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REVIEW

Diseases of Echinodermata. II. Agents metazoans (Mesozoa to Bryozoa)

Michel Jangoux

Laboratoire de Biologie marine (CP 160), Université Libre de Bruxelles, Ave F. D. Roosevelt 50, B-1050 Bruxelles, Belgium

ABSTRACT: The only species of Mesozoa known to parasitize echinoderms is clearly pathogenic; it causes the regression of ovaries of infested ophiuroids. Symbiotic turbellarians have been reported for each echinoderm group; they mainly infest the gut and coelom of aspidochirote holothuroids and regular echinoids. Echinoderms generally act as second intermediary host for trematodes; the latter are known mostly from echinoids and ophiuroids which constitute the most frequent echinoderm prey for fishes. Records of echinoderm-infesting nematodes are rather scarce; they usually infest either the coelom or the gonads of their host. Many eulimid gastropods have been reported to parasitize echinoderms; however, most of them do not seem to seriously alter the echinoderm life cycle. They are no bivalves parasitic on echinoderms except a few species inhabiting the gut of holothuroids. Associations between echinoderms and sponges, cnidarians, entoprocts or bryozoans have been casually reported in the literature.

INTRODUCTION

The present paper is the second of a series of 4 that review the diseases of Echinodermata. It considers the disease agents belonging to the Mesozoa, Parazoa, Cnidaria, Acoelomata (Turbellaria and Trematoda), Nematoda, Mollusca (Gasteropoda and Bivalvia), Entoprocta and Bryozoa. As discussed in Part I (Jangoux 1987), I have adopted the definition of parasites proposed by Kinne (1980, p. 19) and used it in a very broad sense, considering disease agents (parasites *sensu lato*) to represent any kind of a harmful associate which affects, if even slightly, the echinoderm's tissues or internal fluids (i.e. coelomic and hemal fluids).

DISEASES CAUSED BY METAZOANS

Agents: Mesozoa

The Mesozoa, a small group of uncertain taxonomic affinity, comprise about 50 species of minute animals parasitic on marine invertebrates. One species, *Rhopalura ophiocomae*, parasitizes ophiuroids. Its most frequent host is the small cosmopolitan incubating amphiurid *Amphipholis squamata* (Caullery & Mesnil 1901, Kozloff 1969, Rader 1982) but it may – if very rarely – also affect other ophiurid species, namely *Ophiothrix fragilis* and *Ophiura albida* (respectively Fontaine 1968, Bender 1972). *R. ophiocomae* is mostly known from European localities (Atlantic coast of France, North Sea, northwest Mediterranean Sea; for reviews see Kozloff 1969, Barel & Kramers 1977), and also from 2 Pacific localities along the coast of Washington (Kozloff 1969, Rader 1982).

Structure and life cycle of *Rhopalura ophiocomae* were studied intensively at the begining of this century, mainly by Caullery & Mesnil (1901) and Caullery & Lavallée (1908, 1912) (Fig. 1). Mature adults of *R. ophiocomae* are free living. Adults, either male or female, develop in *Amphipholis squamata* and are emitted through the ophiuroid's bursal slits. Their life span is short (a few days) and they give rise to ciliated larvae. These infesting larvae penetrate the ophiuroid bursal slits and intimately contact the outer epithelium of the bursae. Soon afterwards, small parasitic 'plasmodia' occur within the epithelium. Subsequently, plasmodia migrate to the coelomic side of the bursae where they remain close to the ovaries. At that time plasmodia often protude into the coelomic cavity. They

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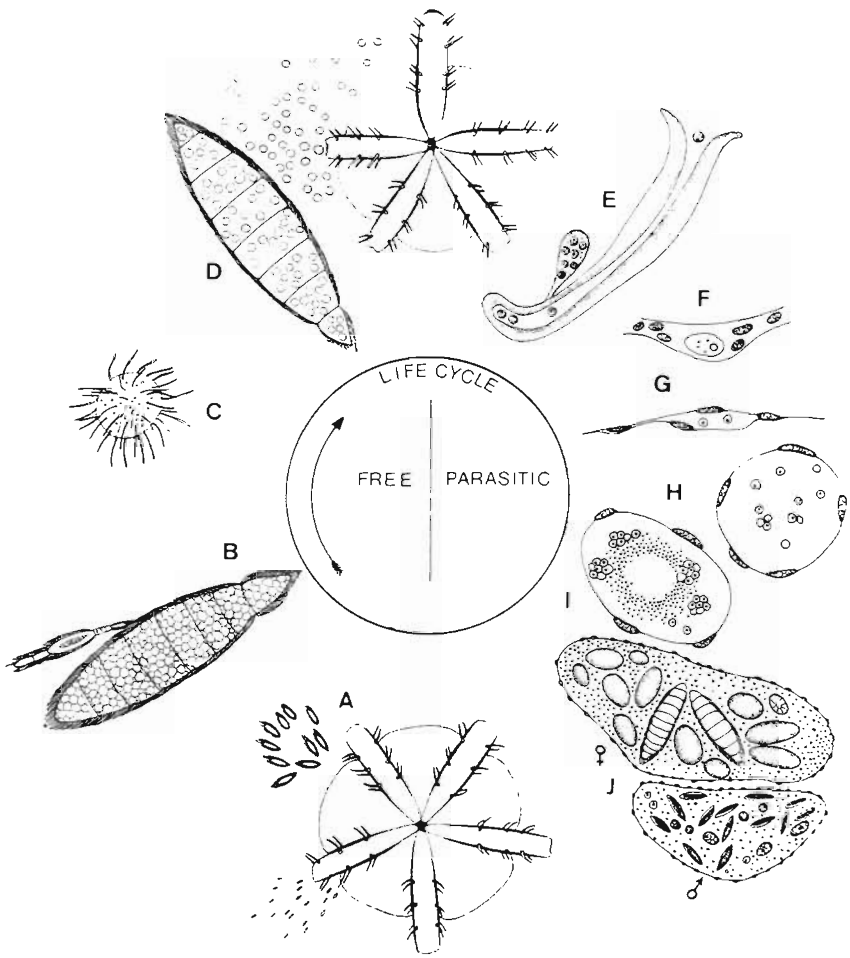

Fig. 1. *Rhopalura ophiocomae*. Life-cycle of a mesozoan parasite of the ophiuroid *Amphipholis squamata* (not to scale). (A) Male and female mesozoans emitted through the genital slits of an infested ophiuroid; (B) fecondation; (C) infesting mesozoan larvae; (D) release of infesting larvae from a female mesozoan; (E) infestation of ophiuroid genital slits; (F) penetration of the larvae in the ophiuroid bursal epithelium; (G to I) developing plasmodia; (J) male and female plasmodia. (After Caullery & Lavallée 1912)

are completely surrounded by an epithelial layer presumably formed by host mesothelium (Caullery & Mesnil 1901, Rader 1982). Whether each plasmodium derived from a whole larva or from one or more cells of that larva is not known. The plasmodia grow and some of them move along the coelomic lining. Fully developed plasmodia consist of an enlarged cytoplasmic (?) mass surrounded by an epithelium of host origin. Each plasmodial mass contains numerous small nuclei (the 'plasmodic' or 'vegetative' nuclei), some germ cells (sometimes called 'agametes') and a few embryos at different developmental stages. These are either males or females, embryos of both sexes within the same plasmodium being exceptional. When mature, the plasmodium presumably disintegrates and numerous adult *R. ophiocomae* are emitted into the outer medium through the host's bursal slit.

The pathogenicity of *Rhopalura ophiocomae* is unquestionable. Its most obvious effect is the regression of host ovaries, while the testes – as noted by several authors – remain functional (*Amphipholis squamata* is hermaphroditic). The parasite does not consume the ovaries; these regress as soon as small plasmodia invade the bursal wall. Ovarian regression implies that infested ophiuroids never harbor incubated embryos. Other consequences of the disease are a decrease in the ophiuroid's regenerative abilities, as well as probably a decrease in its growth rate (Rader 1982).

Agents: Parazoa

There are only 2 sponge species known to parasitize echinoderms. Clark (1896, 1898) reported the occurrence of a *Grantia*-like species firmly attached to the outer body surface of several individuals of the holothuroid *Synapta vivipara*. The sponges always were seen at the base of the holothuroid buccal tentacles. Antarctic ophiuroids of the genus *Ophiurolepis* are very often parasitized by the sponge *Iophon radiatus* (Mortensen 1936, Fell 1961). The parasite fixes itself on the ophiuroid, and infestation is generally very extensive, the whole disc and the basal parts of the arms being involved.

