the Atlantic. *Anisakis* (Type II) larvae occurred in 2% of the *O. bartrami* examined in the Atlantic by Gayevskaya. Normally, only one large (20 mm), pink worm occurred per host, in the lumen of the ovary or testis (Gayevskaya, 1976).

Terranova larvae are rarely found in squids off Japan (Orihara, *et al.*, 1968; Oshima, 1972). However, *Contracaecum* (Type B) larvae are commonly noted in the muscles of *Todarodes pacificus* (see Kikuchi, *et al.*, 1969, 1972; Kosugi, *et al.*, 1970; Oshima, 1972; Shiraki, 1969, 1974). In their review, Norris & Overstreet (1976) indicated that this latter worm represented a member of the genus *Thynnascaris*, whereas Deardorff & Overstreet (1981) transferred it to the genus *Hysterothylacium*. Both publications list *H. reliquens* as occurring in *Lolliguncula brevis* off Mississippi in the Gulf of Mexico. Brunsdon (1956) found *Contracaecum* larvae in the stomach and mesenteries of *Nototodarus sloani* off New Zealand but a positive identification has not been made (Hurst, pers. comm.). Cannon (1977) remarks that *Anisakis* and *Terranova* are typically found in plankton and nekton feeders, whereas *Contracaecum* and *Thynnascaris* occur principally in bottom feeders. In general this fits with the feeding habits of the cephalopods listed above but would be worthy of further investigation.

Unidentified nematodes have been recovered on numerous occasions from cephalopods. Nouvel, working in Monaco, found nematodes encysted in the mantle of *Onychoteuthis banksi* and *Sepia orbignyana*, in the stomach of *S. elegans*, and in the rectum of *Sepiola atlantica* and *Eledone aldrovandi* (see Dollfus, 1958). In France, Dollfus recovered nematodes from the musculature of *Histioteuthis bonelliana* and from the stomach of *Illex coindeti*. Off California and Hawaii, I have observed larval nematodes encysted in the digestive tracts of oceanic squids such as *Abralia*, *Abraliopsis*, *Enoploteuthis*, *Pterygioteuthis*, *Moroteuthis*, *Symplectoteuthis, Chiroteuthis*, *Japatella*, and *Vampyroteuthis*. In the Gulf of California, Mexico, I observed *Loliolopsis diomedeae* to be heavily infected with larval nematodes.

Oshima (1972) reviewed the life cycle of *Anisakis*. Adult worms are present in the stomachs of many cetaceans, especially the small toothed whales, and a few pinnipeds. Embryonated eggs are shed to the exterior with the feces. Following a single molt within the egg, ensheathed second stage larvae emerge in the sea water. The larvae are preyed upon by euphausiid crustaceans. Upon ingestion, the larval nematodes migrate into the hemocoel of the crustacean. Third stage larvae develop following exsheathment and another molt in the hemocoel of the first intermediate host. The prevalence of infection in euphausiids is very low but fishes and squids concentrate larvae as they feed on many hundreds or thousands of euphausiids during their life time. In these second intermediate hosts, the third stage larvae penetrate the alimentary tract and encyst in the organs of the body cavity or in the muscles. Advanced third stage larvae can be serially passed through the oceanic food chain without additional molts occurring. This further concentrates the larvae in a wide diversity of predatory fishes. Squids probably function as obligatory paratenic or transport hosts in the cycle. The cycle is completed when third stage larvae are consumed by marine mammals. Attaching to the stomach wall, the nematodes undergo two more molts, grow and eventually develop into sexually mature adults.

In certain areas of the world such as Japan, Korea, California, Britain, and Scandinavia, where uncooked fishes and squids are eaten anisakiasis is an important human health problem (See Cheng, 1976; Myers, 1975; Oishi, *et al.*, 1969; Okumura, 1967; Oshima, 1966, 1972; Smith & Wootten, 1978; Williams & Jones, 1976). Human infections, attributed to larval ascaridoid nematodes, are characterized by small ulcers or lesions, particularly in the stomach. This disease is typically transmitted through fishes, though squids, especially *Todarodes pacificus*, serve an equally important role (see Doi, 1973; Okumura, 1967; Oshima, 1972). Experimental evidence is lacking to positively link the larval nematodes in cephalopods with pathological symptoms in man, but most clinical parasitologists hold the opinion that species of larval anisakids, normally infective to marine mammal or bird final hosts, may be infective to humans if they ingest raw or partially cooked squids. The numerous reports of larval ascaridoids makes this an area of potential concern especially when considering the increased harvest of squids throughout the world.

