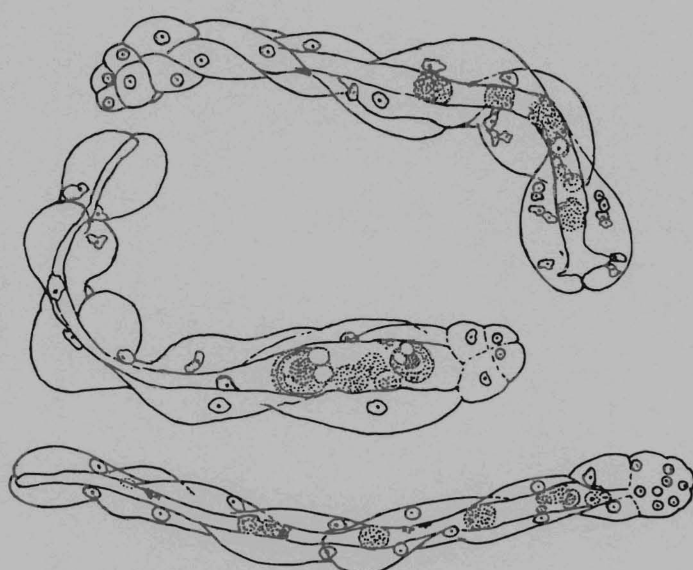
NOAA Technical Report NMFS 100 February 1991

Marine Flora and Fauna of the Eastern United States

Dicyemida

Robert B. Short



U.S. Department of Commerce

NOAA Techncial Report NMFS

The major responsibilities of the National Marine Fisheries Service (NMFS) are to monitor and assess the abundance and geographic distribution of fishery resources, to understand and predict fluctuations in the quantity and distribution of these resources, and to establish levels for their optimum use. NMFS is also charged with the development and implementation of policies for managing national fishing grounds, with the development and enforcement of domestic fisheries regulations, with the surveillance of foreign fishing off U.S. coastal waters, and with the development and enforcement of international fishery agreements and policies. NMFS also assists the fishing industry through marketing service and economic analysis programs and through mortage insurance and vessel construction subsidies. It collects, analyzes, and publishes statistics on various phases of the industry.

The NOAA Technical Report NMFS series was established in 1983 to replace two subcategories of the Technical Report series: "Special Scientific Report—Fisheries" and "Circular." The series contains the following types of reports: scientific investigations that document long-term continuing programs of NMFS; intensive scientific reports on studies of restricted scope; papers on applied fishery problems; technical reports of general interest intended to aid conservation and management; reports that review, in considerable detail and at a high technical level, certain broad areas of research; and technical papers originating in economic studies and in management investigations. Since this is a formal series, all submitted papers, except those of the U.S.-Japan series on aquaculture, receive peer review and all papers, once accepted, receive professional editing before publication.

Copies of NOAA Technical Reports NMFS are available free in limited numbers to government agencies, both federal and state. They are also available in exchange for other scientific and technical publications in the marine sciences. Individual copies may be obtained for the U.S. Department of Commerce, National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161. Although the contents of these reports have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

Recently Published NOAA Technical Reports NMFS

90. **Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries**, edited by Harold L. Pratt Jr., Samuel H. Gruber, and Toru Taniuchi. July 1990, 518 p.

91. **Marine flora and fauna of the northeastern United States—Echinodermata: Crinoidea**, by Charles G. Messing and John H. Dearborn. August 1990, 30 p.

92. **Genetics in aquaculture: proceedings of the sixteenth U.S.-Japan meeting on aquaculture; Charleston, South Carolina, 20–21 October, 1987**, edited by Ralph S. Svrjcek. November 1990, 81 p.

93. **Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985**, by William G. Pearcy and Joseph P. Fisher. November 1990, 83 p.

94. **An economics guide to allocation of fish stocks between commercial and recreational fisheries**, by Steven F. Edwards. November 1990, 29 p.

95. **Larval fish recruitment and research in the Americas: proceedings of the thirteenth annual larval fish conference; Merida, Mexico, 21–26 May 1989**, edited by Robert D. Hoyt. January 1991, 147 p.

96. **Marine flora and fauna of the Eastern United States—Copepoda, Cyclopoida: Archinotodelphyidae, Notodelphyidae, and Ascidicolidae**, by Patricia L. Dudley and Paul L. Illg. January 1991, 40 p.

97. **Catalog of osteological collections of aquatic mammals from Mexico**, by Omar Vidal. January 1991, 36 p.

98. **Marine mammal strandings in the United States: proceedings of the second marine mammal stranding workshop; Miami, Florida, 3–5 December, 1987**, edited by John E. Reynolds III and Daniel K. Odell. January 1991, 157 p.

99. **Marine flora and fauna of the Northeastern United States: Erect Bryozoa**, by John S. Ryland and Peter J. Hayward. February 1991, 48 p.

100. **Marine flora and fauna of the Eastern United States: Dicyemida**, by Robert B. Short. February 1991, 16 p.

101. **Larvae of nearshore fishes in oceanic waters near Oahu, Hawaii**, by Thomas A. Clarke. March 1991, 19 p.

NOAA Technical Report NMFS 100

Marine Flora and Fauna of the Eastern United States

Dicyemida

Robert B. Short

February 1991

U.S. DEPARTMENT OF COMMERCE
Robert Mosbacher, Secretary
National Oceanic and Atmospheric Administration
John A. Knauss, Under Secretary for Oceans and Atmosphere
National Marine Fisheries Service
William W. Fox Jr., Assistant Administrator for Fisheries

Foreword

This NOAA Technical Report NMFS is part of the subseries ''Marine Flora and Fauna of the Eastern United States'' (formerly ''Marine Flora and Fauna of the Northeastern United States''), which consists of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the eastern United States. The manuals are published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation. These manuals are intended for use by students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. They can often serve as guides to additional information about species or groups.

The manuals are an outgrowth of the widely used ''Keys to Marine Invertebrates of the Woods Hole Region,'' edited by R.I. Smith, and produced in 1964 under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts. Geographic coverage of the ''Marine Flora and Fauna of the Eastern United States'' is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Florida, but can vary somewhat with each major taxon and the interests of collaborators. Whenever possible, representative specimens dealt with in the manuals are deposited in the reference collections of major museums.

The ''Marine Flora and Fauna of the Eastern United States'' is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual is based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each manual, treating a separate major taxon, includes an introduction, illustrated glossary, uniform originally illustrated keys, annotated checklist (with information, when available, on distribution, habitat, life history, and related biology), references to the major literature of the group, and a systematic index.

Manuals are available from the National Technical Information Service, United States Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161, either as a paper copy or microfiche, for a charge. Manuals are not copyrighted, and so can be photocopied from the NOAA Technical Report NMFS Circulars and Reports available in most major libraries and listed at the end of this manual.

Marine Flora and Fauna of the Eastern United States
Dicyemida

ROBERT B. SHORT

Department of Biological Science B-142
Florida State University
Tallahassee, FL 32306-2043

ABSTRACT

This manual treats the six species of dicyemid mesozoans that have been reported in three species of hosts (*Octopus vulgaris*, *O. joubini*, and *O. briareus*) from the eastern coast of North America and the Gulf of Mexico, including the Florida Keys. All are parasites of species of *Octopus* and are in the genus *Dicyema*, family Dicyemidae. In the introduction, the life cycle, as known, and the general morphology of dicyemids are briefly described, and methods are given for collecting and preparing material for study. These are followed by a key to species and by an annotated checklist, which includes data, some hitherto unpublished, on their known prevalence in hosts from various localities including Bimini and Bermuda.

Introduction

The dicyemid mesozoans are a relatively small group of minute parasites with a simple yet multicellular structure. They parasitize cephalopod molluscs and are found primarily in the fluid-filled renal sacs (renal coelom) or "kidneys." In decapod cephalopods (squids, sepiolids, and teuthoids), they have been found also in the reno-pancreatic coelom and occasionally in the pericardium (Hochberg 1983). Dicyemids were discovered by Cavolini (1787) and were described by Krohn (1839) and Erdl (1843).

The name Mesozoa was proposed by van Beneden (1876) to indicate his belief that the simple structure of these parasites represents an evolutionary stage between the protozoans and metazoans. There has been considerable controversy regarding their taxonomic position. The dicyemids have usually been considered to form, together with the orthonectids (parasites of various invertebrates), the phylum Mesozoa (e.g., Hyman 1940). Stunkard (1954), however, has argued that the mesozoans should be included as a class in the phylum Platyhelminthes. Furthermore, because of differences between the dicyemids and orthonectids in internal structure and the lack of homologies in their life-cycle stages, other workers (e.g., Kozloff 1969; Hochberg 1983) have considered them not to be closely related. Hochberg (1983) suggested that "it is best to treat these two assemblages as separate phyla [Dicyemida and Orthonectida] and to use the term 'Mesozoa' to refer to their grade of organization only." In the present manual this systematic scheme will be followed, and only members of the phylum Dicyemida will be considered.

Recent accounts of the dicyemids have been published by Hochberg (1982, 1983, 1990) and Stunkard (1982). Earlier reviews include those of Hyman (1940), Stunkard (1954), Czihak (1958), Grassé (1961), and McConnaughey (1963, 1968).

A total of about 40 species of cephalopods, representing 15 genera, are currently known to be hosts of dicyemids. The parasites occur mostly in cuttlefishes, sepiolids, and octopods and less frequently in loliginid squids and have been reported from temperate, polar, and subtropical waters in many parts of the world.

This manual deals with the dicyemid mesozoans reported from off the coast of eastern North America and the Gulf of Mexico, including the Florida Keys. All hosts reported herein are species in the genus *Octopus*.