As shown by Mortensen (1932), the bizarre sponge *Microcordyla asteriae* described by Zirpolo (1926) as an ectoparasite of the asteroid *Coscinasterias tenuispina,* actually represents a globiferous pedicellaria of the echinoid *Sphaerechinus granularis.* The pedicellariae probably were detached in a defensive reaction of *S. granularis* (globiferous pedicellariae of echinoids autotomize easily).

Agents: Cnidaria

Several sea anemones attach to the body surface of echinoderms. Gravier (1918) noted the occurrence of the actinid *Sicyopus commensalis* partly embedded in the body wall of the deep-sea holothuroid *Pseudostichopus villosus.* Kropp (1927) reported echinoids of the genus *Diadema* with the sea anemone *Aiptasia tagetas* firmly attached to their body surface near the anal cone. Other cnidarians may incidentally parasitize echinoderms, namely hydrozoans which live attached to the stem or the cirri of crinoids. Four crinoid-associated hydrozoans are known: *Calycella syringa, Cuspidella* sp., *Lafoea fruticosa,* and *Stegopoma fastigiata* (Clark 1921). A case of symbiosis between the hydrozoan *Hydractinia vallini* and several species of the Antarctic ophiuroid genus *Theodoria* has been reported by Smirnov & Stepanyants (1980). This symbiosis is similar to the one between Antarctic ophiuroids and sponges. The single known case of hydrozoans living on asteroids was reported by Madsen (1961) who recorded unidentified athecate hydroids attached to the peristome of the deep-sea asteroid *Eremicaster gracilis.*

Agents: Turbellaria

While Turbellaria are mainly free-living, each order has developed representatives living in close association with other organisms. Symbiotic turbellarians were reviewed by Jennings (1971) (see also Stunkard & Corliss 1951) who noted that echinoderms represent preferential shelters for turbellarians. Table 1 lists symbiotic turbellarians living with echinoderms; of the 68 species, 9 are Acoela, 58 Rhabdocoela (52 species belonging to the family Umagillidae) and 1 Polycladida. With very few exceptions (*Euplana takewakii* and *Acholades asteris*; respectively Kato 1935, Hickman & Olsen 1955), almost all echinoderm-associated turbellarians live either within the digestive tract or within the coelomic cavity of their host. Symbiotic turbellarians have been reported for each echinoderm group, but most of these associates live in aspidochirote holothuroids (mainly Holothuriidae and Stichopodidae) or in regular echinoids. As noted in Table 1, massive turbellarian infestations occur rather frequently in echinoderms. There is, however, no information on the effect of parasitic Turbellaria on the echinoderm life cycle.

Gut-associated umagillids may either occur all along the digestive tract (Smith 1973) or be more or less restricted to some digestive areas (Barel & Kramers 1971, Shinn 1981, Cannon 1982; see also Table 1). Holt & Mettrick (1975) reported that *Syndisyrinx franciscanus* from the gut of *Strongylocentrotus purpuratus* feeds mostly on associated ciliates, harbored by the digestive tract of the echinoid. Snyder (1980) could determine neither beneficial nor detrimental effects due to the occurrence of gut-associated umagillids. He concluded that these symbiotes should be considered simply commensals. In contrast Shinn (1981) reported that the gut-associated umagillids always compete with their host for nutrients and thus may exert adverse effects. He noted that all the umagillids studied by him ingest intestinal host tissue – one of them subsisted entirely on that tissue (see also Cannon 1982). Shinn suggested that gut umagillids parasitise their host to varying degress. Giese (1958) noted that the infestation level of *S. franciscanus* in the gut of *S. purpuratus* remains constant throughout the year and does not differ whatever the size, sex or gonadal stage of the echinoid. In contrast, *Wahlia pulchella* inhabiting the intestine of *Stichopus californicus* displays a distinct annual cycle of infestation related to the annual feeding cycle of its host (worms do not occur in *S. californicus* in fall and winter when the host's viscera are resorbed) (Shinn 1986b). According to Shinn (1980, 1983b) egg capsules of the gut-associating *S. franciscanus* leave the host gut with fecal material. Embryogenesis within capsules lasts approximately 2 mo, and fully-formed embryos (infesting embryos) can survive in their capsule for about 10 additional mo (Fig. 2). Embryos hatch after the capsules were ingested by an echinoid. Hatching is induced by some property of the host's digestive fluid and performed presumably owing to a hatching enzyme secreted by the embryos (Shinn 1983b, 1986a).

Coelomic umagillids swim in the host's body cavity, seemingly without any particular intracoelomic location. Coelomic umagillids directly depend on their host for nutrition – they ingest the host's coelomic fluid together with coelomocytes (Jennings & Mettrick 1968, Shinn 1983b) – or on other coelom-associated organisms such as ciliates (Mettrick & Jennings 1969, Jennings 1980). Egg-capsules of intracoelomic umagillids of holothuroids frequently occur within brown bodies (Briot 1906a, b, Arvy 1957, Changeux 1961, Jespersen & Lützen 1971, Shinn 1983b, 1985a). They are thought to be released into the outer medium through host evisceration (Changeux 1961, Jespersen & Lützen 1971). Shinn (1985a) reported, however, that brown

Table 1. Turbellarians associated with echinoderms (compiled from the sources indicated). Turbellarian species names according to Cannon (1982). Hosts: A, asteroid; C, crinoid; E, echinoid; H, holothuroid; O, ophiuroid

Turbellarian	Host	Location in host	Remarks	Geographical area	Source
I. Acoela					
Aechmalotus pyrula	*Eupyrgus scaber* (H)	Digestive tract and respiratory trees	–	Barents Sea (Murmansk coast)	Beklemishev (1915)
Aphanastoma pallidum	*Myriotrokus rinki* (H)	Digestive tract	–	Barents Sea (Murmansk coast)	Beklemishev (1915)
Aphanostoma sanguineum	*Chirodota laevis* (H)	Posterior part of the digestive tract	–	Barents Sea (Murmansk coast)	Beklemishev (1915)
Avagina glandulifera	*Spatangus purpureus* (E)	Digestive tract	Many echinoids infested	English Channel (Plymouth)	Westblad (1953)
Avagina incola	*Echinocardium cordatum* (E)	Siphon (accessory canal)	5 % of the echinoid population infested	NE Atlantic (Millport)	Leiper (1902, 1904)
Avagina incola	*Echinocardium flavescens, Spatangus purpureus* (E)	Digestive tract	Average infestation: 50 worms echinoid^{-1}	North Sea (Bonden, Norway)	Karling (in Westblad 1948)
Avagina incola	*Echinocardium flavescens* (E)	Digestive tract	3 to 14 worms echinoid^{-1} (50 echinoids investigated)	North Sea (Norwegian coast)	Westblad (1948)
Avagina incola	*Spatangus purpureus* (E)	Digestive tract	–	North Sea (Norwegian coast); English Channel (Plymouth)	Westblad (1948, 1953)
Avagina vivipara	*Echinocardium cordatum* (E)	Esophagus	2 to 5 worms echinoid^{-1} (18 infested/68 investigated)	SW Indian Ocean (Ralph's Bay, Tasmania)	Hickman (1956)
Faerla echinocardii	*Echinocardium flavescens* (E)	Unspecified	–	? North Sea (Norwegian coast)	Dorjes (1972)
Meara stichopi	*Parastichopus tremulus* (H)	Anterior intestine; coelomic cavity	1 to 8 worms holothuroid^{-1}	North Sea (Norwegian coast: Herdla, Trondhjem)	Westblad (1926, 1949)
Meara stichopi	*Parastichopus tremulus* (H)	Esophagus	–	North Sea (Oslofjord)	Jespersen & Lützen (1971)
Meara stichopi	*Mesothuria intestinalis* (H)	Coelomic cavity	Single observation	North Sea (Norwegian coast)	Westblad (1926, 1949)
Octocoelis chirodota	*Chirodota laevis* (H)	Anterior part of digestive tract	–	Barents Sea (Murmansk coast)	Beklemishev (1915)
II. Rhabdoecoela (f. umagillidae)					
Anoplodiera voluta	*Parastichopus tremulus* (H)	Digestive tract	Up to 90 worms holothuroid^{-1}	North Sea (Norwegian coast: Herdla, Trondhjem)	Westblad (1926, 1930)
Anoplodiera voluta	*Parastichopus tremulus* (H)	Anterior part of digestive tract	–	North Sea (Oslofjord)	Jespersen & Lützen (1971)
Anoplodiera sp.	*Holothuria arenicola* (H)	Pharynx	Average infestation: 7 worms holothuroid^{-1} (9 infested/12 investigated)	Tropical W Atlantic (Bermuda)	Snyder (1980)
Anoplodiopsis gracilis	*Holothuria forskali* (H)	Coelomic cavity	Up to 9 worms holothuroids^{-1} (11 infested/47 investigated) (Wahl 1906)	Mediterranean Sea (Naples)	Wahl (1906, 1909), Westblad (1953)
Anoplodium[1] *chirodotae*	*Chirodota pellucida* (H)	Coelomic cavity	Species of doubtful generic affinity	White Sea	Sabussow (1900, quoted by Barel & Kramers, 1977)
Anoplodium evelinae	Unidentified holothuroid	Coelomic cavity	Up to 50 worms holothuroid^{-1}	SW Atlantic (Brazil: Santos Bay)	Marcus (1949)
Anoplodium graffi	*Holothuria impatiens* (H)	Coelomic cavity	–	Mediterranean Sea (Naples)	Monticelli (1892), Westblad (1953)
Anoplodium hymanae	*Parastichopus californicus* (H)	Coelomic cavity	1 to 51 (average 15) worms holothuroid^{-1} (25 infested/27 investigated)	NE Pacific (Washington coast: Cowlitz Bay)	Shinn (1983a; see also Shinn 1985b)