XI. ANNELIDA

A. Hirudinea

Three species of hirudineans have been recovered from cephalopods, in all cases from *Octopus dofleini*. All are piscicolids which have very small posterior suckers and commonly attach to arthropods. Leeches normally obtain blood meals from fishes although some species have been reported to feed on crustaceans. Many of the species which feed on fishes eventually leave to deposit cocoons on hard shelled invertebrates such as crustaceans, pycnogonids, and bivalves (Overstreet, 1983). The association with octopuses appears to be temporary and may or may not involve feeding. Transfer most likely occurs when cephalopods feed on crustaceans.

Borovitzkaya (1949) described *Crangonobdella achmerovi* from *Octopus dofleini* captured in the Okhotsk Sea. According to Epshtein (1962) this species is synonymous with *C. murmanica* which parasitizes the shrimp, *Sclerocrangon*, and the fish, *Myoxocephalus*. The worm is widely distributed in Arctic waters having been reported in Greenland, Alaska and Russia as well as in the Okhotsk and Bering Sea. A second species, *Osterobdella papillata* was described and figured by Burreson (1977) from *O. dofleini* collected off Oregon. A species identified as *Johanssonia arctica* (Burreson, pers. comm.) has been found on *O. dofleini* off California. This latter species commonly attaches to deep sea pycnogonids (i.e., *Nymphon* and *Colossendeis*) and decapod crustaceans (i.e., *Chionoecetes*, *Paralithodes*, and *Hyas*) and is also reported to infest fishes (i.e., *Anarhichas* and *Gadus*). *Johanssonia arctica* is circumpolar in description, occurring throughout the Arctic Ocean, as far south as Newfoundland in the western Atlantic Ocean, and as far south as California in the eastern Pacific Ocean. See Meyer & Khan (1979) for a review of this species.

B. Polychaeta

Polychaetes are not commonly recognized as symbionts of cephalopods. Clark (1956) and Cheng (1967) reviewed the polychaete annelids which live in the gelatinous egg masses of neritic loliginid squids. *Capitella capitata ovincola* was described from the egg fingers of *Loligo opalescens* off California (Hartman, 1947, 1961). Hartman (1959) later described a second subspecies, *C. c. floridana*, obtained from the eggs of an unidentified squid collected off Florida. In France, the egg masses of *Loligo vulgaris* harbor two additional species. Boletzky & Dohle (1967) named *C. hermaphrodita* and Harant & Jecklins (1933) identified *Capitomastus minimus*.

At present these small capitellids are known only from the benthic egg masses of *Loligo*. They have not been encountered in the egg masses of any other cephalopod genera. All the worms live in mucoid tubes which irregularly penetrate the capsular matrix of the squid egg masses. Harant & Jecklins (1933) postulated that *Capitomastus* secretes an enzyme which dissolves the capsular membranes of the squid eggs and makes them suitable for food. *Capitella*, on the other hand, feeds only on the jelly in which the eggs are embedded and apparently does not harm the developing embryos. In the case of *C. c. ovincola*, the worms infest the egg masses at the time they are laid on the bottom. The worms become sexually mature and reproduce about the time the squids hatch (see Fields, 1950, 1965; MacGinitie & MacGinitie, 1968; McGowan, 1954). Though these capitellids are most similar to micropredators and not parasites, the degree of host and substrate specificity and the nature of the synchrony of life histories indicate a complex and highly specialized symbiotic interaction.

XII. ARTHROPODA/CRUSTACEA

Few published reports treat the crustaceans associated with cephalopods. Ten copepods, one branchiuran and three isopods have been described. These occur principally in the mantle cavity and on the gills of their cephalopod hosts. Other potential parasitic arthropods, such as mites and pycnogonids, and crustaceans, such as barnacles and amphipods are not known to infect cephalopods. For reviews see Dollfus (1958), Monod & Dollfus (1932), and Pelseneer (1929).