Morphology and Life Cycle

In the renal sacs, vermiform stages are the conspicuous ones. These occur with the anterior ends adhering to, and more or less embedded in, the renal appendages (venous appendages) of the host, with most of the body floating freely in the host urine within the sac. They may also be seen swimming slowly in the urine, propelled by their cilia. Vermiform stages have a simple multicellular structure (Figs. 1, 2). A single elongated axial cell (except in stem

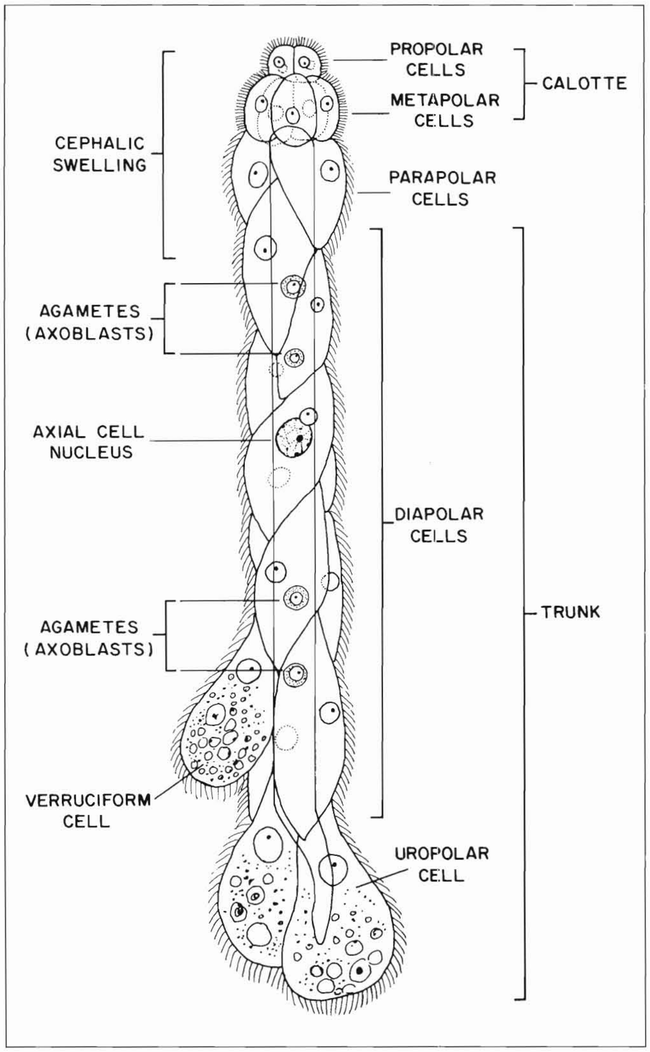


Figure 1
Generalized drawing of a young dicyemid (*Dicyemennea*) showing terms for various parts. Modified slightly from McConnaughey (1951).

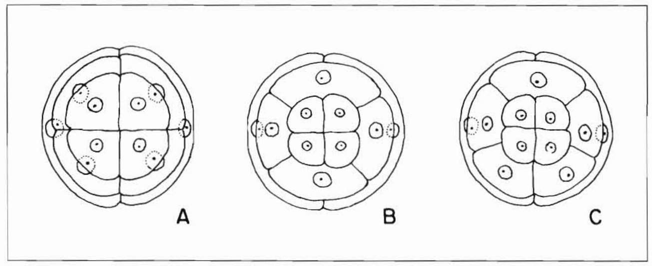


Figure 2
Diagrams of anterior end views of primary and secondary nematogens and rhombogens of the genera *Dicyema* (**A**), *Pseudicyema* (**B**), and *Dicyemennea* (**C**). Calotte patterns and parapolar cells shown. Redrawn from Nouvel (1947). Cilia not drawn.

Figure 3 (Facing page, top)
Photographs. (**A**) *Dicyema typoides* rhombogens. (**B**) *D. hypercephalum* rhombogens. (**C**) *D. apalachiensis* nematogens. In part from Short (1962, 1964). Scale in micrometers.

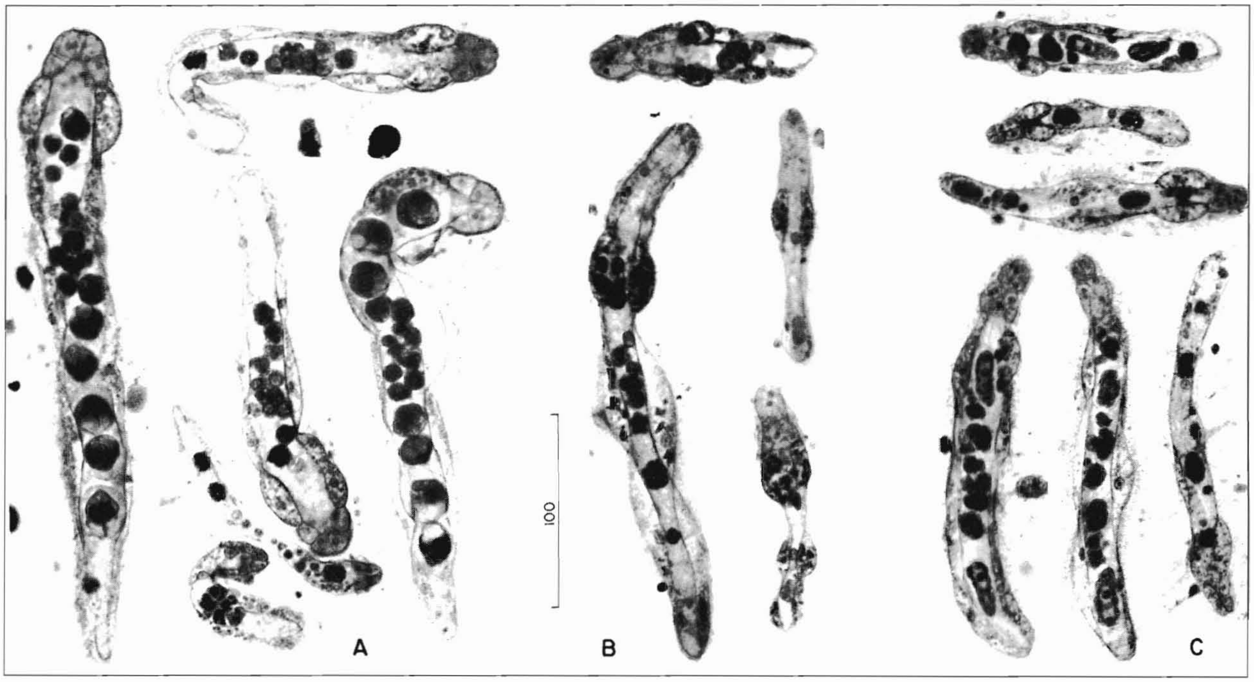
Figures 4–8 (Facing page, bottom)
Fig. 4. Vermiform embryos of *D. bilobum*. (**A**) Surface view. (**B**) Optical section. (**C**) Optical section of anterior end of *Dicyemennea eledones*, showing anterior abortive axial cell (arrow). (A and B) redrawn from Couch and Short (1964); (C) modified from Nouvel (1947). **Fig. 5.** Infusorigens within axial cells of rhombogens. (**A**) *Dicyema briarei*. (**B**) *D. aegira*. (A) redrawn from Short (1961); (B) redrawn from Short and Damian (1967). **Figs. 6–8.** Infusoriform larvae. (**6**) *Dicyema aegira*, optical sagittal section (to same scale as Fig. 5). (**7** and **8**) *Dicyema briarei*. (7) Dorsal view within axial cell of rhombogen. (8) Optical sagittal section. a = refringent body; b = capsule cell; c = urn cell. (6) modified from Short and Damian (1966). (7 and 8) from Short (1961). Scales in micrometers. Cilia not shown.