Table 1 (continued)

Turbellarian	Host	Location in host	Remarks	Geographical area	Source
Anoplodium longiductum	*Actinopyga* sp. (H)	Unspecified	–	SW Indian ocean (Madagascar: Nossy-Bé)	Hyman (1960)
Anoplodium mediale	*Stichopus japonicus* (H)	Coelomic cavity	–	NW Pacific (Japan: Hiroshima)	Ozaki (1932)
Anoplodium myriotrochi	*Myriotrochus rincki* (H)	Digestive tract	Infestation frequent	Arctic Seas (Spitzbergen)	Barel & Kramers (1977)
Anoplodium parasita	*Holothuria tubulosa*, *Holothuria poli* and *Holothuria stellati* (H)	Coelomic cavity; rarely digestive tract or respiratory trees	1–4 worms holothuroid^{-1} (16 infested/26 investigated) (Changeux)	Mediterranean Sea (Banyuls, Naples, Trieste)	Schneider (1858), Monticelli (1892), Briot (1906b), Wahl (1906), Westblad (1953), Changeux (1961)
Anoplodium ramosum	*Stichopus variegatus* (H)	Unspecified (endoparasitic)	–	SW Indian Ocean (Madagascar: Nossi-Bé)	Hyman (1960)
Anoplodium stichopi	*Parastichopus tremulus* (H)	Coelomic cavity	Up to 30 worms holothuroid^{-1} (Westblad)	North Sea (Norwegian coast)	Bock (1926), Westblad (1926), Jespersen & Lützen (1971)
Anoplodium tubiferum	*Holothuria forskali* (H)	Digestive tract	–	English Channel (Plymouth)	Westblad (1953)
'*Anoplodium*' sp.[1]	*Leptosynapta bergensis*, *Leptosynapta galliennei*, *Leptosynapta inhaerens* (H)	Digestive tract	Rather frequent	NE Atlantic (Plymouth, Roscoff)	Cuénot (1912), Barel & Kramers (1970, 1977), Kramers (1971)
Bicladus metacrini	*Metacrinus rotundus* (C)	Digestive tract	'Occur in enormous number'	N Pacific (Japan: Sagami Sea)	Kaburaki (1925)
Cleistogamia heronensis	*Holothuria atra*, *Holothuria leucospilota* (H)	Anterior to midpart of digestive tract	–	Great Barrier Reef (Australia)	Cannon (1982)
Cleistogamia holothuriana	*Actinopyga mauritiana* (H)	Digestive tract	50 worms in a single individual (Faust)	NE Indian Ocean (Andaman Islands)	Faust (1924, 1927), Baer (1938)
Cleistogamia holothuriana	*Actinopyga echinites* (H)	Unspecified (endoparasitic)	–	SW Indian Ocean (Madagascar: Nossi-Bé)	Hyman (1960)
Cleistogamia longicirrus	*Stichopus chloronotus*, *Stichopus horrens*, *Stichopus variegatus* (H)	Anterior to midpart of digestive tract	–	Great Barrier Reef (Australia)	Cannon (1982)
Cleistogamia louftia	*Holothuria* sp.	Unspecified (endoparasitic)	–	Red Sea	Khalil (1938, quoted by Stunkard & Corliss 1951)
Cleistogamia pallii	*Bohadschia argus* (H)	Anterior to midpart of digestive tract	–	Great Barrier Reef (Australia)	Cannon (1982)
Cleistogamia pulchra	*Actinopyga echinites*, *Actinopyga lecanora*, *Actinopyga miliaris* (H)	Midpart of digestive tract	–	Great Barrier Reef (Australia)	Cannon (1982)
Cleistogamia pyriformis	*Holothuria impatiens* (H)	Anterior part of digestive tract	–	Great Barrier Reef (Australia)	Cannon (1982)
Desmote inops	*Florometra serratissima* (C)	Digestive tract	10 to 30 worms crinoid^{-1} (49 infested/60 investigated)	NE Pacific (British Columbia: satellite Channel)	Kozloff (1965)
Desmote vorax	*Heliometra glacialis* (C)	Unspecified (endoparasitic)	1 to 20 worms crinoid^{-1} (9 infested/100 investigated)	Barents Sea (Kola Bay)	Beklemishev (1916)
Fallacohospes inchoatus	*Florometra serratissima* (C)	Digestive tract	2 to 15 worms crinoid^{-1} (59 infested/60 investigated)	NE Pacific (British Columbia: satellite Channel)	Kozloff (1965)
Macrogynium ovalis	*Isostichopus badionotus* (H)	Coelomic cavity; digestive tract	15 worms holothuroid^{-1} (average number); 36 holothuroids investigated (Snyder)	Tropical W Atlantic (Bermuda)	Meserve (1934), Snyder (1980)

Table 1 (continued)

