Dicyemids

11

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Abstract

Dicyemids are the most common and characteristic endosymbionts found in the renal sac of benthic cephalopods. In this chapter, we introduce biology and diversity of dicyemids of European typical cephalopods, *Octopus vulgaris* and *Sepia officinalis*. The diphasic life cycle of dicyemids consists of vermiform stages formed asexually and an infusoriform stage developed sexually. Their morphology varies depending on the development stage. Recent molecular studies suggested that dicyemids belong to lophotrochozoans. In Europe, 16 dicyemid species were described from 17 cephalopod species.

Keywords

Dicyemids • Mesozoa • Vermiform • Infusoriform • Renal sac

11.1 Introduction

The renal organs of cephalopods are the renal complex (renal and pancreatic appendages) and the branchial heart complex (branchial heart and pericardial appendage). Prior to release, urine is collected in a renal sac, the fluid-filled coelom of which is a unique environment providing living space for a diversity of endosymbionts (Hochberg 1982; Furuya et al. 2004b). There are phylogenetically distant parasitic organisms, trematodes, dicyemids, and chromidinids, in the kidney of cephalopods (Nouvel 1945; Hochberg and Short 1983; Hochberg 1990; Furuya et al. 2004a). Dicyemids (Phylum Dicyemida) are the commonest and most characteristic endosymbionts that are found in the renal sac of benthic

cephalopod molluscs. The body length of dicyemid species ranges from 0.1 to 10 mm. Typically, two or three dicyemid species are found in individuals of each cephalopod species and most are host specific (Furuya 1999). Currently, about 140 dicyemid species have been recorded from cephalopod hosts distributed in a variety of geographical localities: the Okhotsk Sea, Japan Sea, western and eastern North Pacific Ocean, waters around New Zealand, North Indian Ocean, Mediterranean, western North and eastern Atlantic Ocean, Gulf of Mexico, and Antarctic Ocean (Catalano 2013; Castellanos-Martinez et al. 2016; Furuya 1999; Furuya and Tsuneki 2003; Hochberg 1990; McConnaughey 1951; Nouvel 1947; Short 1991). The dicyemids are heavily infecting the renal organs in their host cephalopods (Fig. 11.1). However, this is somewhat surprising; no damage has ever been observed in the tissues. This means that dicyemids are not pathogens to their cephalopod hosts. There must be interaction between dicyemids and their host renal organs; it is possible that dicyemids are beneficial for their hosts.

In this chapter, we introduce biology of dicyemids and dicyemid species of European typical cephalopods, *O. vulgaris* and *S. officinalis*.

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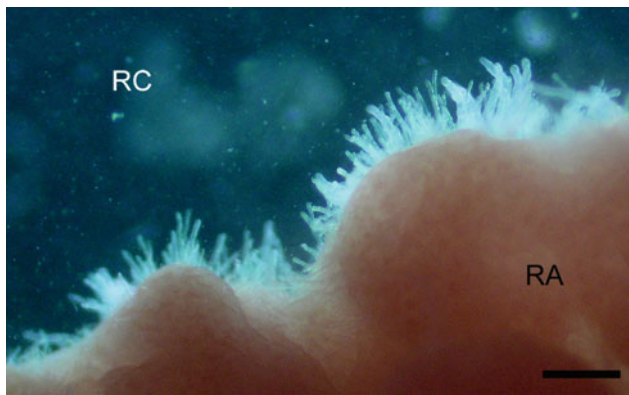e-mail: dhikra.souidenne@mnhn.fr

Fig. 11.1 Dicyemids on the renal appendage of *Amphioctopus fangsiao*. The dicyemids attach on the surface areas of renal appendages. Scale bar: 1000 μm. *Abbreviations* RA, renal appendage; RC, renal coelom

11.2 Life Cycle

The diphasic life cycle of dicyemids, with a characteristic asexual phase, likely evolved as an adaptation to parasitism (Fig. 11.2), presumably to enable them to adapt to the cephalopod renal organs. The life cycle of dicyemids consists of two phases of different body organizations (Fig. 11.2). The first phase is the vermiform stages, in which the dicyemid exists as a vermiform embryo formed asexually, and as a final form, the nematogen, or rhombogen. The second phase is the infusoriform embryo that develops from a fertilized egg. The shift from an asexual mode to a sexual mode of reproduction may be caused by a high population density in the cephalopod kidney (Lapan and Morowitz 1975). Vermiform stages are restricted to the renal sac of cephalopods, whereas the infusoriform embryos escape from the host into the sea to search for a new host. However, it is not clear how infusoriform larvae develop into vermiform stages in the new host.