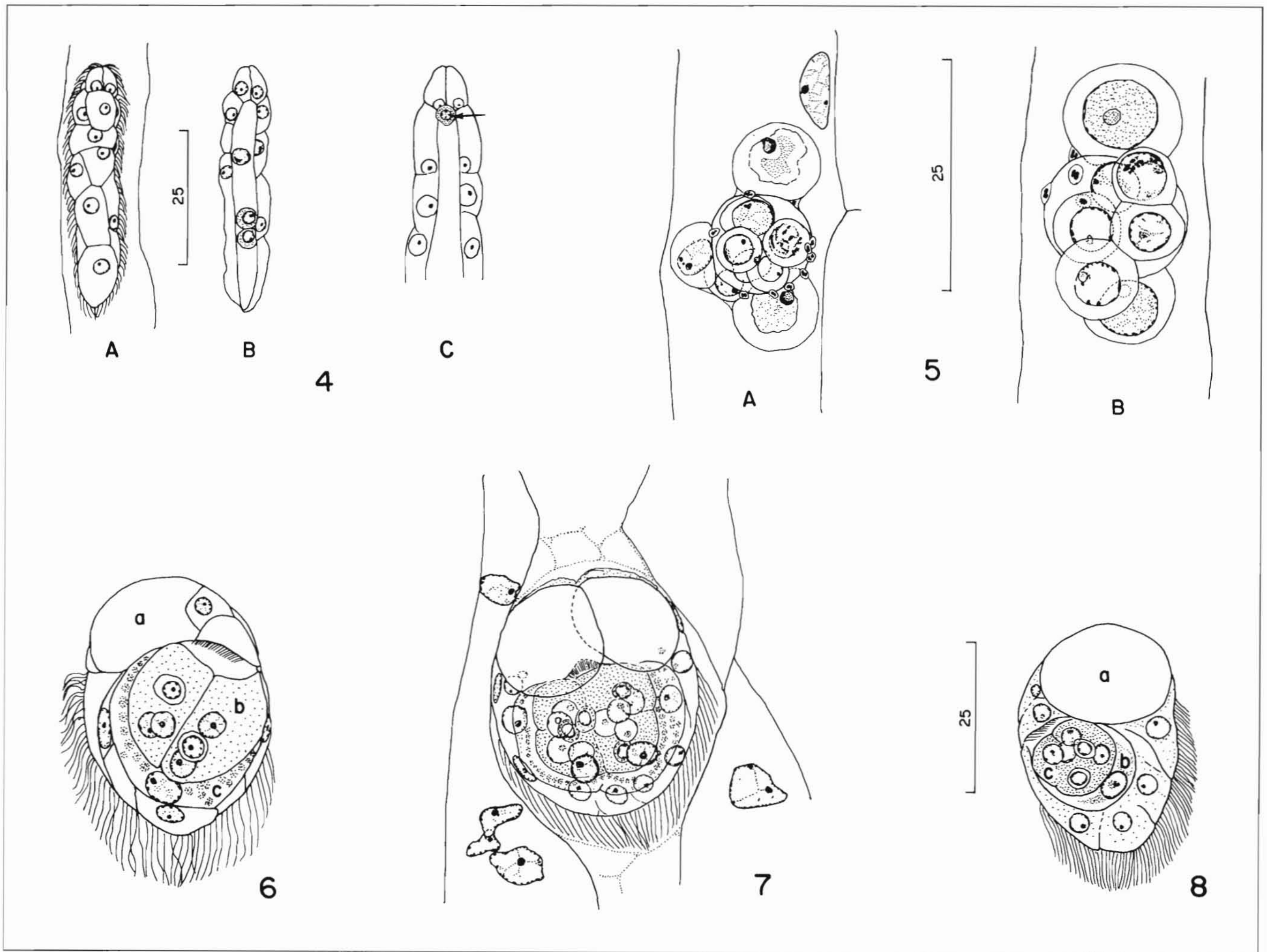
nematogens, which may have two or three axial cells; *see* below) is surrounded by a single layer of ciliated peripheral (somatic) cells. Somatic cells are arranged in groups. The anterior or "head" group is modified into a calotte consisting (typically) of two tiers of cells, the propolar and metapolar cells. These cells have shorter, denser cilia than other somatic cells. Immediately behind the calotte are the parapolar cells (usually two), then trunk cells, consisting of several diapolars, and two posterior uropolar cells covering the posterior end of the axial cell. Parapolar and trunk cells often contain refractive granular material in their cytoplasm (*see* Figs. 3, 20). The diapolar and uropolar cells of certain species become so laden with such material that they are swollen; if this is the case, they are termed verruciform cells (Fig. 1).

The number and arrangement of somatic cells is rather constant for a species but may vary within narrow limits. Somatic cell numbers range among species from 14 to 40. Lengths of adult vermiform stages vary from about 260 to 10,000 μm, depending on the species.

Typical mature vermiform stages encountered are of two types or phases: nematogens and rhombogens. Besides a nucleus, the axial cells of nematogens contain within their cytoplasm agametes (axoblasts), which are asexual reproductive cells, and vermiform embryos (Figs. 3C, 4) in various stages of development. Axial cells of young nematogens may contain only agametes (as in Fig. 1). Axial cells of rhombogens contain one or more of a bisexually reproductive stage (or gonad), the infusorigen (Fig. 5), and also infusoriform larvae (Figs. 3A, 6–8), which are ciliated when fully developed. A diagram of the life cycle is shown in Figure 9.

Vermiform embryos develop within axial cells of nematogens from mitotic division of agametes. Early in development, they attain the definitive somatic cell number; they


100
A
B
C


25
A
B
C
4
25
A
5
B
a
b
c
6
7
25
a
b
c
8

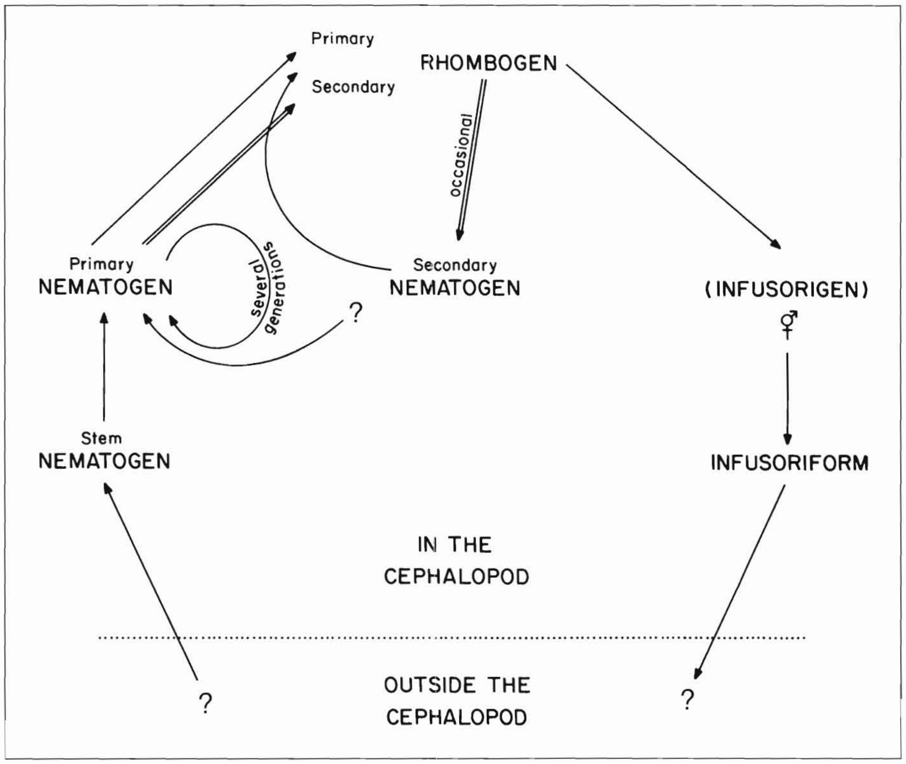


Figure 9
Diagram of the life cycle. Single straight line from primary NEMATOGEN indicates development of vermiform embryos into primary rhombogens; double lines indicate transformation of recognizable nematogens into secondary rhombogens and of rhombogens into secondary nematogens. From McConnaughey (1951).

then continue to grow in size and, at a certain stage, escape from the parent nematogen (a process called eclosion). They further mature to become nematogens and produce vermiform embryos within their axial cells. By this means, large numbers of primary nematogens populate the cephalopod kidney. Vermiform embryos of some species of dicyemids (in the genus *Dicyemennea*) at eclosion possess, in addition to the usual single elongated axial cell, a small "abortive" axial cell located immediately anterior to the larger axial cell (Fig. 4C). This abortive axial cell degenerates soon after the embryo escapes from the nematogen. When a large number of primary nematogens have been built up in the cephalopod kidney by production of vermiform embryos, a change in the population occurs such that the predominant mature phase becomes the rhombogen. Rhombogens may originate in two ways: 1) from immature vermiform stages (primary rhombogens) and 2) by transformation of functional nematogens to rhombogens (secondary rhombogens). During this transformation, some transitional stages may have large numbers of single cells (agametes?) in their axial cells; other transitional stages may contain both vermiform embryos and infusorigens.

The infusorigen (Fig. 5), as mentioned above, is a hermaphroditic individual or stage (probably more properly called a gonad) that remains within the axial cell of a rhombogen. Each infusorigen is composed of a more or less spherical "axial" cell, with male reproductive cells inside and female cells more or less surrounding it. The male cells consist of spermatogonia, spermatocytes, and tailless spermatozoa; female cells are oogonia and oocytes. Spermatozoa, formed within the "axial" cell, emerge and penetrate oocytes. When fertilization is completed, the zygote develops into an infusoriform larva (Figs. 6–8), which, when mature, escapes from the rhombogen and from the cephalopod host with the urine. Rhombogens typically have one to a few infusorigens (Fig. 3A), and sometimes in larger individuals a series of developmental stages of infusoriform larvae extend in opposite directions from each infusorigen.

The infusoriform (Figs. 6–8) is morphologically the most complex stage in the cycle and is rather similar in structure among a wide variety of species. It is ovoid or pyriform and has cilia over the posterior region and a large part of the dorsal and lateral surfaces. A characteristic feature is the presence of two relatively large "refringent bodies," each located within an anterodorsal apical cell and surrounded by a thin layer of this cell's cytoplasm. Refringent bodies are often crystalline. In some species of dicyemids, however, the bodies are not refractive and are termed mucoid; in other species bodies are absent or at least not readily apparent. In the interior of infusoriforms are two large capsule cells that form the so-called urn. These cells often contain conspicuous granules and appear in lateral view relatively thin and more or less C-shaped (Figs. 6, 8); they surround four urn cells posteriorly, dorsally, and to a large degree laterally. Cytoplasm of the urn cells usually stains more darkly than that of other cells. Each urn cell usually contains two nuclei and one smaller cell interpreted as a germinal cell. Two germinal cells per urn cell have been reported in a few species.

As indicated by Figure 9, the life cycle of dicyemids is not completely known. That part within the host is pretty well understood, but little or nothing is known about the mode of entry into new hosts and initiation of infection. The earliest known stage seen in young cephalopods is termed the stem nematogen. It differs from other nematogens chiefly in having two or three axial cells instead of one. Stem nematogens, at first very small, may grow to be considerably larger than other nematogens. Agametes in their axial cells develop into vermiform embryos that emerge and become primary nematogens, each with a single axial cell. Presumably, the infusoriform larva, which leaves the cephalopod, is responsible for infecting new hosts, but whether it infects a cephalopod directly or uses an intermediate host is not clear, nor is it known whether infection occurs by means of the entire larva or by only certain cells (germinal cells?).

Dicyemid Families and Genera

To date 68 species of dicyemids have been described in the two families and eight genera listed below.