Turbellarian	Host	Location in host	Remarks	Geographical area	Source
Monticellina longituba[2]	*Holothuria impatiens, Holothuria poli* (H)	Coelomic cavity	–	Mediterranean Sea (Naples)	Westblad (1953)
Notothrix inquilina	*Mensamaria thompsoni* (H)	Digestive tract (anterior part)	Up to 22 worms holothuroid^{-1} (121 investigated/51 infested)	Tasmania	Hickman (1955)
Ozametra arborum	*Stichopus japonicus* (H)	Digestive tract	–	NW Pacific (Japan: Hiroshima)	Ozaki (1932)
Ozametra sp.	*Parastichopus californicus* (H)	Digestive tract	–	Pacific coast of N America	Kozloff in Shinn (1983a)
Paranotothrix queenslandensis	*Actinopyga echinites, Actinopyga miliaris, Bohadschia argus, Holothuria atra, Holothuria hilla, Holothuria impatiens, Holothuria leucospilota, Stichopus chloronotus, Stichopus horrens, Stichopus variegatus, Thelonota ananas* (H)	Posterior part of digestive tract	–	Great Barrier Reef (Australia)	Cannon (1982)
Seritia elegans	*Parastichopus tremulus* (H)	Digestive tract (anterior part)	Rather frequent	North Sea (Norwegian coast)	Westblad (1926, 1953), Jespersen & Lützen (1971)
Seritia striata	*Stichopus mollis* (H)	Digestive tract (anterior part)	–	Tasmania	Hickman (1955)
Syndesmis alcalai	*Heterocentrotus mammillatus* (E)	Digestive tract and coelomic cavity	–	NW Pacific (Philippines: Sumilon Island)	Komschlies & Vande Vusse (1980a)
Syndesmis compacta	*Echinometra oblonga* (E)	Digestive tract and coelomic cavity	–	NW Pacific (Philippines: Cebu Province)	Komschlies & Vande Vusse (1980b)
Syndesmis dendrastromum	*Dendraster excentricus* (E)	Digestive tract	Up to 23 worms echinoid^{-1} (Smith); worms consistently present in large number (Orihel)	E Pacific (California; Washington State)	Stunkard & Corliss (1950, 1951), Orihel (1952), Smith (1973), Shinn (1981)
Syndesmis echinorum	*Echinus acutus, Echinus esculentus, Paracentrotus lividus, Psammechinus microtuberculatus, Psammechinus miliaris, Sphaerechinus granularis, Strongylocentrotus droebachiensis* (E)	Digestive tract and coelomic cavity	Infestation rate highly variable (see Barel & Kramers 1977)	European Seas	Silliman (1881), François (1886), Cuénot (1891), Shipley (1901), Briot (1906b), Westblad (1926), Barel & Kramers (1970, 1977), Lama Seco & Rodriguez Babio (1978)
Syndesmis aff. *echinorum*	*Strongylocentrotus droebachiensis, Strongylocentrotus pallidus* (E)	Digestive tract	–	NE Pacific (Washington: San Juan Island)	Shinn (1981)
Syndesmis glandulosa	*Diadema setosum, Echinothrix calamaris* (E)	Digestive tract and coelomic cavity	–	SW Indian Ocean (Madagascar: Nossi-Bé)	Hyman (1960), Komschlies & Vande Vusse (1980a)
Syndesmis mammillata	*Echinometra oblonga* (E)	Digestive tract and coelomic cavity	–	NW Pacific (Philippines: Negros Oriental Province)	Komschlies & Vande Vusse (1980a)
Syndesmis philippinensis	*Echinometra oblonga* (E)	Digestive tract and coelomic cavity	–	NW Pacific (Philippines: Negros Oriental Province)	Komschlies & Vande Vusse (1980a)
'*Syndesmis*' sp.	*Evechinus chloroticus, Heliocidaris erythrogramma* (E)	Digestive tract	–	New Zealand	McRae (1959)

Table 1 (continued)

Turbellarian	Host	Location in host	Remarks	Geographical area	Source
Syndisyrinx antillarum	*Diadema antillarum* (E)	Coelomic cavity	60 worms echinoid^{-1} (average number; 3 infested/9 investigated) (Snyder)	Tropical Atlantic (off Florida: Bermuda)	Powers (1935), Stunkard & Corliss (1951), Mettrick & Jennings (1969), Snyder (1980)
Syndisyrinx antillarum	*Lytechinus variegatus* (E)	Digestive tract and coelomic cavity	Up to 205 worms echinoid^{-1} (475 investigated/350 infested)	Jamaica	Nappi & Crawford (1984)
Syndisyrinx antillarum	*Echinometra viridis* (E)	Digestive tract and coelomic cavity	Up to 5 worms echinoid^{-1} (219 investigated/87 infested)	Jamaica	Nappi & Crawford (1984)
Syndisyrinx atriovillosa	*Spatangus purpureus* (E)	Digestive tract	–	English Channel (Plymouth)	Westblad (1953)
Syndisyrinx franciscanus	*Strongylocentrotus franciscanus, Strongylocentrotus purpuratus, Strongylocentrotus droebachiensis, Strongylocentrotus pallidus, Lytechinus anamesus* (E)	Digestive tract	Often up to 30 worms in infested echinoid (Lehman, Shinn)	Pacific coast of N America (California, Washington)	Lehman (1946), Stunkard & Corliss (1951), Giese (1958), Jennings & Mettrick (1968), Barnes (1969), Mettrick & Jennings (1969), Mettrick & Boddington (1972), Holt & Mettrick (1975), Shinn (1981, 1983b)
Syndisyrinx franciscanus	*Allocentrotus fragilis* (E)	Digestive tract	Maximum 3 worms echinoid^{-1} (5 infested/75 investigated) (Giese)	NE Pacific (off Californian coast)	Giese (1958), Hyman (1960)
Syndisyrinx franciscanus	*Lytechinus variegatus* (E)	Digestive tract and coelomic cavity	29 worms echinoid^{-1} (average number)	Tropical W Atlantic (Jamaica)	Jennings & Mettrick (1968), Jones & Canton (1970)
Syndisyrinx pallida	*Echinocardium cordatum* (E)	Digestive tract	1 to 4 worms echinoid^{-1} (10 infested/68 investigated)	Tasmania (Ralph's Bay)	Hickman (1955)
Syndisyrinx punicea	*Heliociaris erythrogramma, Amblypneustes ovum* (E)	Digestive tract	Infestation very frequent; up to 18 worms echinoid^{-1}	SE Indian Ocean (Tasmania: Ralph's Bay)	Hickman (1956)
Umagilla forkalensis	*Holothuria forskali* (H)	Digestive tract	Up to 14 worms holothuroid^{-1} (29 infested/47 investigated) (Wahl 1909)	Mediterranean Sea (Naples); North Sea (Norwegian coast); English Channel (Plymouth)	Wahl (1906, 1909), Westblad (1953)
Wahlia macrostylifera	*Isostichopus tremulus* (H)	Digestive tract	Infestation rather frequent	North Sea (Norwegian coast)	Westblad (1926, 1930), Jespersen & Lützen (1971)
Wahlia macrostylifera	*Parastichopus badionotus* (H)	Digestive tract and coelomic cavity	15 worms holothuroid^{-1} (average number) (33 infested/36 investigated)	Tropical W Atlantic (Bermuda)	Snyder (1980)
Wahlia pulchella	*Stichopus californicus* (H)	Anterior part of investine	2 to 5 worms holothuroid^{-1} (infestation level: 62 to 100 % in spring & summer; 0 % in fall and winter when host's viscera are resorbed)	NE Pacific (coast of Washington)	Shinn (1986b)
Wahlia stichopi	*Stichopus chloronotus, Stichopus horrens, Thelonota ananas* (H)	Anterior to midpart of digestive tract	–	Great Barrier Reef (Australia)	Cannon (1982)
III. Rhabdocoela (f. acholadidae and pterastericolidae)					
Acholades asteris	*Coscinasterias calamaria* (A)	Encysted in tube feet wall	20 or more worms asteroid^{-1} (216 infected/267 investigated)	SW Indian Ocean (Tasmania: D'Entrecasteaux Channel)	Hickman & Olsen (1955)

Table 1 (continued)

Turbellarian	Host	Location in host	Remarks	Geographical area	Source
Pterastericola australis	*Patiriella calcar* (A)	Pyloric caeca	Up to 10 worms asteroid^{-1} (407 investigated/28 infested)	Hasting Point (New South Wales, Australia)	Jennings & Cannon (1985)
Pterastericola fedotovi	*Pteraster militaris, Pteraster obscurus, Pteraster pulvillus* (A)	Unspecified (endoparasitic)	–	Barents Sea (Murmansk); White Sea (Kandalaksha Bay)	Beklemishev (1916), Karling (1970)
Pterastericola vivipara	*Acanthaster planci* (A)	Pyloric caeca	Infested asteroid may have large number of worms	W Pacific (Australia: central Great Barrier Reef)	Cannon (1978), Jennings & Cannon (1985)
Triloborhynchus astropectenis	*Astropecten irregularis* (A)	Pyloric caeca	5 to 10 worms per pyloric caecum in infested asteroid	North Sea (Norwegian and Swedish coasts); English Channel (Plymouth)	Bashirudin & Karling (1970), Jennings & Cannon (1985)
Triloborhynchus psilastericola	*Psilaster andromeda* (A)	Pyloric caeca, coelomic cavity (juvenile forms)	Infestation frequent (sometimes more than 10 worms asteroid^{-1})	North Sea (Oslo fjord)	Jespersen & Lützen (1972)
IV. Polycladida					
Euplana takewakii	*Ophioplocus japonicus* (O)	Bursae	20 infested / 200 investigated	NW Pacific (Japan: Mitsui)	Kato (1935)

[1] Species of doubtful validity (Shinn pers. comm.)
[2] Synonym of *Umagilla forskalensis*, according to Cannon (1982)

bodies containing egg capsules of the coelom-associating *Anoplodium hymanae* may pass out of intact hosts – the holothuroid *Parastichopus californicus* – through any of a series of pores that connect the coelom to the posterior end of the rectum. Embryogenesis of *A. hymanae* lasts about 1 mo, and embryos remain quiescent in their capsule until they are ingested by a holothuroid (developed embryos can survive in their capsules for 10 to 11 mo; Shinn 1985b). Hatching is stimulated by some property of the host's digestive