11.3 General Morphology

Vermiform stages, vermiform embryos, nematogens, and rhombogens are similar in shape (Fig. 11.2). The body surface of dicyemids has numerous cilia and the folded structure, which is considered to contribute to absorb nutrients more efficiently from urine (Bresciani and Fenchel 1965; Ridley 1968; Furuya et al. 1997). The number of peripheral cells is species specific and constant. At the anterior region, 4–10 peripheral cells form the calotte, of which cilia are shorter and denser than in more posterior peripheral cells (Fig. 11.2). The calotte shape varies, depending on the species, and adapts to attach to the various regions of renal tissues in the host kidneys (Furuya et al. 2003a) (Figs. 11.3 and 11.4). There is a central

cylindrical cell called the axial cell, which extends to 100 mm in length in the largest dicyemid.

Regarding the number of somatic cells, the dicyemid is a multicellular animal that is composed of the fewest in number of cells in metazoans except for aberrant myxozoans. This organization does not correspond to metazoan two-layered construction of endoderm and ectoderm, and dicyemids have neither body cavities nor differentiated organs.

Infusoriform embryos are ovoid and have both antero-posterior axis and dorsoventral axis. Embryos mostly consist of 37 or 39 cells (Short 1971; Furuya 1999), which are more differentiated than those of vermiform stages (Matsubara and Dudley 1976; Furuya et al. 2004b). Internally, there are four large cells called urn cells, each containing a germinal cell that probably gives rise to the next generation (Fig. 11.2). At the anterior region of embryo, there is a pair of unique cell called the apical cell (Fig. 11.5), each containing a refringent body composed of magnesium inositol hexaphosphate (Lapan 1975a). The external cells are mostly ciliated. Infusoriform embryos swim while spinning the body.

The bodies of vermiform stages might be simplified as a reflection of their specialization in their parasitic habitat composed of renal tubules (Nouvel 1947). By contrast, infusoriform embryos seem to represent the true level of organization due to free-swimming organisms (Furuya et al. 1997). However, the body organization of infusoriform embryos cannot be regarded as achieving the grade of tissue level.

11.4 Relationship with Cephalopods

Dicyemids are usually found to be heavily infecting the renal organs in their host cephalopods (Fig. 11.1). No damage has ever been observed in the infected renal tissue, so dicyemids apparently do no harm to their cephalopod hosts. Lapan (1975b) has even suggested that dicyemids facilitate host excretion of ammonia by contributing to acidification of the urine. In addition to the normal muscular contraction of the renal appendages, the ciliary activity of dicyemids present in the kidneys maintains a constant flow of urine, and as a result dicyemids assist in removal of urine. Thus, dicyemids are symbiotic, rather than parasitic, in their relationship with cephalopods.