A. Copepoda

The copepods associated with cephalopods do not form a systematic unity. The majority of species have been classified with the poecilostomatoids but siphonostomatoids and harpacticoids are also represented. Most of the species are commensals and not true parasites (i.e., they do not injure the host) though in the majority of cases the relationships are highly host specific.

Members of two genera of siphonostomatoid copepods are reported from cephalopods. Tiny 'tad-pole like creatures' originally discovered by Smith (1887) on *Nautilus*, are now known to be caligid copepods of the genus *Anchicaligus*. Ho (1980) recently redescribed the single species, *A. nautili*, which had not been studied in detail since the time of Stebbing (1900). *Anchicaligus nautilii* is the only caligid known to parasitize a deep-water molluscan host. All the nearly 400 other species in the family infect coastal or oceanic fishes. The copepod infects *N. pompilius* and probably *N. macromphalus*. It is distributed throughout the range of both hosts in the Indo-Pacific. Little is known about the biology of the copepod. In his letters from New Guinea, Wiley (1896) reported that *A. nautili* attaches to the gills and moves around in the mantle cavity. Haven (1972) indicated that the 'commensal copepod' was common inside the funnel and on the inner surfaces of the ala infundibulae of *N. pompilius* in the Philippines. Wiley and others have noted that when nautiluses are placed in containers of water, the copepods emerge in large numbers from the mantle cavity and actively swim about. Although not completely known for *A. nautili*, the life cycle of some caligid copepods involves an intermediate host to which a series of chalimus larval stages are attached.

Larval stages of the pennellid '*Pennella varians*' have been repeatedly noted on the gills of *Eledone moschata*, *Sepia officinalis*, *S. elegans*, *Loligo vulgaris* and *Todaropsis eblane* (see Rose & Hamon, 1953; Rose & Vaissiere, 1953; and Wierzejski, 1877). All published reports indicate that only cephalopods from the Mediterranean are infected with this siphonostomatoid copepod. Originally described by Steenstrup & Lütken (1861), adults of this parasite typically occur on a variety of fishes. The presence of *Pennella* on cephalopods has been contested by Stock (1960). However, a specimen which I recovered from the gills of *Alloteuthis subulata* off Plymouth, England, was recently identified as a male *Pennella* (Ho, pers. comm.).

Two species of harpacticoid copepods in the tisbid genus, *Cholidya*, are known from the deep benthic octopods. Faran (1914) described *C. polypi* from specimens taken off the inner surface of the arm web of *Benthoctopus ergasticus* (= *Polypus profundicola*). The host was captured off the coast of Iceland. Bresciani (1970) described *C. intermedia* from an unidentified cirroteuthid collected off Britain in the Channel between the Faroe and Shetland Islands. This latter species occurred in the mantle cavity and on the gills. Nothing is known about the biology or life history of either copopod species.

The lichmologids are highly mobile poecilostomatoid copepods which actively move about over the suface of invertebrate hosts feeding on mucus. In their review of the family, Humes & Stock (1973) discussed the species known to live on cephalopods. *Lichomolgus longicauda* (= *Sepicola longicauda* and *L. sepicola*), is found on the gills and in the mantle cavity of *Sepia officinalis* and *S. filliouxi* wherever these two species of cuttlefishes occur (see Claus, 1960; Cuenot, 1927; Pesta, 1909; Stock, 1956, 1960; Wiezejski, 1877). Ho (pers. comm.) considers the copepod to belong to the genus *Doridicola* and not *Lichomolgus*. Another species of *Doridicola*, *D. sepiae* (= *Lichomolgus sepiae*), was reported by Izawa (1976) from *Sepia esculenta* in Japan. Stock (1960, 1964) recovered a single specimen of *Doridicola* ? *agilis* from the gills of *Todarodes sagittatus* at Rosas, Spain.

Members of the genus *Octopicola* live in specific association with octopuses. In the English Channel and in the Mediterranean *Octopus vulgaris* is infected with *O. superbus superbus*. In the West Indies, at Barbados and Curaçao, the same species (?) of host harbors *O. s. antillensis*. Humes & Stock (1973) identified the latter subspecies from *Octopus briareus* collected at several sites in Florida. *Octopus cyaneus* captured off Madagascar were infested with *O. stocki*, whereas *O. regalis* was present in the same host in the Pacific Ocean at New Caledonia and Eniwetok Atoll. For additional details on descriptions and distributions see: Bocquet & Stock (1960); Delamare Deboutteville, *et al.* (1975); Humes (1957, 1963, 1974); Humes & Stock (1972); and Stock, *et al.* (1963).