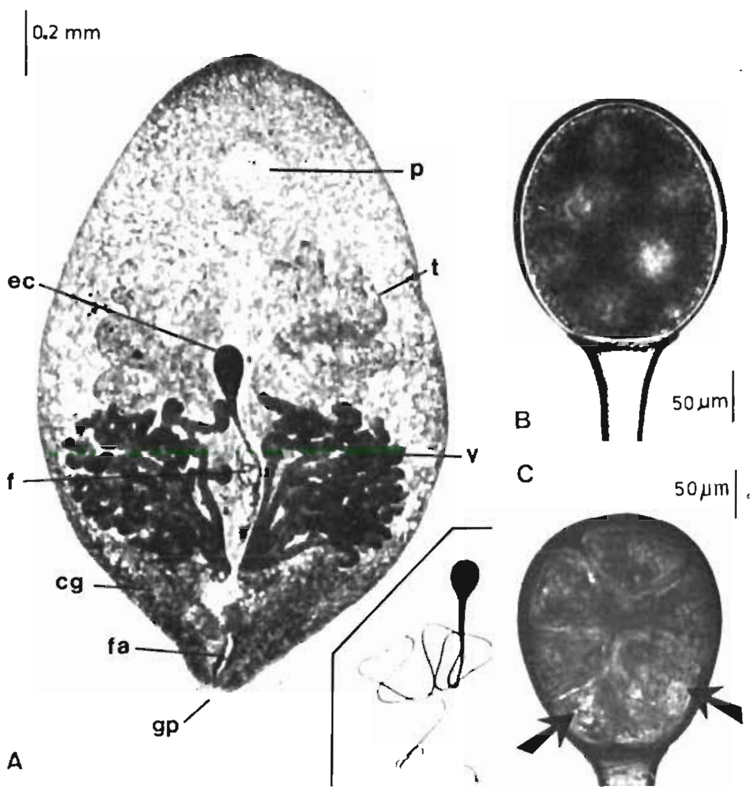

Fig. 2. *Syndisyrinx franciscanus*, a symbiotic turbellarian from the intestine of echinoids (*Strongylocentrotus* spp.). (A) Ventral view of a live adult individual. cg: cement glands; ec: bulb of egg capsule; f: filament of egg capsule; fa: female antrum; gp: location of common gonophore; p: pharynx; t: left testis; v: vitellaria. Insert: egg capsule showing bulb and filament. (B) Bulb of a newly produced egg capsule. (C) Bulb of a 2 mo old egg capsule containing 6 fully developed embryos (arrows). (After Shinn 1983b)

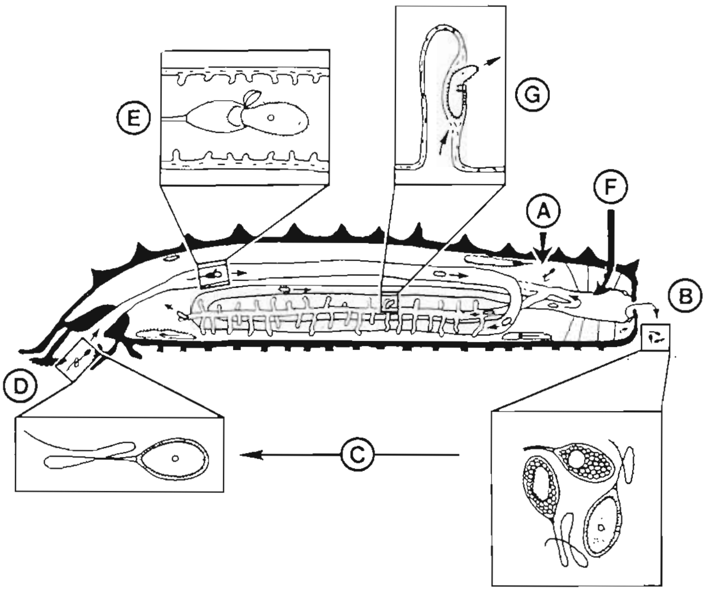

Fig. 3. *Anoplodium hymanae.* Life cycle of a coelom-associated umagillid from the holothuroid *Parastichopus californicus.* (A) Release of umagillid egg capsules into the host's coelom; (B) ensheathment of egg capsules into brown bodies; (C) completion of embryos' development outside the host; (D) ingestion by the new host of egg capsules containing embryos; (E) hatching of larvae in the upper intestine; (F) migration of larvae towards the respiratory trees; (G) larvae penetrate the wall of the respiratory trees and enter the coelom. (After Shinn 1985b)

fluid. Larvae penetrate the wall of the posterior intestine or, more commonly, that of the respiratory trees to reach the coelom (Fig. 3). As demonstrated by Shinn (1985b), the size of *A. hymanae* infesting *P. californicus* varies seasonally and is correlated with the seasonal feeding behavior of the host.

Investigations by Shinn (1983b, 1985a, b, 1986b) on echinoderm-associated umagillids showed that hatchings are not adversely affected by the host's digestive fluids whatever the final location of the worms in the host. However, adult worms of coelom-inhabiting species are killed by the host's digestive fluid but appear to have some mean of avoiding attack by coelomocytes. Considering the number of species of umagillids that are reported to inhabit both the coelom and gut of the host (see Table 1), careful re-examination is needed 'to determine if the worms clearly are adapted to inhabiting very differents sites in their hosts, or whether the reports are the results of improper dissection techniques' (Shinn 1985b, p. 213).

Non-umagillid rhabdocoels associated with echinoderms have been reported only from asteroids (Table 1). The acholadid *Acholades asteris* was always found encysted in the connective tissue layer of the tube feet of *Coscinasterias calamaria.* Nothing is known on the life cycle of this aberrant rhabdocoel. All pterastericolids found thus far were associated with asteroid pyloric caeca on which they feed (feeding on energy-rich epithelial cells; Cannon 1975, 1978, Jennings & Cannon 1985) (Fig. 4 & 5). According to Jennings & Cannon (1985), the occurrence of pterastericolids is independent of host size and sex. These workers noted that the worms neither affect the host's reproductive potential nor produce any marked damages to the asteroid's pyloric caeca. Digestion in

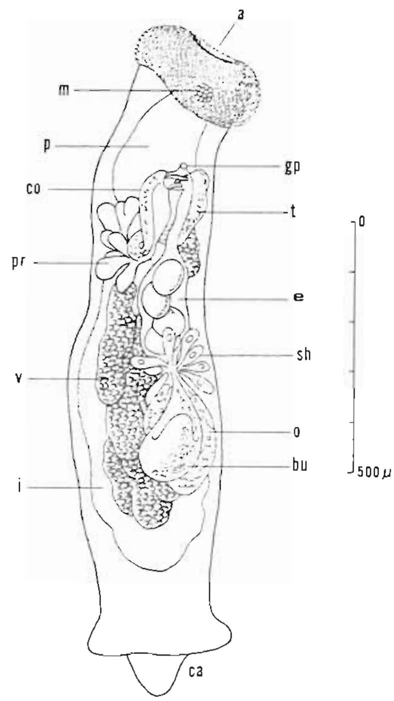

Fig. 4. *Triloborhynchus psilastericola.* Ventral view of a turbellarian parasite of the pyloric caeca of the asteroid *Psilaster andromeda.* a: entrance to apical organ; bu: bursa; ca: caudal adhesive disk; co: copulatory bulb; e: egg capsule in uterus; gp: common genital pore; i: intestine; m: mouth; o: ovary; p: pharynx; pr: prostatic glands; sh: shell glands; t: testis; v: yolk glands. (After Jespersen & Lützen 1972)

asteroid pterastericolids is predominantly intracellular (their gut is deprived of gastrodermal glands), and Jennings & Cannon suggest this would be 'an adaptative simplification related to the particular diet of host storage and digestive cells, which provides all necessary dietary components plus the enzymes necessary for their digestion and assimilation' (p. 211). The only polyclad species known to be an echinoderm parasite, *Euplana takewakii*, feeds on ophiuroid gonads, the infested bursae always being castrated (Kato 1935).