The majority of the dicyemid species studied were found to be host specific (Furuya 1999). Typically, two or more species of dicyemids are present in each host species or each host individual. There is a certain relationship between the calotte configuration of vermiform stages and the co-occurrence pattern in hosts (Fig. 11.6). Vermiform individuals live specifically within the renal sac. Their anterior region, termed a "calotte", is critical in adapting to their habitats in the renal sac. They insert the distinct anterior region into renal tubules or crypts of the renal appendages of
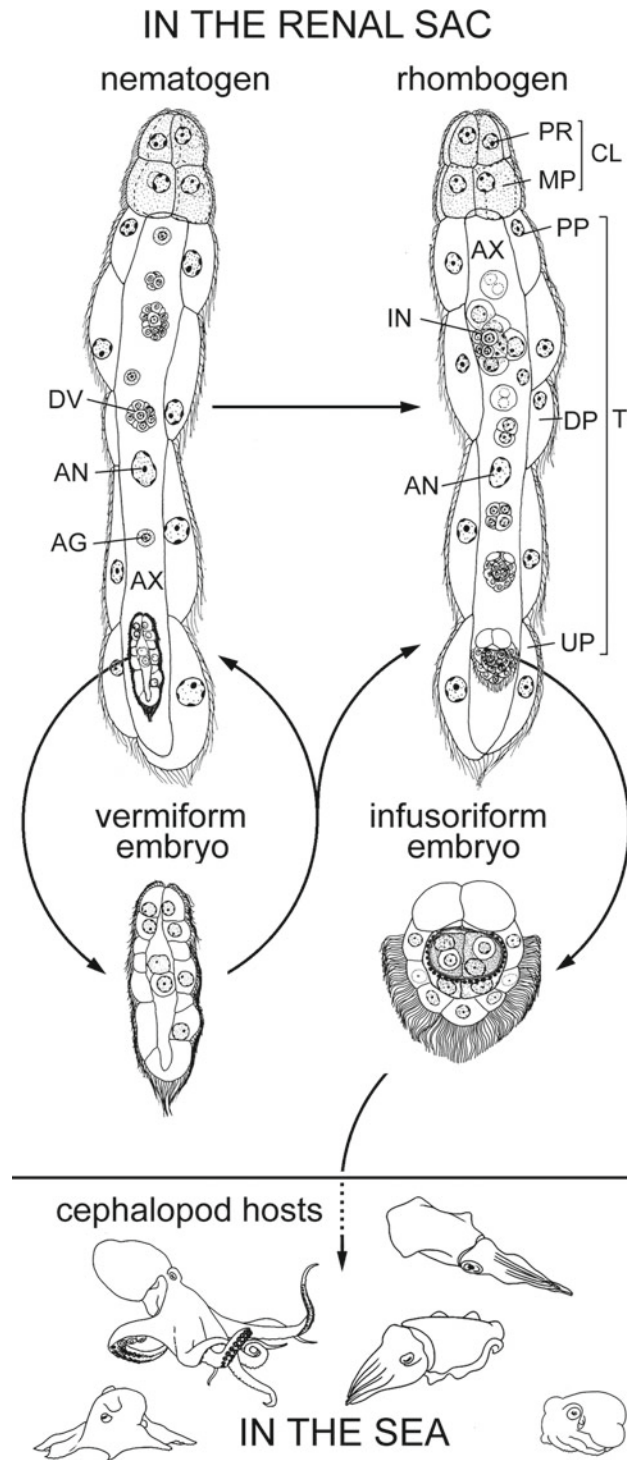
Fig. 11.2 Dicyemid life cycle (modified from Furuya 2016). The dashed line indicates an unknown process involved in the infection of a new cephalopod and development into adult forms. In vermiform stages (nematogen, rhombogen, and vermiform embryo), a large cylindrical axial cell is surrounded by peripheral cells. A calotte is formed by four to ten anterior peripheral cells (propolars and metapolars). The other peripheral cells are diapolars and two of those posterior cells are somewhat specialized as uropolars. The development of hermaphroditic gonads (infusorigens), gametegenesis around the gonads and development of two types of embryos all proceed within the cytoplasm of the axial cell. *Abbreviations* AG, agamete; AN, axial cell nucleus; AX, axial cell; CL, calotte; DP, diapolar cell; DV, developing vermiform embryo; IN, infusorigen; MP, metapolar cell; PP, parapolar cell; PR, propolar cell; T, trunk; UP, uropolar cell
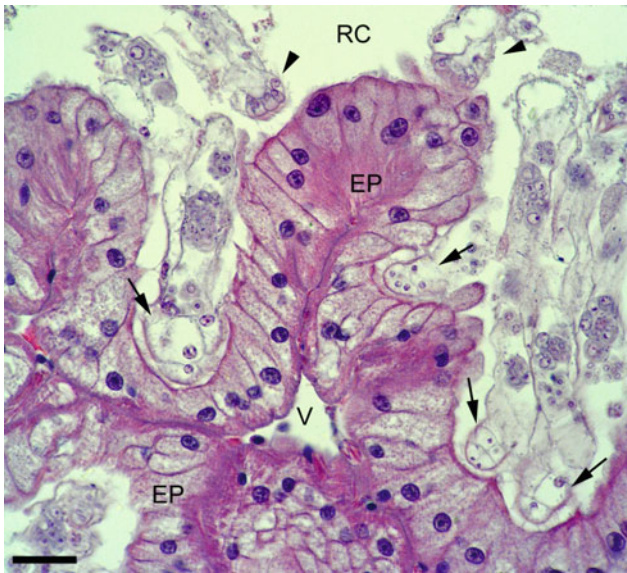
Fig. 11.3 Light micrographs of stained sections through the renal organ of *A. fangsiao*. The niche separation occurs between dicyemid species inhabiting in the renal appendages. *Dicyema akashiense* (arrowhead) lives in the fold of renal appendages, while *D. helocephalum* (arrow) attached on the surface of renal appendages. Scale bar: 20 μm. *Abbreviations* EP, epithelial cell of renal appendage; RC, renal coelom; V, vein

the host (Ridley 1968; Furuya et al. 1997) or attach to surfaces of the renal appendages with a flat anterior region (Furuya et al. 2003a; Furuya 2005, 2006) (Fig. 11.3).