	No. of species
Family Dicyemidae	
Dicyema von Kölliker, 1849	33
Pseudicyema Nouvel, 1933	1
Dicyemennea Whitman, 1883	26
Dicyemodeca Wheeler, 1897	1
Pleodicyema Nouvel, 1961	1
Dodecadicyema Kalavati and Narasimhamurti, 1980	1
Family Conocyemidae	
Conocyema van Beneden, 1882	4
Microcyema van Beneden, 1882	1

Members of the family Conocyemidae differ from those of the family Dicyemidae in one major way: peripheral cells of adult vermiform stages lose their cilia and fuse to form a syncytium covering the axial cell, whereas in the Dicyemidae peripheral cells of adult vermiform stages retain their cilia and their individual identity.

Genera in the Dicyemidae have been determined usually by the number and arrangement of cells in the calottes of the primary and secondary nematogens and rhombogens. The situation in the Conocyemidae is not clear, and the systematics of this group needs revision. The calottes of genera in the family Dicyemidae have the following configurations:

Dicyema: 8 polar cells (4 propolar, 4 metapolar), polar and metapolar cells opposite each other (Fig. 2A).

Pseudicyema: same as *Dicyema* except that polar cells alternate with metapolar cells (Fig. 2B).

Dicyemennea: 9 polar cells (4 propolar, 5 metapolar) (Figs. 1, 2C).

Dicyemodeca and *Pleodicyema*: 10 polar cells (4 propolar, 6 metapolar).

Dodecadicyema: 9 to 14 polar cells (4 propolar, 6 metapolar, plus, in most individuals, 3 (occasionally 2) much smaller cells forming the anterior tip of the calotte).

An important species character is the peripheral (somatic) cell number. This can be determined accurately for vermiform embryos and generally for young or small nematogens because each cell has a single nucleus, which is easily visible. Care should be taken, however, in determining cell numbers for rhombogens (and sometimes also large nematogens) because in certain species (e.g., *Dicyema aegira*) peripheral trunk cells sometimes contain accessory nuclei, i.e., nuclei in addition to the original cell nucleus (*see* Fig. 15). Accessory nuclei apparently arise by mitotic budding that may produce daughter nuclei of very unequal size (McConnaughey 1951), and their presence may cause difficulty in obtaining reliable cell counts.

Species are characterized also by the size and general shape of adult vermiform and infusorigen stages, the shape of the calotte, the anterior extent and degree of branching of the axial cell, the presence or absence of verruciform cells, and the structure of the infusoriform larva.

Only species in the genus *Dicyema* have been reported from the coast of eastern North American and the Gulf of Mexico, and in this genus abortive axial cells have not been reported nor has branching of the axial cell. As mentioned above, the genus *Dicyema* is characterized by 4 propolar and 4 metapolar cells.

Collection and Preparation of Dicyemids for Study

The following procedure is used commonly for preparation of dicyemids. The octopod host, if active, can be anesthetized by addition of 70% ethanol to sea water. It then is laid on its back and a midventral cut of the mantle is made from its anterior edge posteriorly to expose the conspicuous, fluid-filled renal sacs, which lie at the surface of the visceral mass. The renal sacs are semitransparent, and within them lie the renal appendages (*see* Fig. 39), which are outpocketings of the venae cavae. Vermiform dicyemids adhere to the renal appendages, often with their calottes embedded in depressions in the renal epithelium. Smaller vermiform individuals occur within the folds and crevices of the appendages, and a few dicyemids may also occur free in the urine.

The renal sacs are cut open and the appendages removed, *en masse* or a piece at a time, with the attached dicyemids. Octopods, especially more mature ones, often harbor heavy dicyemid infections, and the vermiform stages can be seen easily with the lower powers of a dissecting microscope appearing as ''hairs'' projecting from the edges of the renal appendages. Occasionally light infections occur and are more difficult to detect. Smears with pieces of renal appendage are made on coverslips or slides and, when fixed, stained, and mounted, are useful for study. Bouin's fixative is satisfactory and can be followed by staining with hematoxylin (e.g., Ehrlich's acid hematoxylin or Heidenhain's iron hematoxylin) and, if desired, by counterstaining with eosin. Care should be taken not to let the coverslip smears become dry at any time during the process from fixative to mounting medium.

Key to the Dicyemid Mesozoa of the East Coast of North America and the Gulf of Mexico

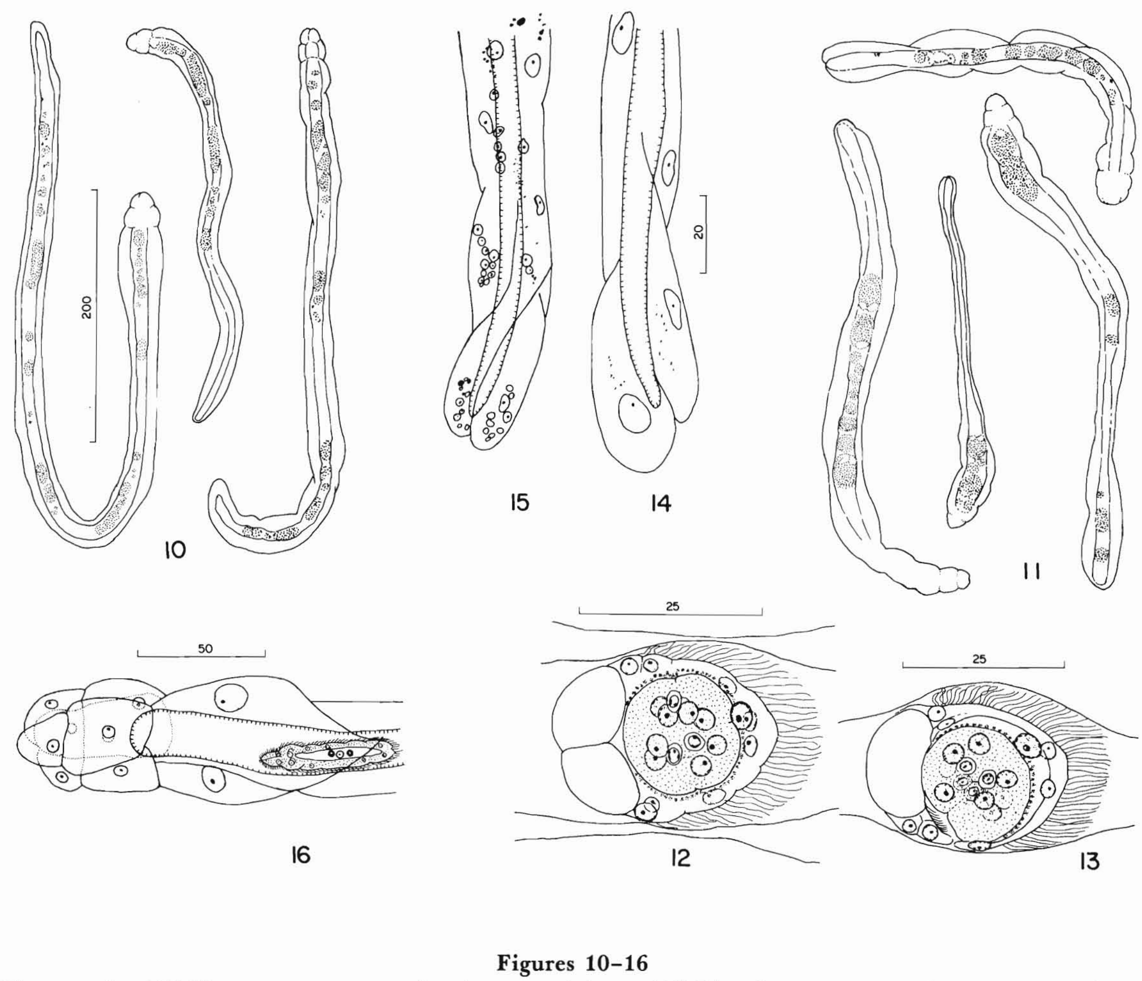
Genus *Dicyema* von Kölliker, 1849

1 Somatic cells of vermiform stages most often 22, varying from 20 to 25 (very seldom 18 and 19) 2

1 Somatic cells fewer than 20 3

2(1) Adult vermiform stages usually 400 to 1500 µm in length; somatic cell number 22, seldom 21 to 25; tendency for infusorigens and their products to be located well forward in axial cell of rhombogens causing a swelling behind the calotte (cephalic swelling); somatic cells not conspicuously charged with granules, a pronounced tendency to produce accessory nuclei in the posterior diapolar and uropolar cells. Vermiform embryos 40 to 50 µm at eclosion. Refringent bodies, in infusoriforms viewed laterally, appearing smaller than the cluster of 4 urn cells (*see* Figs. 5B, 6) . . . . *Dicyema aegira* **(Figs. 10–16)**