These small, cyclopiform copepods normally live in the mantle cavities of their octopus hosts though they may also be found on the body surfaces and amongst the eggs. In the mantle cavity they move about freely over the gills or attach, by means of the second antennae, to the arterial stems beneath the branchial leaflets. No damage to the tissues of the gills or the mantle cavities has been reported. Delamare Deboutteville, *et al.* (1957) noted that the European species, *O. superbus*, inhabits the mantle cavity during the day but moves out on the arms and over the head and mantle after dark.

All lichomolgids have a single host life cycle. Delamare Deboutteville and coworkers demonstrated that *Octopicola* exhibits a strong chemotaxis to the egg masses of the octopus. They are probably correct in assuming that autoinfestation regularly takes place. Gotto (1962) suggested that the reproductive rates of lichomolgids (i.e. egg number) reflects the mobility and habits of the host. He compared *Doridicola* (= *Lichomolgus*) which infects the cuttlefish, *Sepia*, and has a high egg count, with *Octopicola* which occurs in association with the more sedentary *Octopus* and produces a much smaller number of eggs.

B. Branchiura

The branchiurans are small copepod-like crustaceans which are external parasites of teleost fishes. However, a single species, *Argulus arcassonensis*, lives on the skin of *Sepia fillioux*i. It has, thus far, only been reported from Arcachon, France (see Argilas, 1936; Ceunot, 1912, 1927). Like other ectoparasitic crustaceans this species is dorsoventrally flattened and has developed modifications to enhance the efficiency of attachment and feeding. The second maxillae are greatly enlarged and modified as suckers to aid in attaching to the skin of the host and the mouth parts are adapted for piercing and sucking the blood and body fluids of the host.

C. Malacostraca

Of the parasitic malacostracans only a few isopods have been discovered on cephalopods. Though rare, they occur principally in the mantle cavity. *'Aegathoa occulata'* (=*A. loliginea*) infests *Loligo pealei* as well as a number of species of fishes found along the Atlantic and Gulf coast of the United States, Mexico and the West Indies (see Harger, 1878; Richardson, 1905). However, additional study is needed since the genus *Aegathoa* is considered to be a group name which represents a complex of young isopods of several genera and species. A second species, *Nerocila orbignyi*, was collected by Szidat (1955) from *Loligo* off the coast of Argentina. A single individual of an undetermined species of *Codonophilus* (=*Meinertia*) was taken by Dollfus (1958) from a specimen of *Sepia elegans* captured at Port-Vendres, France. And, a single individual of an unidentified isopod has been recovered from *Abraliopsis felis* in the North Pacific.

All the isopods named above are cymothoids, which as adults typically inhabit the gill chambers, skin and fins of fishes. Narrow host specificity is generally not observed, since these parasites are not permanently attached. Sexual dimorphism is the rule and the life cycle is protandric. Males are similar in size and shape to juveniles whereas females are very much larger and their bodies asymmetrically proportioned. Female isopods brood their eggs in a special marsupium under the thorax. Following hatching a free-swimming, manca stage is released. During juvenile development, the aegathoid stage attaches to a fish or cephalopod host. After settling on the host adult male characters are attained with the next molt. The male phase continues through several additional molts until a second individual lands on the host. At this point the larger of the two isopods is transformed into a functional female and begins to produce eggs. If the female dies, the male which remains begins to molt and eventually assumes the role of the female when another isopod settles on the host. For examples of cymothoid life cycles see Bowman (1960) and Brusca (1978).

In a few cases, brachyuran malacostracans have been reported as commensals in the mantle cavity of squids. Fischer (1943) found specimens of the galatheid, *Munida bamffia*, in the mantle cavity of *Alloteuthis subulata* being dissected by his students in Paris. Serene (1961) discovered megalopa larvae of an unknown crab in a number of *Loligo* captured off Viet Nam. On the surface these would appear to be 'accidental' associations, but Serene indicated that, in all cases, only one megalopa was found per host and that, in each case, the coloration blended perfectly with that of the host cephalopod.

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