11.5 Systematic Position

Van Beneden (1876) regarded the dicyemids as intermediate in the body plan between Protozoa and Metazoa, and thus gave them the name Mesozoa. This phylum included other several microscopical enigmatic organisms, *Trichoplax*, *Haplozoon*, *Neresheimeria*, *Salinella*, and orthonectids, which were not assignable to any of phyla. Most of these organisms were subsequently belonged to the other phyla (Hyman 1940). Only dicyemids and orthonectids were often united into a single phylum Mesozoa. Later, Hochberg (1990) and Kozloff (1990) treated them independently as a separate phylum, Dicyemida and Orthonectida, in each review. However, they were still treated as the Mesozoa in the many zoological textbooks, because of their unclear relationships among animals. Several zoologists regard the simple organization of dicyemids to be the result of specialization for parasitism (Nouvel 1947; Stunkard 1954; Ginetsinskaya 1988). However, Hyman (1956), Lapan and Morowitz (1975), and Ohama et al. (1984) concurred that dicyemids are primitive multicellular organisms. Since dicyemids have several protozoan-like features, an affinity to the protozoans has been pointed out (Czaker 2006; Noto and Endoh 2004). Current analyses of molecular sequences have revealed that, rather than truly primitive animals that deserve the name "mesozoan", they probably belong to the lophotrochozoans (Katayama et al. 1995; Kobayashi et al. 1999; Aruga et al. 2007; Suzuki et al.