Hosts: *Octopus vulgaris* Cuvier, 1797; *Octopus joubini* Robson, 1929

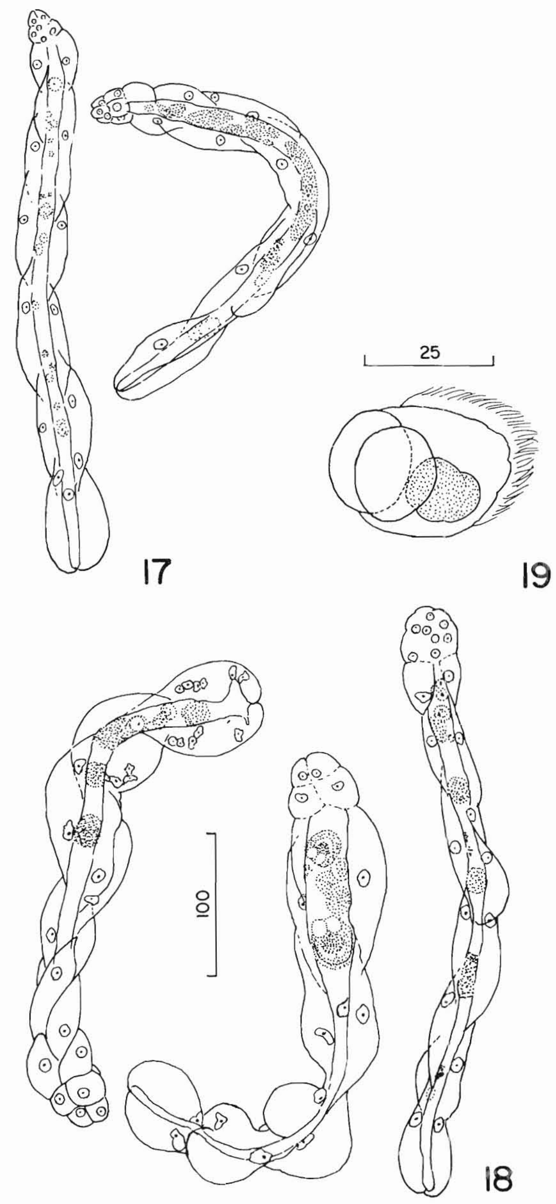


Figures 10–16

Dicyema aegira. (**10**) Nematogens, mature, showing general shape. (**11**) Rhombogens, mature showing general shape. (**12** and **13**) Infusoriform larvae, frontal view (12), sagittal optical section (13). (**14**) Posterior portion of trunk of young nematogen. (**15**) Posterior portion of trunk of rhombogen showing fragmentation of nuclei in somatic cells (**16**) Anterior end of large nematogen showing calotte and its relation to the axial cell, which contains a vermiform embryo. (14–16) redrawn from McConnaughey and Kritzler (1952). Scales in micrometers. Cilia not shown on mature vermiform stages.

2(1) Adult nematogens from about 300 to slightly over 1000 μm in length; largest adult rhombogens about 1000 μm, often smaller; somatic cell number usually 20 to 22, most often 22, seldom 18, 19, 23, 24; body usually about the same width throughout with no conspicuous cephalic swelling; cytoplasm of somatic cells, especially uropolar and posterior diapolar, characteristically charged with particulate matter variously appearing as fine granules or small globules of spherical, oval, or irregular shape (Fig. 20); granular material usually denser and more conspicuous in rhombogens than in nematogens, with tendency toward formation of verruciform cells. Vermiform embryos about 60 to 70 μm at eclosion. Refringent bodies, in infusoriforms viewed laterally, appearing larger than the cluster of 4 urn cells (*see* Figs. 5A, 7, 8)... ***Dicyema briarei*** **(Figs. 17–20)**

Host: *Octopus briareus* Robson, 1929



Figures 17–19
Dicyema briarei. (**17**) Nematogens (to same scale as Fig. 18). (**18**) Rhombogens. (**19**) Infusoriform larva, side view, showing refringent bodies and urn cells (stippled). (17–19) redrawn from Short (1961). Cilia not shown on vermiform stages.

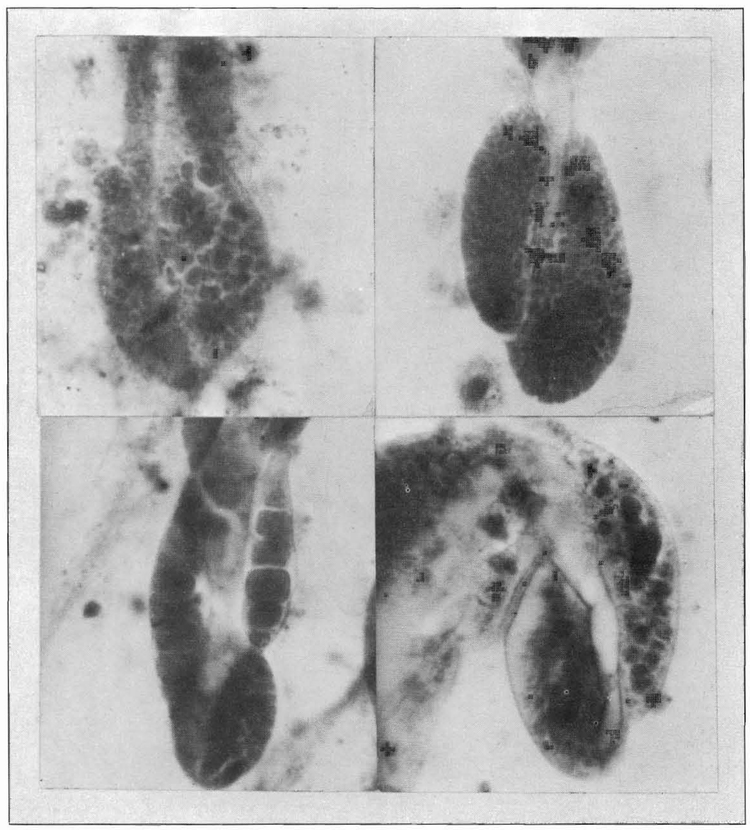


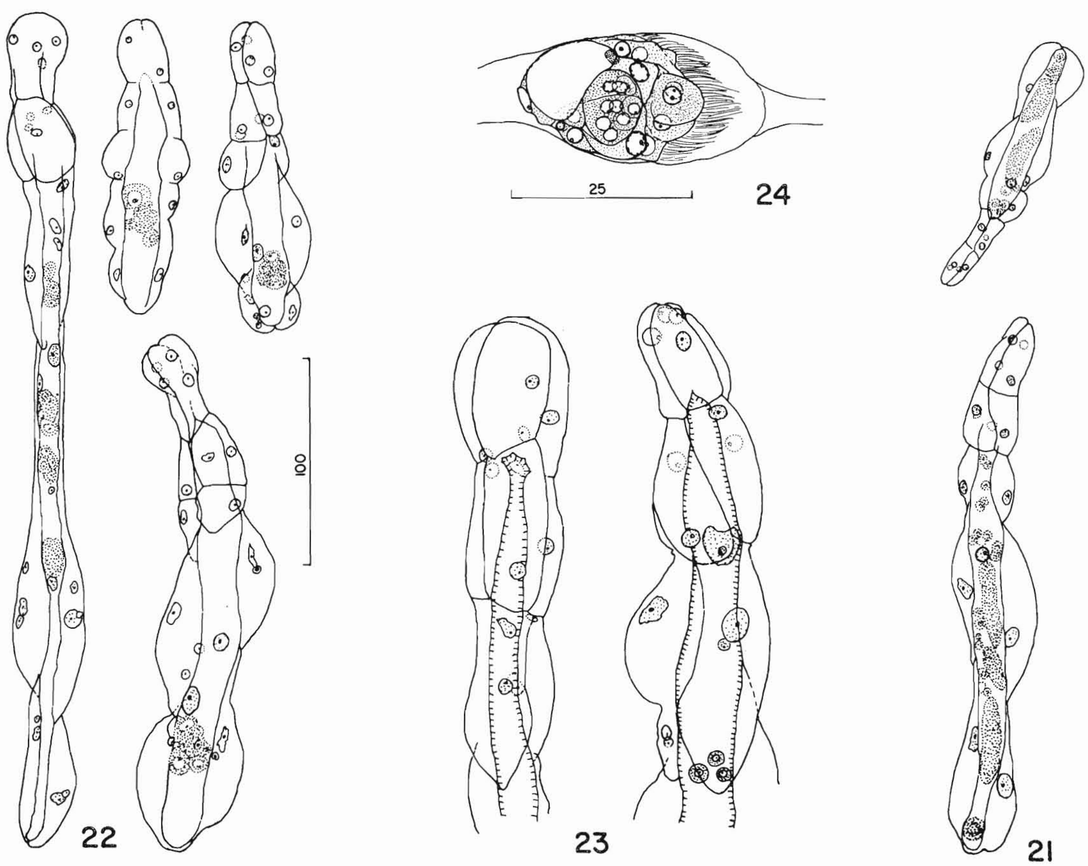
Figure 20
Dicyema briarei. Posterior ends of rhombogens showing variation in material in uropolar cells. From published photographs (Short 1961).

3(1) Somatic cells usually 14 4

3(1) Somatic cells usually 16 to 18 5

4(3) Lengths of mature nematogens 254 to 264 μm, mature rhombogens 438 to 657 μm. Somatic cell number almost invariably 14. Calotte markedly elongate; in young vermiform individuals often 30 to 50% of total length, in largest vermiforms 14 to 20% of total length. Parapolar cells usually shorter than calotte. Vermiform embryos about 40 to 50 μm long at eclosion. Refringent bodies, in infusoriforms viewed laterally, appearing larger than cluster of urn cells (*see* Fig. 3B) .... ***D. hypercephalum*** **(Figs. 21–24)**