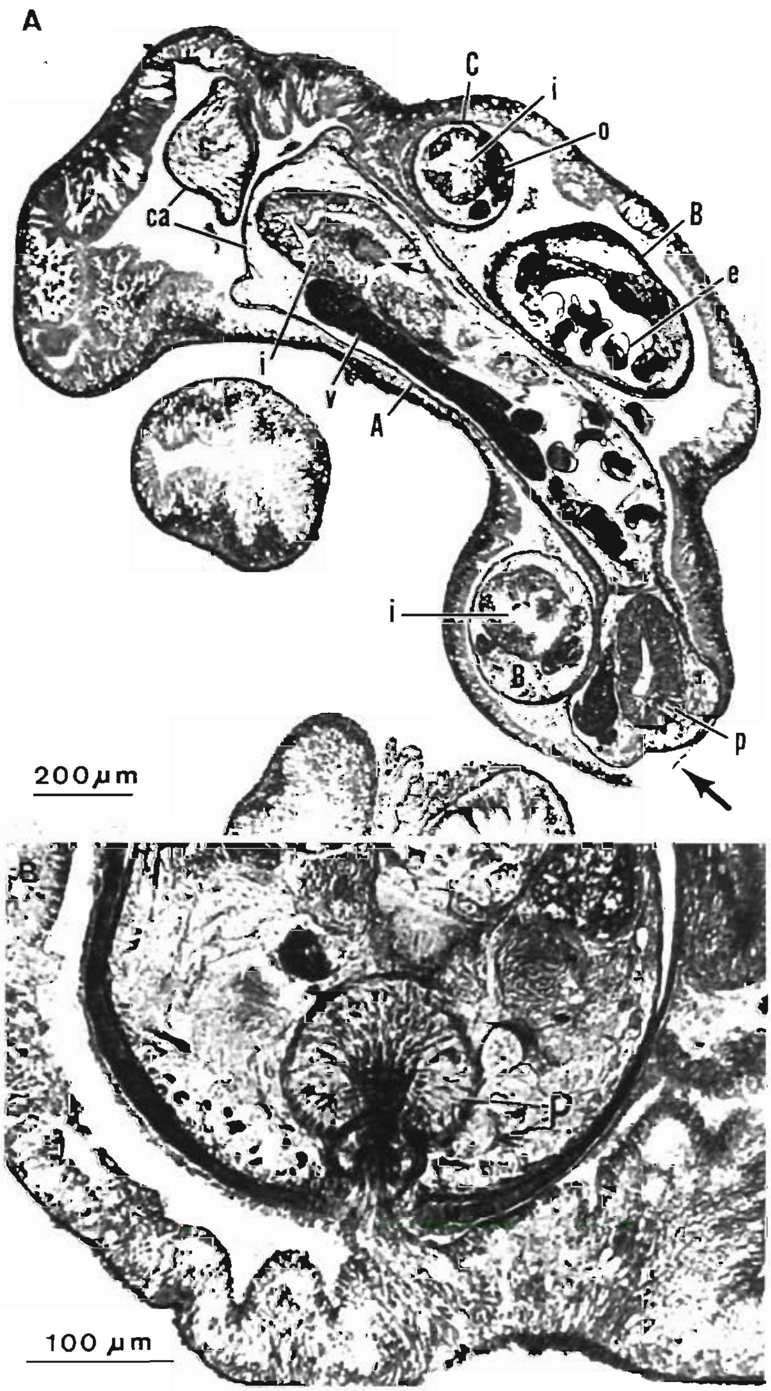

Fig. 5. Infestation of asteroid pyloric caeca by pterastericolid turbellarians. (A) *Psilaster andromeda*. Section through pyloric diverticulum containing 3 specimens (A, B, C) of *Triloborhynchus psilastericola*. ca: caudal adhesive disk; e: egg capsule in uterus; i: intestine; o: ovary; p: pharynx; v: yolk glands; large arrow: area of pyloric diverticulum demolished by specimen; small arrow: piece of ingested tissue from pyloric diverticulum. (B) *Acanthaster planci*. Section through a pyloric diverticulum showing an individual of *Pterastericola vivipara* ingesting pyloric tissues. P: pharynx. ([A] after Jespersen & Lützen 1972; [B] after Cannon 1978)

Table 2. Parasitic trematodes from echinoderms (compiled from the sources indicated). Hosts: C, crinoid; E, echinoid; H, holothuroid; O, ophiuroid

Trematode	Host	Location in host	Primary host	Remarks	Geographical area	Source
Diphterostomum brusinae	*Antedon mediterranea* (C)	Inside crinoid calyx (within connective tissue strings)	Several species of benthic fishes	1 to 15 trematodes crinoid^{-1}; first intermediary host would be a gastropod mollusc (*Nassa* sp., *Natica* sp.)	Mediterranean Sea (Marseille)	Prévot (1966a; see also Palombi 1930)
Fellodistomum fellis[1]	*Ophiura albida*, *Ophiura sarsi* (O)	In wall of digestive sac	Fishes (*Anarrhicas lupus*, *Platessa platessa*; Mortensen)	1 to 13 trematodes ophiuroid^{-1}; the first intermediary host is bivalve *Nucula nucula* (Chubrik)	Barents Sea (Kola Bay); North Sea (Gullmarfjord)	Tauson (1917), Mortensen (1921a), Chubrik (1952, see also Barel & Kramers 1977)
Himasthla leptosoma	*Leptosynapta galliennei*, *Leptosynapta inhaerens* (H)	In body wall, at base of buccal tentacles; sometimes within coelomic brown bodies	Sea birds (*Tringa variabilis*, *Calidris leucophoea*)	Alternative intermediary hosts: bivalve *Scrobicularia tenuis*, polychete *Arenicola marina*, sipunculid *Phascolosoma vulgare* (Cuénot 1912)	NE Atlantic (Arcachon, Roscoff)	Cuénot (1892, 1912), Timon-David (1938)
'Metacercaria' *psammechini*	*Psammechinus microtuberculatus*, *Sphaerechinus granularis* (E)	In muscles of Aristotle's lantern	Presumably echinoid-eating fishes of the family Labridae	Infestation may be very heavy	Mediterranean Sea (Banuyls, Marseille)	Timon-David (1934, 1938)
Monorchis monorchis	*Antedon mediterranea* (C)	Inside crinoid calyx (within connective tissue strings)	Sparid fishes, in particular *Spondyliosoma cantharus*	5 to 60 trematodes crinoid^{-1} (17 infested/151 investigated)	Mediterranean Sea (Marseille)	Prévot (1966a, b)
?*Nidrosia ophiurae*[2]	*Ophiura sarsi* (O)	In gonads	–	–	North Sea (Trondhjem fjord)	Mortensen (1933a)
Paralepidapedon hoplognathi	*Anthocidaris crassispina* (E)	Mostly in gonads; also in muscles of Aristotle's lantern and in ampullae of tube feet	Fish *Hoplognathus punctatus*	1 to 66 trematodes echinoid^{-1} (22 infested/29 investigated)	Misaki (Japan)	Shimazu & Shimura 1984
Proctoeces maculatus	*Anthocidaris crassispina*, *Diadema setosum*, *Hemicentrotus pulcherrimus* (E)	In gonads	–	–	Misaki (Japan)	Shimazu & Shimura (1984)
Protoeces sp.	*Strongylocentrotus intermedius* (E)	In gonads	–	Gastropod *Haliotis discus hannai* is alternative intermediary host	Japan Sea (off Maehama, Hokkaido)	Shimazu (1979)
?*Tetrarhynchus holothuriae*[3]	*Molpadia* sp. (H)	Body wall (?)	–	–	NE Indian Ocean (Malaysian coast)	Shipley (1903)
Zoogonoides viviparus[4]	*Ophiura albida*, *Ophiothrix fragilis*, *Leptosynapta galliennei*, *Leptosynapta inhaerens* (O, H)	In gonads and coelom wall of ophiuroids; in body wall of holothuroids (at base of buccal tentacles)	–	Might also occur in *Mysis* sp.	NE Atlantic (Arcachon, Roscoff)	Cuénot (1892, 1912)
Zoogonoides viviparus	*Ophiura albida*; rarely *Ophiura texturata* and *Ophiura robusta* (O)	Mostly between arm vertebrae (natural infestation); also within disc (gonads, water vascular system, mesenteries) (experimental infestation)	Fishes: posterior intestine and rectum of plaice, flounder, dab and long rough dab from Øresund	First intermediary host is gastropod *Buccinum undatum*, *O. albida* is the most important second intermediary host. 1 to 30 trematodes ophiuroid^{-1}; up to 250 in experimentally infested ones	North Sea (Kattegat, Øresund)	Køie (1976)