Fig. 11.4 European dicyemid species. **a** *C. polymorpha*; **b** *M. vespa*; **c** *D. typus*; **d** *Dicyema moschatum*; **e** *Dicyemennea eledones*; **f** *P. truncatum*
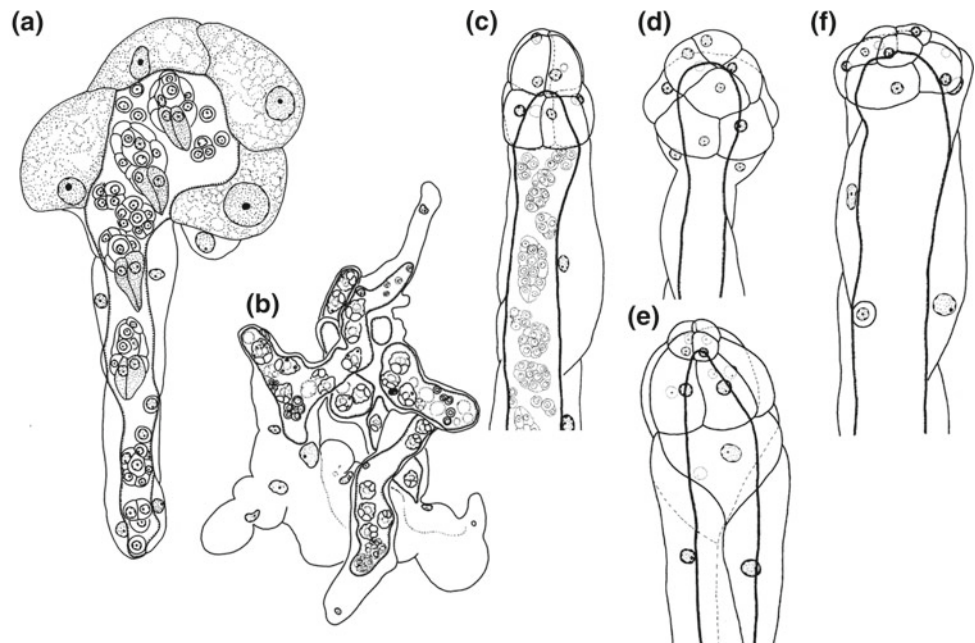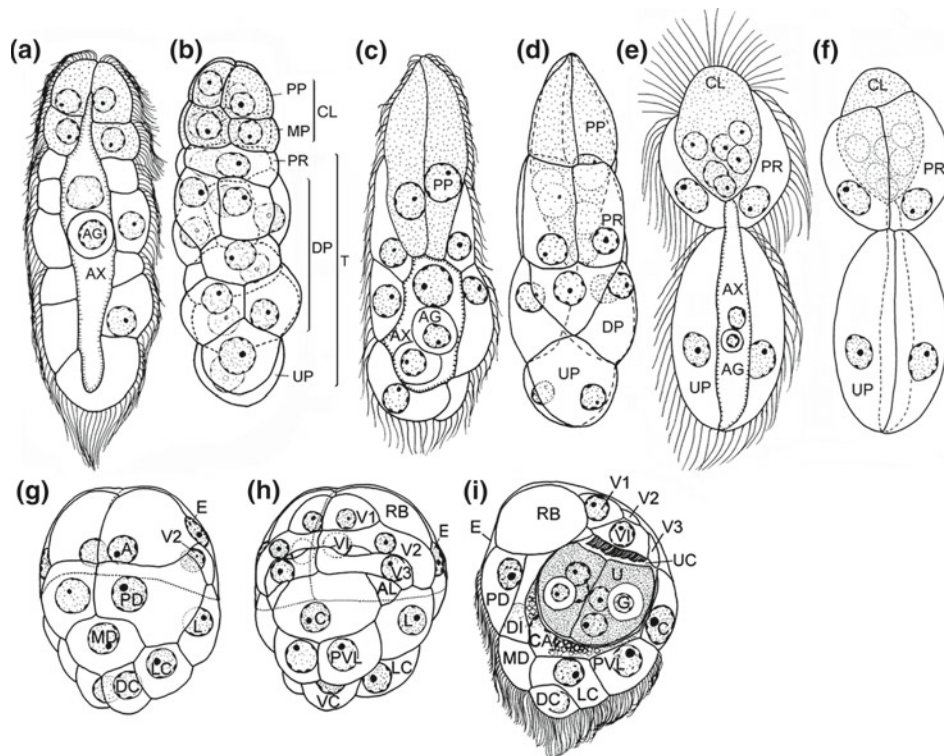
Fig. 11.5 Schematic drawings of vermiform larvae with 22 peripheral cells (**a**, **b**), vermiform larvae of *C. polymorpha* (**c**, **d**), vermiform larvae of *M. vespa* (**e**, **f**), infusoriform larvae with 39 cells (**g–i**) (modified from Furuya and Tsuneki 2003; Furuya 2016). **a**, **f**, lateral view; **b**, **c**, sagittal section; **d**, ventral view; **e**, dorsal view. *Abbreviations* A, apical cell; AG, agamete; AX, axial cell; C, couvercle cell; CA, capsule cell; CL, calotte; DC, dorsal caudal cell; DI, dorsal internal cell; DP, diapolar cell; E, enveloping cell; G, germinal cell; L, lateral cell; LC, lateral caudal cell; MD, median dorsal cell; MP, metapolar cell; PD, paired dorsal cell; PP, parapolar cell; PR, propolar cell; PVL, posteroventral lateral cell; RB, refringent body; SC, short cilia; T, trunk; U, urn cell; UC urn cavity; UP, uropolar cell; VC, ventral caudal cell; VI, ventral internal cell; V1, first ventral cell; V2, second ventral cell; V3, third ventral cell

2010; Mikhailov et al. 2016; Lu et al. 2017). Despite their extremely reduced body plan, dicyemids still appear to exhibit some degree of cell differentiation (Ogino et al. 2011). In this reason, the name Mesozoa is not suited for their phylogenetic place; the Dicyemida, which is the first name of dicyemids by Khrone (1839), has been used as the phylum name of dicyemids in 1999 (Furuya 1999).

11.6 Diversity of Dicyemids in Europe

Cephalopods are commercially important in European countries. Many species of cephalopods have been examined for parasites in European waters. Sixteen species of dicyemids were described from 17 species of cephalopods, so far (Table 11.1). From one to four dicyemid species have been recorded in a single species of cephalopods. Most dicyemid species are host specific. However, 18 dicyemid species are known to have a relatively wide host range (Furuya 1999). In European dicyemids, for instance, *Dicyema macrocephalum* van Beneden (1876) appears to infect five cephalopod species belonging to three genera. The other species with a wide host range have been described mostly without using characters of the infusoriform embryos, so it will be necessary to examine the cellular composition of the infusoriform embryos of these other species to confirm their occurrence in more than one species.