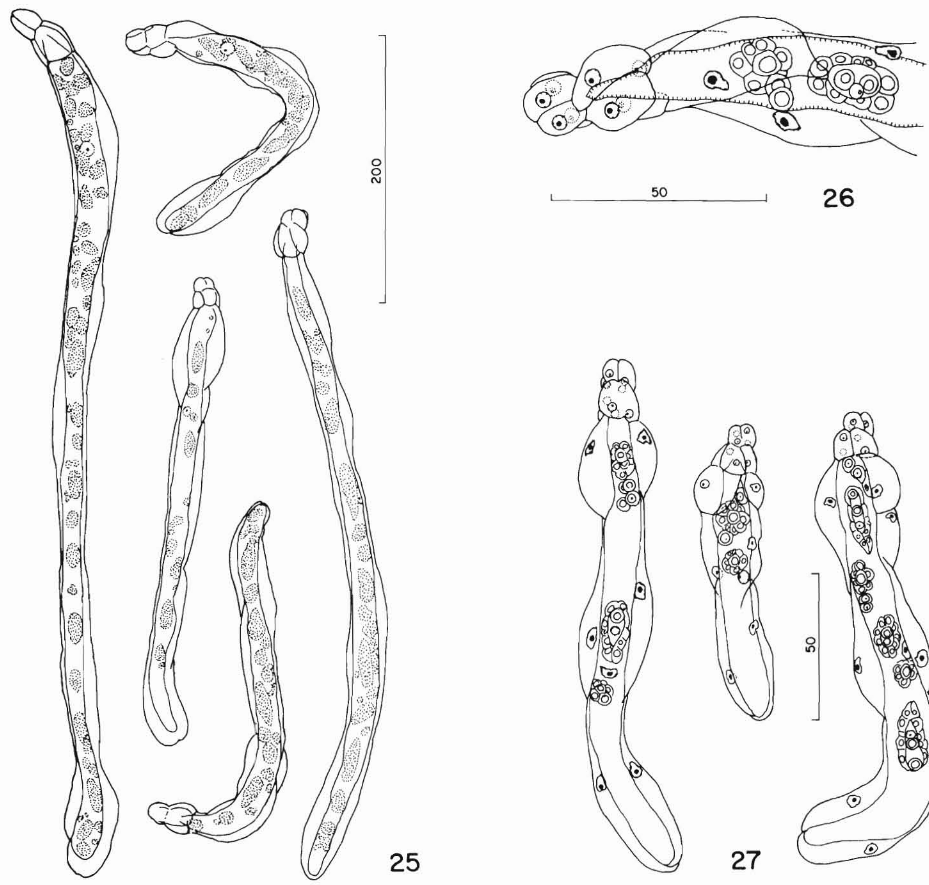
Host: *Octopus joubini* Robson, 1929



Figures 21–24
Dicyema hypercephalum. (**21**) Nematogens. (**22**) Rhombogens. (**23**) Anterior ends of rhombogens. (**24**) Infusoriform within axial cell of rhombogen, sagittal optical section. All figures from Short (1962). Scales in micrometers. Cilia not shown on vermiform stages.

4(3) Largest mature nematogens 299 to 645 μm long, seldom longer than 350 μm; rhombogens unknown. Somatic cell numbers usually 14, sometimes 15, very occasionally otherwise. Calotte not markedly elongate; parapolar cells usually as long as or longer than calotte. Vermiform embryos about 20 to 25 μm long at eclosion (*see* Fig. 3C) . . . . *D. apalachiensis* **(Figs. 25–27)**

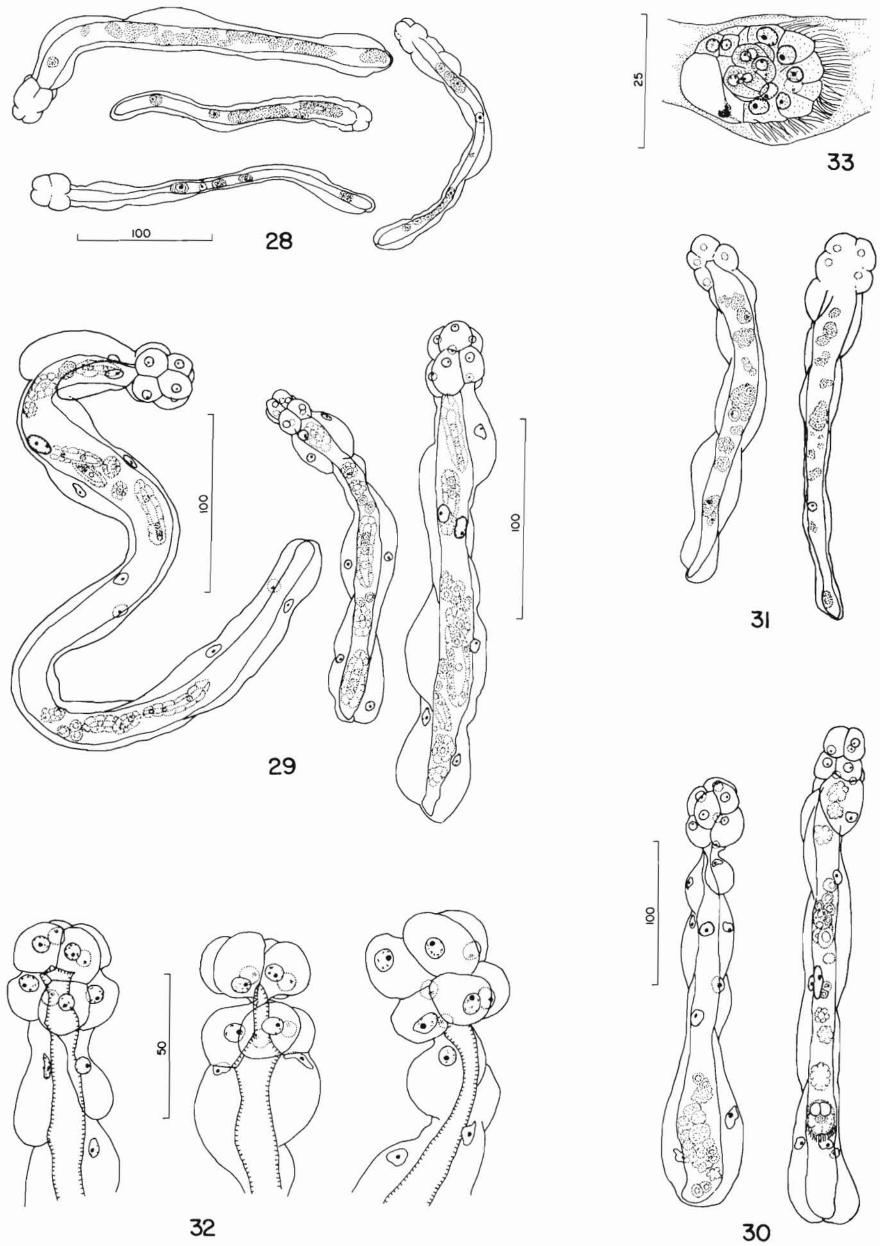
Host: *Octopus joubini* Robson, 1929



Figures 25–27
Dicyema apalachiensis. Nematogens. (**26**) Anterior end only. All redrawn from Short (1962). Scales in micrometers. Cilia not shown.

5(3) Largest nematogens 432 to 610 μm; largest rhombogens 514 to 802 μm; somatic cells 16 to 18, occasionally 15 or 19. Calotte large and conspicuous in older vermiform stages, appearing ellipsoidal to bilobed, often with a constriction between propolar and metapolar cells, anterior end of calotte in older vermiforms sometimes rather blunt with propolar region as broad as metapolar. Vermiform embryos 40 to 60 μm long at eclosion. Refringent bodies, in infusoriform viewed laterally, appearing about same size or only slightly larger than cluster of urn cells (*see* Fig. 4, A and B) .... ***Dicyema bilobum*** **(Figs. 28–33)**

Host: *Octopus vulgaris* Cuvier, 1797

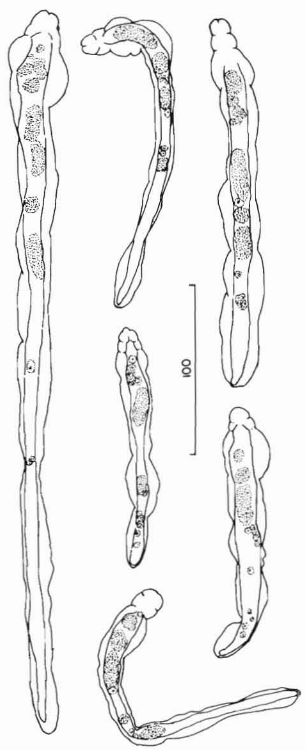


Figures 28–33

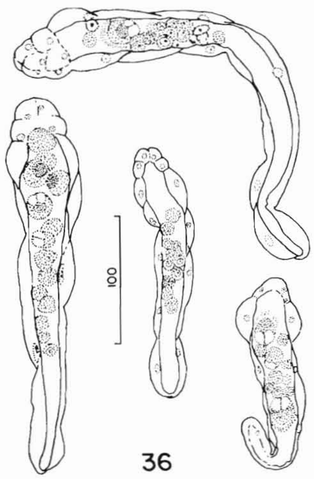
Dicyema bilobum. (**28** and **29**) Nematogens. (**30–32**) Rhombogens. (32) Anterior ends only. (**33**) Infusoriform, optical sagittal section. All figures except 31 from Couch and Short (1964), mostly redrawn. Scales in micrometers. Cilia not shown on vermiform stages.

5(3) Largest nematogens 193 to 414 μm; largest rhombogens 450-689 μm; somatic cells almost always 18. Calotte relatively smaller than that of *D. bilobum* and with no tendency toward constriction between propolar and metapolar cells; often with cephalic swelling in parapolar region; in older rhombogens propolar and metapolar cells sometimes alternately arranged (in contrast to usual opposite arrangement in this and most other species of *Dicyema*). Vermiform embryos about 35 μm long at eclosion. Refringent bodies of infusoriform appear considerably larger than the cluster of urn cells viewed laterally (*see* Fig. 3A) . ***Dicyema typoides*** **(Figs. 34–38)**

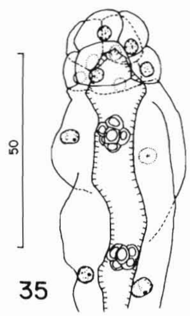
Host: *Octopus vulgaris* Cuvier, 1797



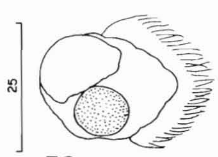
34



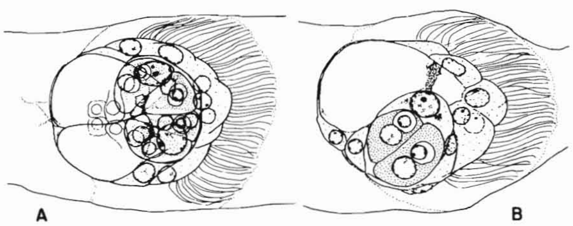
36



35



38



37

Figures 34–38

Dicyema typoides. (**34**) Nematogens. (**35**) Anterior end of nematogen. (**36**) Rhombogens. (**37**) Infusoriforms in axial cell of rhombogens: (**A**) Frontal view; (**B**) Sagittal optical section. (**38**) Infusoriform side view. Urn cell stippled. Note unusually large refringent bodies. Except for (36), all from Short (1964). Scales in micrometers. Cilia not shown on vermiform stages.