Table 2 (continued)

Trematode	Host	Location in host	Primary host	Remarks	Geographical area	Source
Zoogonus mirus	*Arbacia lixula, Paracentrotus lividus, Sphaerechinus granularis* (E)	In muscles of Aristotle's lantern	Fishes: *Labrus merula* (natural infestation), *Blennius gattorugine* (experimental infestation)	1 to 30 trematodes echinoid^{-1}; heavy infestation with *P. lividus*, slight infestation with *A. lixula*	Mediterranean Sea (Banyuls, Marseille)	Timon-David (1933, 1934, 1936, 1938)
Zoogonus rubellus	*Arbacia punctulata* (E)	Presumably in muscles of Aristotle's lantern	Eel (natural infestation); toadfish (experimental infestation)	First intermediary host gastropod *Nassa obsaleta*; usual second intermediary host: polychete *Nereis virens*. Experimental use of *A. punctulata* as alternative second intermediary host was partly successful	N W Atlantic (Woods Hole)	Stunkard (1941; see also Stunkard 1938)
Zoogonus sp.	*Psammechinus miliaris* (E)	In muscles of Aristotle's lantern	–	1 to 36 trematodes echinoid^{-1}	North Sea (Boulogne, Wimereux)	Stunkard (1941)

[1] Previously identified by Tauson (1917) as *Adolescaria ophiurae*
[2] The parasite has been tentatively ascribed to trematodes by Mortensen; it causes destruction of infested gonads
[3] Described as encysted larvae of cestode (Shipley 1903)
[4] Identified by Cuénot (1892, 1912) as *Cercaria capriciosa*

Agents: Trematoda

Trematodes reported from echinoderms are listed in Table 2. Unidentifed metacercariae were noted by Schneider (1858), in the body cavity of *Holothuria tubulosa;* by Schurig (1906), in the gut of a deep-sea echinoid; by Ohshima (1911), in stomach and mesenchyme of a planktonic holothuroid larva; by Mortensen (1921b), in gonads of the Japanese echinoid *Mespilia globulus;* and by Johnson (1971), in gonads of *Strongylocentrotus purpuratus.*

Echinoderms generally act as second intermediary host (Fig. 6). The echinoderm's reaction to invading cercariae or to encysted metacercariae is largely unknown. According to Prévot (1966a) host tissues form a 'xenocyst' of dense connective tissue around metacercariae (Fig. 7), but Køie (1976) reported that infested ophiuroids do not respond to trematode cysts. Effects of metacercariae on their echinoderm host appear to be rather unimportant. According to Køie (1976), heavily infested *Ophiura albida* tend to autotomize their arms. This is presumably linked to the cysts' location at the joints between the arm vertebrae. One may also suggest that, when heavily infested, the jaw muscles of echinoids become less functional (Table 2; *Zoogonus mirus* and *Zoogonus* sp.); thus the cysts may affect echinoid feeding.

The location of metacercarian cysts (in muscles or within the body wall) may partly explain why relatively few species of echinoderm-infesting trematodes have been recorded. Whatever the cause, it seems rather obvious that echinoderms are very suitable intermediary hosts for marine digenic trematodes. Not only do echinoderms occur frequently in very dense populations, but some of their representatives also form part of the diet of many fishes. As seen in Table 2, most echinoderm-infesting trematodes are known from echinoids and ophiuroids which constitute the most frequent echinoderm prey for fishes. The role of echinoderms as potential vectors of trematode-caused fish diseases requires further attention.

Agents: Nematoda

Rather few nematodes have been reported to occur in echinoderms (e.g. Fig. 8). In addition to the species listed in Table 3, unidentified – and presumably undescribed – nematodes were found inside the host's body (mostly the coelomic cavity): Antarctic asteroids *Hymenaster perspicuus* and *Diplasterias luetkeni* (see Ludwig 1903); echinoids *Echinus esculentus* and *Brissopsis lyrifera* (respectively Shipley 1901, Brattström 1946); holothuroids *Leptosynapta* spp., *Holothuria* spp. and *Aslia lefevrei* (respectively Monticelli 1892, Briot 1906a, Hérouard 1923); and North Sea ophiuroids *Asteronyx loveni* and *Ophiura albida* (respectively Jungersen 1912, Mortensen 1921a).

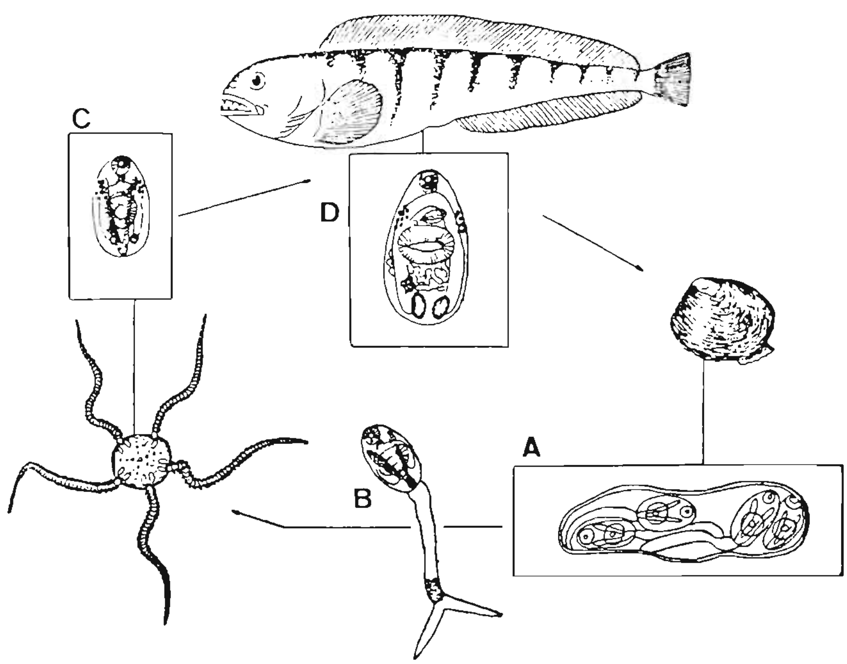

Fig. 6. *Fellodistomum fellis*. Life-cycle of a marine digenic trematode with 2 intermediary hosts: bivalve mollusc *Nucula tenuis* and ophiuroid *Ophiura sarsi*. (A) Redia; (B) cercaria; (C) metacercaria; (D) late metacercaria and adult worm. (After Chubrik 1952)