O. vulgaris, the common octopus, is the commercially most important species in the European cephalopods. Therefore, this species has been well studied for the parasite. Four species of dicyemids, *Conocyema polymorpha*, *Dicyema paradoxum*, *Dicyema typus*, and *Dicyemennea lameerei,* have been described from *O. vulgaris* in the Mediterranean Sea, the English Channel, and the Eastern North Atlantic Ocean (Table 11.1). Typically, two or three species of dicyemids are present in each host species or each
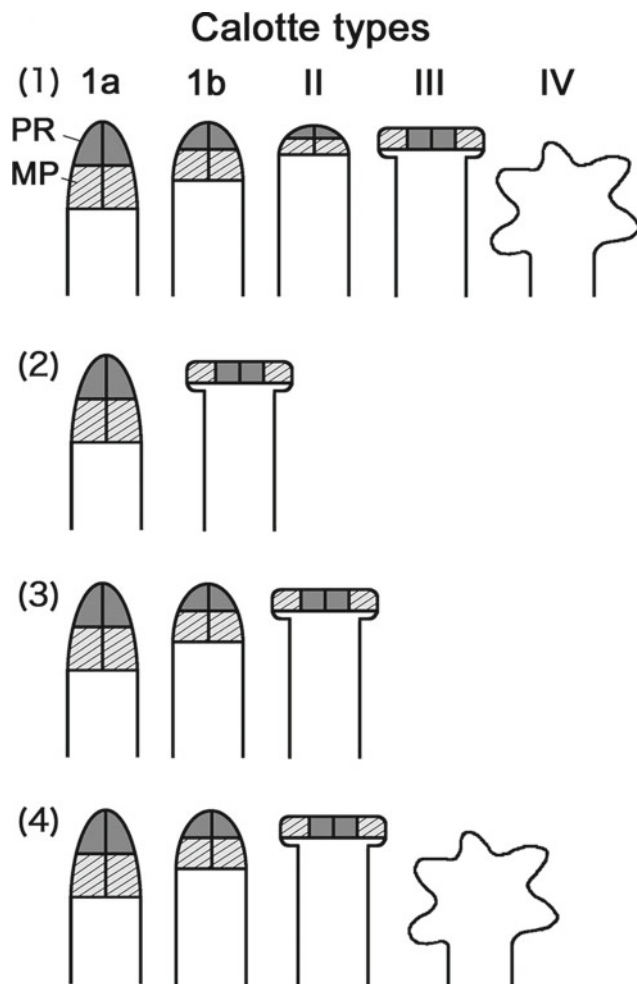
Fig. 11.6 Co-occurrence pattern of calotte shapes usually detected within host individual. (1) Stylized drawings of the main three types of regular calotte configurations and a type of irregular configuration found in vermiform stages. Type I, conical-shaped, is divided into two types (Type Ia and Ib); Type II, cap-shaped; Type III, discoidal; Type IV, an irregular configuration. Shaded and striped areas indicate propolar cells and metapolar cells, respectively. (2) When two species of dicyemids are present, two distinct calotte shapes, conical and discoidal, are usually observed. (3) When three species of dicyemids are present, three types of calotte configurations are usually observed, conical (two grades) and discoidal. (4) When more than four species of dicyemids are present, at least one species is characterized by its rare irregular shaped calotte that spreads, connects with other individuals, and forms a syncytium

host individual, all four species were never simultaneously present in a single-host individual (Furuya et al. 2003b). *Dicyema* and *Dicyemennea* are common, and the largest number of species is placed in these genera. Several other genera are monotypic or contain only a small number of species. *C. polymorpha* is the unusual dicyemid, which is irregular in shape and lacking external cilia (Fig. 11.7). It has relatively small-sized species with 12 peripheral cells. The vermiform larvae are cuneiform and have distinct calottes, which consist of only single tier of four propolar cells. In this species, four parapolar cells are located in the posterior part of propolar cells instead of metapolar cells (Fig. 11.5).