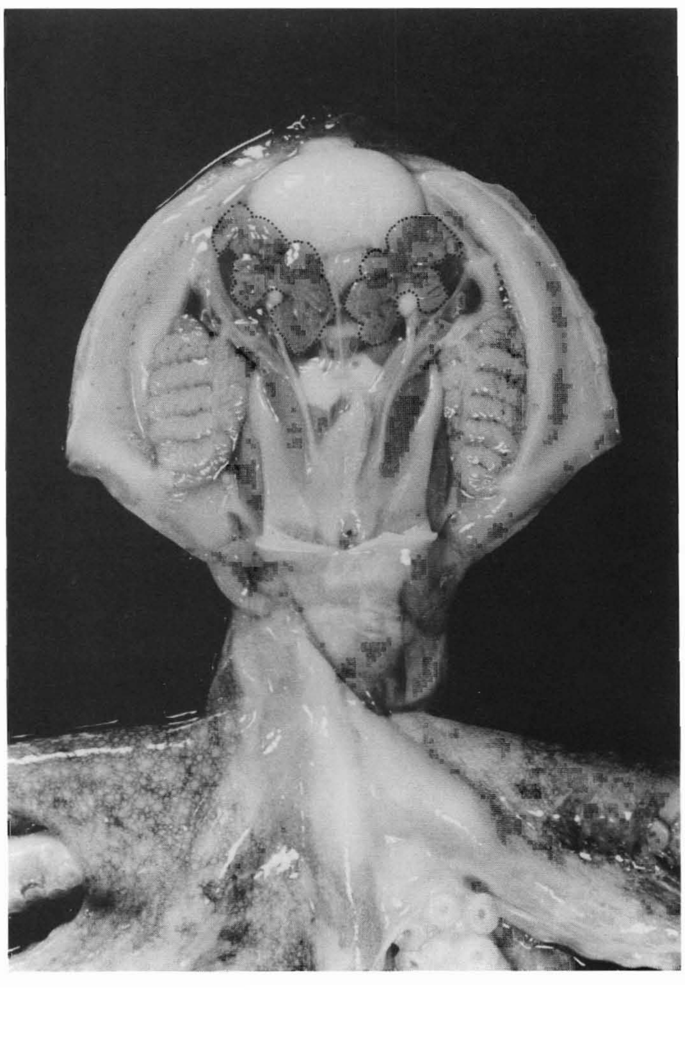


Figure 39 (right)

Octopus vulgaris, ventral view. Dissected to show renal appendages (dotted outlines) within semitransparent renal sacs.

Annotated Systematic List

In addition to the six species in the genus *Dicyema* (family Dicyemidae) that have been reported from off the coasts of eastern North America and the Gulf of Mexico, Aldrich (1964) recorded a single dicyemid in a single specimen of the squid *Illex illecebrosus* from Newfoundland, and in 1989 I recovered an as yet unidentified species of *Dicyemennea* from a specimen of *Bathypolypus arcticus* (furnished by Professor M.D.B. Burt) from off Grand Manan Island, south of St. Andrews, N.B., Canada.

As indicated above, the dicyemids are here considered to represent the phylum Dicyemida. In this system to my knowledge no class or order names have been assigned in the literature and it seems inappropriate to designate them in this manual. The species in this list are arranged alphabetically. Except for type host and locality, the locality and prevalence records summarize published and unpublished data (mostly from the present author's records). These records should not, of course, be interpreted as representing the true range of the parasites. It is my impression that octopods have not been examined systematically for dicyemids over most of the eastern and Gulf coasts of North America, and it is expected that at least some of the dicyemid species range much more widely than here indicated and that undescribed species remain to be discovered. Hochberg (E. Hochberg, Curator, Dept. of Invert. Zoology, Santa Barbara Mus. Nat. History, 2559 Puesta del Sol Rd., Santa Barbara, CA 93105, pers. commun., 1990) has pointed out that apparently unexamined potential octopod hosts in the region include *Octopus macropus*, *O. burryi*, *O. defilippi*, *O. cardinensis*, and *O. mercatoris*.

Family DICYEMIDAE E. van Beneden, 1882

***Dicyema aegira* McConnaughey and Kritzler, 1952**—(Figs. 5B, 6, 10–16).

Stages Known—nematogen (primary), rhombogen, vermiform embryo, infusorigen, infusoriform larva.

Type Host and Locality—*Octopus vulgaris* Cuvier, 1797. Western North Atlantic Ocean, offshore from St. Augustine, Florida.

Additional Host—*Octopus joubini* Robson, 1929 (Short 1957).

Additional Localities—*Octopus vulgaris*, Western North Atlantic Ocean, coast of North Carolina, near Cape Lookout; Northern Gulf of Mexico, coast of Florida, Apalachee Bay west to Pensacola Bay. *Octopus joubini*, Northern Gulf of Mexico, coast of Florida, Apalachee Bay, near St. Teresa.

Prevalence (in *Octopus vulgaris*)—Of 26 hosts from the type locality examined, 25 were infected with dicyemids. The species of dicyemid was determined in 22. *Dicyema aegira* was in 17, 6 of which also harbored *D. typoides* (= *D. typus* of McConnaughey and Kritzler, 1952, *see* below).

Two hosts from the North Carolina coast near Cape Lookout were examined. Both were infected with *D. aegira*.

From the northern Gulf of Mexico off Florida, 147 hosts were examined; 144 were infected with dicyemids. The dicyemid species was determined in 122 hosts; *D. aegira* was present in 93, 18 of which also harbored *D. typoides*.

Prevalence (in *Octopus joubini*)—Four hosts from Apalachee Bay were examined; 2 harbored dicyemids that appeared to be *D. aegira*.

Other Reports—Austin (1964) reported on gametogenesis and Short and Damian (1966, 1967) on morphology of the infusoriform larva, oogenesis, fertilization, and first cleavage. Transmission electron microscopical studies were published by Ridley (1968, 1969).

***Dicyema apalachiensis* Short, 1962**—(Figs. 3D, 25–27).

Stages Known—stem nematogen, nematogen (primary), vermiform embryo. The stem nematogen was described from an entire small specimen and part of a larger one.

Type Host and Locality—*Octopus joubini* Robson, 1929. Northern Gulf of Mexico, off Franklin Co., Florida, about 6 miles south of Light House Point.

Additional Hosts—none.

Additional Localities—none.

Prevalence—From the type locality, 13 hosts were examined; 12 were small, immature specimens, and all were infected with *D. apalachiensis*. One additional, larger specimen from the same locality was negative for *D. apalachiensis* but harbored *D. hypercephalum*.

***Dicyema bilobum* Couch and Short, 1964**—(Figs. 4, A and B, 28–33).

Stages Known—nematogen (primary), rhombogen, vermiform embryo, infusorigen, infusoriform larva.

Type Host and Locality—*Octopus vulgaris* Cuvier, 1797. Northern Gulf of Mexico, off Pensacola Florida.

Additional Hosts—none.

Additional Localities—Northern Gulf of Mexico off Panama City, Florida.

Prevalence—Ten hosts from the type locality were examined; all were infected with dicyemids. In 2 hosts the species of parasites were not determined; of the remaining 8, 5 had *D. bilobum* alone and 3 *D. typoides* alone.

Other Report—Ridley (1968) reported transmission electron microscopical studies.

***Dicyema briarei* Short, 1961**—(Figs. 5A, 7, 8, 17–20).

Stages Known—nematogen (primary), rhombogen, vermiform embryo, infusorigen, infusoriform larva.

Type Host and Locality—*Octopus briareus* Robson, 1929. Gulf of Mexico, inshore near Long Key, Florida Keys.

Additional Hosts—none.

Additional Localities—none.

Prevalence—Two of 16 adult octopuses from the type locality were infected in 1958. From 1959 to 1963, the following numbers of *O. briareus* from other locations were found not to be infected: 43 from areas in the Florida Keys; 12 from Bear Cut, Biscayne Bay, near Miami; and 3 from Bimini.

Dicyema hypercephalum **Short, 1962**—(Figs. 3B, 21-24).

Stages Known—nematogen (primary), rhombogen, vermiform embryo, infusorigen, infusoriform larva.

Type Host and Locality—*Octopus joubini* Robson, 1929. Northern Gulf of Mexico, off Franklin Co., Florida, about 6 miles south of Light House Point.

Additional Hosts—none.

Additional Localities—Northern Gulf of Mexico, off Franklin Co., Florida, south of Dog Island.

Prevalence—From the type locality, 13 hosts were examined; 1 harbored *D. hypercephalum* alone, 12 had *D. apalachiensis*, and 7 of these also had an unidentified species of dicyemid.

From south of Dog Island, 2 hosts were examined; both were infected with *D. hypercephalum*.

Dicyema typoides **Short, 1964**—(Figs. 3A, 34-38).

Stages Known—nematogen (primary), rhombogen, vermiform embryo, infusorigen, infusoriform larva.

Type Host and Locality—*Octopus vulgaris* Cuvier, 1797. Northern Gulf of Mexico, offshore about 3 miles from Panama City, Florida.

Additional Hosts—none.

Additional Localities—Northern Gulf of Mexico: Pensacola Bay; St. Joseph's Bay; Apalachee Bay—off Panacea, Alligator Point, Dog Island, St. George Island. Western Atlantic Ocean: offshore from St. Augustine, Florida; Bimini, Bahama Is., Bermuda Is.

Prevalence—From the northern gulf coast of Florida, 144 of 147 hosts were infected with dicyemids; of these 144, the species of dicyemid present was determined in 122 hosts. *Dicyema typoides* occurred in 48 hosts, 18 of which also harbored *D. aegira*.

From off St. Augustine, Florida, 12 of 13 hosts were infected; dicyemids were identified in 9; *D. typoides* occurred in 7, 3 of which also had *D. aegira*. McConnaughey and Kritzler (1952) reported *Dicyema typus* van Beneden, 1876, *sensu* Nouvel, 1946, from *Octopus vulgaris* offshore from St. Augustine, Florida. I believe that these authors were dealing with *D. typoides*, at that time (1952) not described. Four of 13 hosts were reported infected with "*D. typus*"; 3 of the 4 also had *D. aegira*.

Bimini. Of 24 hosts examined, 13 were parasitized by dicyemids; in 11 the species was determined; all harbored *D. typoides*.

Bermuda. Of 3 hosts examined, all harbored *D. typoides*.

Other reports—Ridley (1968, 1969) reported transmission electron microscopical studies of this species.

Citations

Aldrich, F.A.
1964. Observations on the Newfoundland bait squid (*Illex illecebrosus* LeSueur, 1821), and the netting of squid in Newfoundland bays. (Ms.) Spec. Rpt. Canad. Fish Indust. Develop Branch, Ottawa, p. 1-22.

Austin, C.R.
1964. Gametogenesis and fertilization in the Mesozoan *Dicyema aegira*. Parasitology 54:597-600.

Cavolini, F.
1787. Memoria sulla generazione dei pesci et dei granchi. Napoli (cited after Nouvel, 1948).

Couch, J.A., and R.B. Short.
1964. *Dicyema bilobum* sp. n. (Mesozoa: Dicyemidae) from the northern Gulf of Mexico. J. Parasitol. 50:641-645.

Czihak, G.
1958. Morphologie und Entwicklungsgeschichte der Wirbellosen. Forschritte der Zoologie 11:1-34.

Erdl, Professor.
1843. Ueber die beweglichen Fäden in den Venenanhängen der Cephalopoden. Arch. Naturgesch. 1:162-167.

Grassé, P.-P.
1961. Classe des dicyémides. *In* Traité de zoologie: anatomie, systématique, biologie, vol. IV (P.-P. Grassé, ed.), p. 707-729. Masson, Paris.

Hochberg, F.G.
1982. The "kidneys" of cephalopods: a unique habitat for parasites. Malacologia 23:121-134.
1983. The parasites of cephalopods: a review. Mem. Natl. Mus. Victoria 44:109-145.
1990. Diseases of Mollusca: Cephalopoda. Diseases caused by protistans and metazoans. *In* Diseases of marine animals, vol. III (O. Kinne, ed.). Biologisches Anstalt Helgoland, Hamburg.

Hyman, L.H.
1940. Phylum Mesozoa. *In* The invertebrates: Protozoa through Ctenophora, p. 233-247. McGraw-Hill, New York and London.

Kozloff, E.N.
1969. Morphology of the orthonectid *Rhopalura ophiocomae*. J. Parasitol. 55:171-195.

Krohn, A.
1839. Über das Vorkommen von Entozoen und Krystallablagerungen in den schwammigen Venenanhängen einiger Cephalopoden. Froriep's "Neue Notizen" 11:213-216.

McConnaughey, B.H.
1951. The life cycle of the dicyemid Mesozoa. Univ. Calif. Publ. Zool. 55:295-336.
1963. The Mesozoa. *In* The lower Metazoa: comparative biology and phylogeny (E.C. Dougherty, ed.), p. 151-165. Univ. California Press, Berkeley and Los Angeles.
1968. The Mesozoa. *In* Chemical zoology, Vol. II: Porifera, Coelenterata, and Platyhelminthes (M. Florkin and B.T. Scheer, eds.), p. 557-570. Acad. Press, New York.

McConnaughey, B.H., and H. Kritzler.
1952. Mesozoan parasites of *Octopus vulgaris*, Lam. from Florida. J. Parasitol. 38:59-64.

Nouvel, H.
1947. Les Dicyémides. 1re partie: systématique, générations vermiformes, infusorigène et sexualité. Arch. Biol. 58:59-219.

Ridley, R.K.
1968. Electron microscopic studies on dicyemid Mesozoa. I: Vermiform states. J. Parasitol. 54:975-998.
1969. Electron microscopic studies on dicyemid Mesozoa. II: Infusorigen and infusoriform stages. J. Parasitol. 55:779-793.

Short, R.B., and R.T. Damian.
1966. Morphology of the infusoriform larva of *Dicyema aegira* (Mesozoa: Dicyemidae). J. Parasitol. 52:746-751.
1967. Oogenesis, fertilization, and first cleavage of *Dicyema aegira* McConnaughey and Kritzler, 1952 (Mesozoa: Dicyemidae). J. Parasitol. 53:186-195.
Stunkard, H.W.
1954. The life-history and systematic relations of the Mesozoa. Q. Rev. Biol. 29:230-244.
1982. Mesozoa. *In* Synopsis and classification of living organisms, vol. 1 (S.P. Parker, ed.), p. 853-855. McGraw-Hill, New York.
van Beneden, E.
1876. Recherches sur les dicyémides. Bull. Acad. Roy. Belg., A. Sci., (sér. 2) 41:1160-1205 and 42:35-97.

Systematic Index

Acknowledgments

Preparation of this manual was supported in part by a grant from the National Science Foundation to the Editorial Board of the "Marine Flora and Fauna of the Eastern United States."

Thanks are given to Drs. F.G. Hochberg and Eugene N. Kozloff for critically reading the manuscript and making helpful suggestions. Especial appreciation is expressed to Dr. Hochberg for helpful discussions and aid with literature. Anne Thistle's preparation of the manuscript and Arthur K. Womble's help in preparing Figure 8 and in labeling the figures are acknowledged with gratitude. Also much appreciated is the contribution of many students and colleagues for their help over the years with collection and preparation of material for study.

Preparation of manuals in the "Marine Flora and Fauna of the Eastern United States" subseries is coordinated by the following Board.

In addition to establishing the format for the "Marine Flora and Fauna of the Eastern United States," the Board invites systematists to collaborate in the preparation of manuals, review manuscripts, and advise the Scientific Editor of the National Marine Fisheries Service.

Coordinating Editor's Comments

Publication of the "Marine Flora and Fauna of the Eastern United States" is most timely in view of the growing universal emphasis on work in the marine environment and the crucial need for precise and complete identification of organisms related to this work. It is essential, if at all possible, that organisms be identified accurately to species. Accurate scientific names of plants and animals unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been adequately studied.

Robert B. Short received the M.S. degree in biology from the University of Virginia in 1945 and the Ph.D. degree in zoology, with emphasis on parasitology, in 1950 from the University of Michigan. He was on the faculty of Florida State University from 1950 to 1990 and is now Professor Emeritus. His research interests have included the schistosomes as well as the dicyemid mesozoans.

Published Manuals

Marine Flora and Fauna of the Northeastern United States

	NOAA Tech Rep. NMFS Circular no.	NTIS no.
Annelida: Oligochaeta *Cook, David G., and Ralph O. Brinkhurst*	374	COM 73 50670
Protozoa: Ciliophora *Borror, Arthur C.*	378	73 50888
Higher Plants of the Marine Fringe *Moul, Edwin T.*	384	74 50019
Pycnogonida *McCloskey, Lawrence R.*	386	74 50014
Crustacea: Stomatopoda *Manning, Raymond B.*	387	74 50487
Crustacea: Decapoda *Williams, Austin B.*	389	74 51194
Tardigrada *Pollock, Leland W.*	394	PB 257 987
Cnidaria: Scyphozoa *Larson, Ronald J.*	397	261 839
Higher Fungi: Ascomycetes, Deuteromycetes, and Basidiomycetes *Cavaliere, A. R.*	398	268 036
Copepoda: Harpacticoida *Coull, Bruce C.*	399	268 714
Sipuncula *Cutler, Edward B.*	403	273 062
Echinodermata: Holothuroidea *Pawson, David L.*	405	274 999
Copepoda: Lernaeopodidae and Sphyriidae *Ho, Ju-Shey*	406	280 040
Copepoda: Cyclopoids Parasitic on Fishes *Ho, Ju-Shey*	409	281 969
Crustacea: Branchiura *Cressey, Roger F.*	413	222 923
Protozoa: Sarcodina: Amoebae *Bovee, Eugene C., and Thomas K. Sawyer*	419	285 538
Crustacea: Cumacea *Watling, Les*	423	296 460
Arthropoda: Cirripedia *Zullo, Victor A.*	425	297 676
Cnidaria: Scleractinia *Cairns, Stephen D.*	438	124 520
Protozoa: Sarcodina: Benthic Foraminifera *Todd, Ruth, and Doris Low*	439	225 053
Turbellaria: Acoela and Nemertodermatida *Bush, Louise F.*	440	219 387
Lichens (Ascomycetes) of the Intertidal Region *Taylor, Ronald M.*	446	124 735

	NMFS no.	
Echinodermata: Echinoidea *Serafy, D. Keith, and F. Julian Fell*	33	PC A03/MF A01
Echinodermata: Crinoidea *Messing, Charles G., and John H. Dearborn*	91	PB 86 156 395
Erect Bryozea *Ryland, John S., and Peter J. Hayward*	99	

Marine Flora and Fauna of the Eastern United States

Cephalopoda *Vecchione, Michael, Clyde F. E. Roper, and Michael J. Sweeney*	73	PB 89 189 583
Copepoda, Cyclopoida: Archinotodelphyidae, Notodephyidae, and Ascidicolidae *Dudley, Patricia L., and Paul L. Illg*	96	
Dicyemida *Short, Robert B.*	100	