S. officinalis is also commercial species in Europe countries; it is a common inhabitant of the English Channel and Mediterranean Sea. Four species of dicyemids are also recorded from this host cephalopod, namely, *Dicyemennea gracile*, *Pseudicyema truncatum*, *Dicyema whitmani*, and *Microcyema vespa* (Table 11.1). *M. vespa* is unusual in that the body forms a syncytium and the calotte is irregular (Fig. 11.7). In *M. vespa*, the calotte region can only be recognized in the larval stage (Fig. 11.5) (Furuya et al. 2001). *P. truncatum* is the most common species observed with the highest prevalence, nearly 80%. In contrast, *D. whitmani* is a very rare species that has been found in only one cuttlefish host individual collected off Naples, Italy (Furuya and Hochberg 1998).

The dicyemid fauna in the coastal areas of the United States and Japan has been well studied (Furuya 2016), as well as in European waters. The cephalopod fauna in European waters is similar to the Japanese waters, not to the United States, because no cuttlefish (*Sepia*) lives in the coastal areas of the United States. From the ecological viewpoint, *O. vulgaris* and *S. officinalis* are comparable to the Japanese species, *Octopus sinensis* and *Sepia esculenta*, respectively. *O. sinensis* has been regarded as the same species as *O. vulgaris* (Gleadall 2016). *S. esculenta* is a common cuttlefish in Japanese waters. However, *Conocyema* and *Microcyema* species have never been found in these host species and the other Japanese cephalopods. The presence of various genera may be characteristic of the dicyemid fauna in Europe.

**Table 11.1** Dicyemids from cephalopod species in European waters

Cephalopods	Dicyemids	Locality	References
Octopoda			
Bathypolypus sponsalis	*Dicyemodeca delamarei*	Mediterranean (Spain)	Nouvel (1961)
Eledone cirrhosa	*D. eledones*	Eastern North Atlantic Ocean (Sweden, Norway), English Channel (France), Mediterranean (Italy, France)	Wagener (1857); Whitmann (1883); Hartmann (1906); Nouvel (1947); Dhikra et al. (2016)
	D. lameerei	English Channel (France)	Nouvel (1947)
Eledone moschata	*D. moschatum*	Mediterranean (Italy, France)	van Beneden (1876); Whitmann (1883); Hartmann (1906); Nouvel (1947)
	D. eledones	Mediterranean (Italy, France)	Wagener (1857); Whitmann (1883); Nouvel (1947)
Octopus defilippi	*Dicyema microcephalum*	Mediterranean (Italy, France)	Whitmann (1883); Nouvel (1947)
Octopus macropus	*D. paradoxum*	Mediterranean (Italy, Monaco, France)	van Beneden (1876); Whitmann (1883), Nouvel (1947)
Octopus salutii	*Dicyema banyulensis*	Mediterranean (Italy, France)	Furuya and Hochberg (1998)
	Dicyema benedeni	Mediterranean (Italy, France)	Furuya and Hochberg (1998)
	D. eledones	Mediterranean (Italy, France)	Wagener (1857); Whitmann (1883); Hartmann (1906); Nouvel (1947)
O. vulgaris	*C. polymorpha*	Mediterranean (Italy, Monaco, France)	Whitmann (1883); Hartmann (1939); Nouvel (1947)
	D. paradoxum	English Channel (France), Mediterranean (Italy, France)	von Kolliker (1849); van Beneden (1876); Whitmann (1883); Nouvel (1947)
	D. typus	English Channel (France, England), Eastern North Atlantic Ocean (France), Mediterranean (Italy, Monaco, France)	van Beneden (1876); Nouvel (1947)
	D. lameerei	English Channel (France), Eastern North Atlantic Ocean (France), Mediterranean (Italy, Monaco, France)	Nouvel (1947)
Sepioidea			
Sepia elegans	*D. macrocephalum*	Mediterranean (Italy, Monaco, France)	van Beneden (1876); Whitmann (1883); Hartmann (1906); Nouvel (1947)
	Dicyema schulzianum	Mediterranean (Italy, Monaco, France)	van Beneden (1876); Nouvel (1947)
S. officinalis	*D. whitmani*	Mediterranean (Italy, France)	Furuya and Hochberg (1998)
	D. gracile	English Channel (France), Mediterranean (Italy, Monaco, France)	Wagener (1857); Whitmann (1883); Nouvel (1947)
	M. vespa	English Channel (France), Mediterranean (Italy, Monaco, France)	van Beneden (1882); Nouvel (1947)
	P. truncatum	English Channel (France), Eastern North Atlantic Ocean (France), Mediterranean (Italy, France, Spain)	Whitmann (1883); Nouvel (1947)
Sepia orbignyana	*D. gracile*	Mediterranean (France, Spain)	Wagener (1857); Whitmann (1883); Nouvel (1947)
	P. truncatum	Mediterranean (Italy, Monaco, France)	Whitmann (1883); Nouvel (1947)
Sepiolioidea			
Rondeletia minor	*Dicyema rondeletia*	Mediterranean (Italy, Monaco, France)	Nouvel (1944)
	D. schulzianum	Mediterranean (Italy, Monaco, France)	van Beneden (1876); Whitmann (1883); Nouvel (1947)

(continued)

Table 11.1 (continued)

Cephalopods	Dicyemids	Locality	References
Rossia macrosoma	*P. truncatum*	Mediterranean (Italy, Monaco, France)	Whitmann (1883); Nouvel (1947)
Sepetta neglecta	*D. rondeletiolae*	Mediterranean (Italy, Monaco, France)	Nouvel (1944)
Sepietta obscura	*D. macrocephalum*	Mediterranean (Italy, Monaco, France)	van Beneden (1876); Whitmann (1883); Nouvel (1947)
Sepietta oweniana	*D. macrocephalum*	Mediterranean (Italy, Monaco, France)	van Beneden (1876); Whitmann (1883); Nouvel (1947)
	D. rondeletiolae	Mediterranean (Italy, Monaco, France)	Nouvel (1944)
Sepiola rondeleti	*D. moschatum*	Mediterranean (Monaco, France)	Whitmann (1883); Nouvel (1947)
Sepiola steenstrupiana	*D. macrocephalum*	Mediterranean (Italy, Monaco, France)	van Beneden (1876); Whitmann (1883); Nouvel (1947)
	D. microcephalum	Mediterranean (Italy, Monaco, France)	Whitmann (1883); Nouvel (1947)

Fig. 11.7 Light micrographs of *C. polymorpha* (**a**, **b**) and *M. vespa* (**c**). Scale bars represent 20 μm. *Abbreviations* AX, axial cell; CL, calotte; IF, infusoriform embryo; IN, infusorigen; V, vermiform embryo
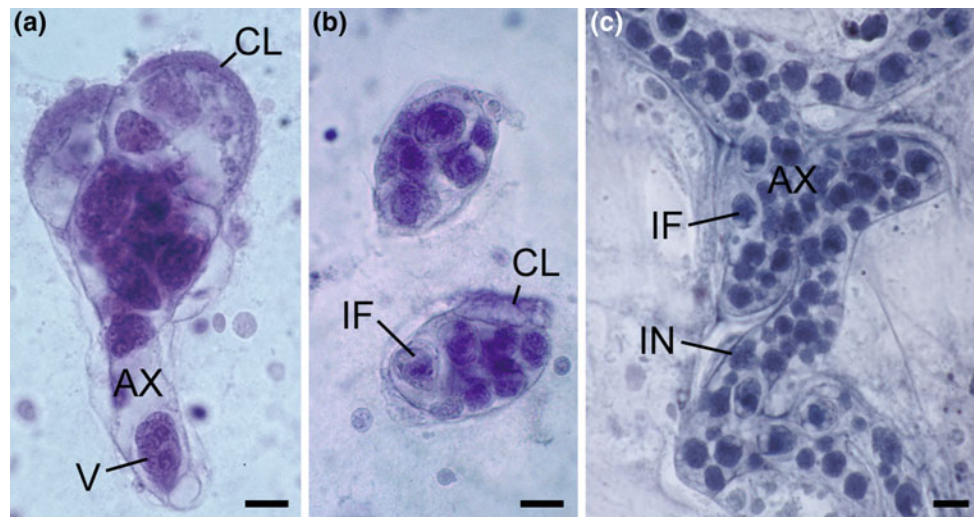
11.7 Concluding Remarks

What I always consider first is when they met cephalopods and where dicyemids come from. The earliest dicyemids must be harmful as well as many other parasites. However, it seems that dicyemids took a new way of life call the "symbiosis". Now dicyemids do no harm to their host cephalopods, rather may give benefits. In this sense, dicyemids are considered to be one of the most advanced parasites.

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