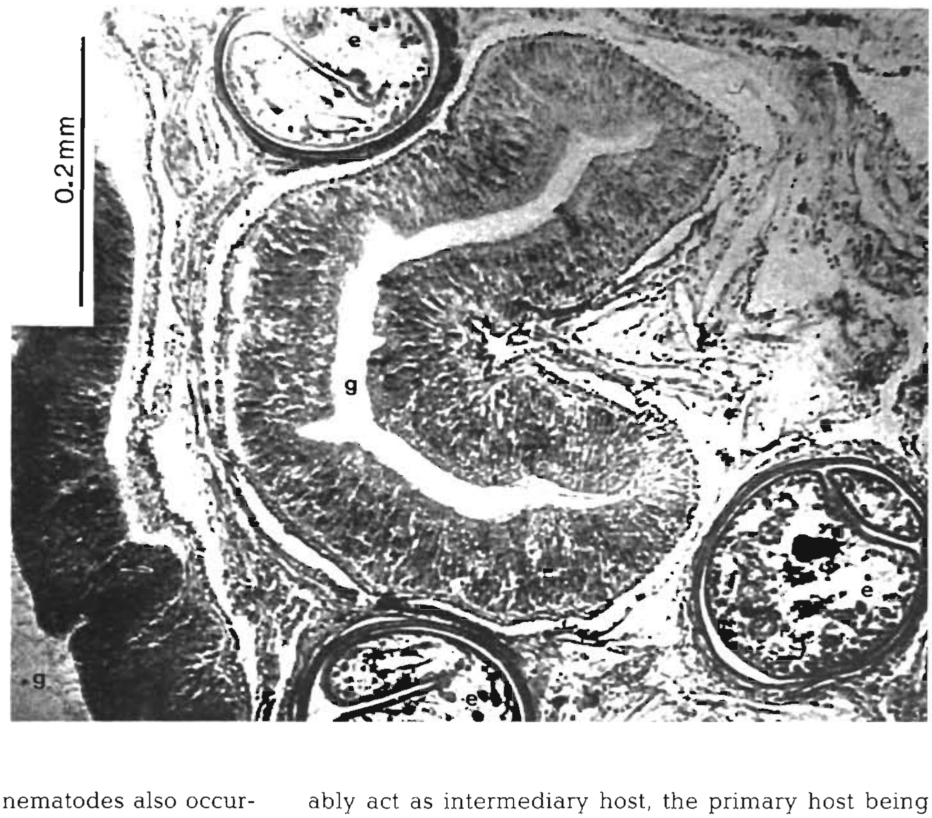

Fig. 7. *Monorchis monorchis* (Trematoda). Metacercariae encysted within connective tissue strings of the calyx of the comatulid crinoid *Antedon mediterranea*. e: encysted metacercariae; g: gut of the crinoid. (After Prévot 1966a)

Intense infestations by juvenile nematodes also occurred within the digestive wall of the abyssal holothuroids *Kolga hyalina*, *Trochostoma thompsoni* and *Elpidia glacialis* (Danielssen & Koren 1882, Massin pers. comm.).

As seen from Table 3 echinoderm-associated nematodes are mostly juveniles. Echinoderms presumably act as intermediary host, the primary host being fishes. This was suggested by Ward (1933) and demonstrated by Pearse & Timm (1971) who identified the primary host of the echinoid parasite *Echinocephalus pseudouncinatus* as the California horned shark *Heterodontus francisci*. Host reactions were noted only by Pearse & Timm (1971) who reported the encystment

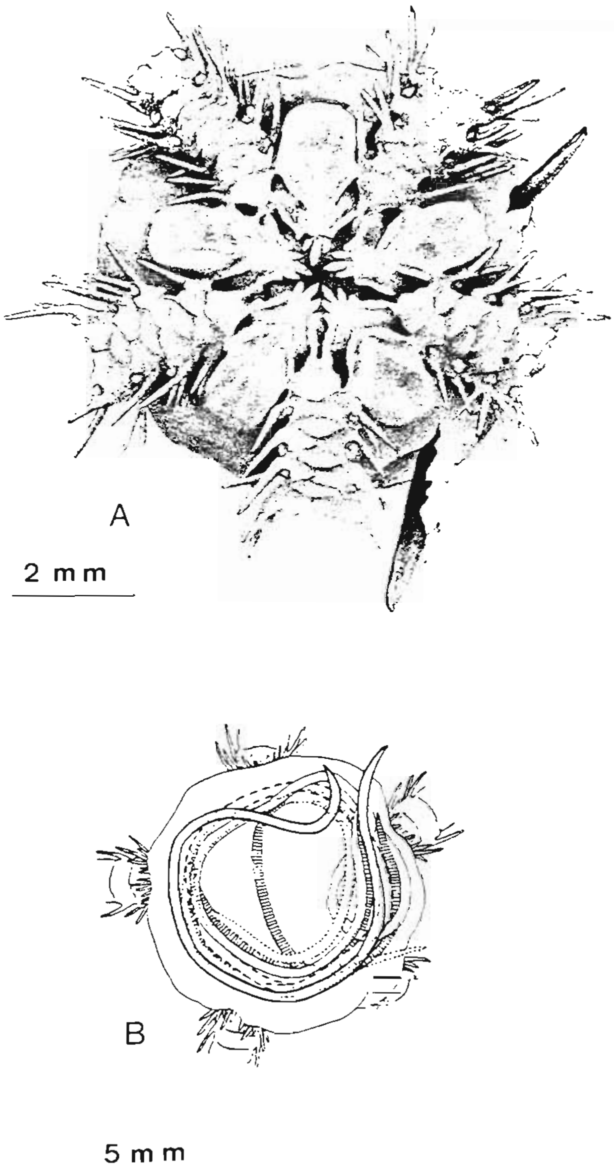

Fig. 8. *Thalassonema ophioctinis,* a nematode parasite of the ophiuroid *Ophiocten amitinum.* (A) Oral view of ophiuroid showing ends of nematode protruding through the wall of disc; (B) 5 nematodes coiled within the ophiuroid body cavity. (After Ward 1933)

of juvenile nematodes within echinoid gonads. The cyst is host-produced and made of dense connective tissue. Effects of nematodes on their hosts are obvious when the worms destroy the echinoderm's body wall, an injury reported by Ludwig (1903), Ward (1933) and Rubstov (1977). Another, less conspicuous, effect was noted by Pearse & Timm (1971) on gonads of *Centrostephanus coronatus:* growing juvenile nematodes progressively invaded the gonadal tubules (small juveniles are confined to the gonad wall) and negatively affected host gametogenesis. Gametogenesis is suppressed in the infested tubules, especially above the parasite, *viz.* in the oral or distal part of the tubule. Pearse & Timm suggested that encysted juveniles block the passage through the tubules of some hormonal substance that regulates echinoid gametogenesis. Hagen (1985)implied that infestation of *Strongylocentrotus droebachiensis* by the nematode *Philotrema* sp. (= *Echinomermella* sp.) could be lethal for the echinoid upon hatching of the juvenile nematodes.

Agents: Mollusca, Gastropoda

Gastropods living symbiotically with echinoderms belong almost exclusively to the family Eulimidae. According to Warén (1984) there are about 800 species (43 genera) of extant eulimids of which all except 2 are associated with echinoderms. Table 4 lists both ecto- and endoparasitic eulimids (species classified as ectoparasites clearly behave as parasites or entertain morphological relations with their host which imply parasitism).

Most ectoparasitic eulimids live attached to the echinoderm's body surface, by either their snout or their proboscis (Vaney 1915, Warén 1984). They feed on the host's tissues or fluids using their proboscis which penetrates more or less deeply into the echinoderm's body wall or crosses it to reach the coelomic cavity, the water-vascular system, or the hemal system. However, unattached ectoparasites also occur, e.g. *Pulicicochlea calamaris* and *Vitreobalcis temnopleuricola* which browse over the epidermis of the echinoids *Echinothrix calamaris* and *Temnopleurus toreumaticus* (Ponder & Gooding 1978, Fujioka 1985, respectively) and *Peastilifer nitidulus* which moves over the entire body surface of *Holothuria atra,* periodically puncturing the body wall of its host (Hoskin & Cheng 1970).

Some attached ectoparasitic eulimids are said to feed exclusively on echinoderm dermal tissues. Among them are those belonging to the gallicole genus *Stilifer* (Tullis & Cheng 1971, Warén 1980a) (Fig. 9), as well as representatives of the genera *Pelseneeria* (Koehler & Vaney 1908) and *Monogamus* (Lützen 1976). These authors reported that the proboscis is inserted into the dermis but they did not discuss the way in which the dermal tissue is ingested. Dermal-tissue-feeding eulimids may induce conspicuous host reactions (Lützen 1976): the formation of swollen areas which are basically disorganized outgrowths of the connective tissue upon which the parasite feed (Fig. 10).

Fluid-feeding ectoparasitic eulimids have also been reported (e.g. Warén 1981c). According to Bacci (1948)

Table 3. Parasitic nematodes from echinoderms (compiled from the sources indicated). Hosts: A, asteroid; E, echinoid; O, ophiuroid

Nematode	Host	Location in host	Remarks	Geographical area	Source
Ananus asteroideus	*Diplopteraster perigrinator* (A)	Coelomic cavity	One nematode in each asteroid arm	Antarctic seas (off Kerguelen Islands)	Rubstov (1977)
Echinocephalus pseudouncinatus	*Arbacia punctulata* (E)	Gonad	Only juvenile nematode observed	NW Atlantic (Woods Hole)	Hopkins (1935), Millemann (1951)
Echinocephalus pseudouncinatus	*Centrostephanus coronata* (E)	Gonads	Most infested echinoids had several juvenile nematodes in each of their 5 gonads (142 infested/213 investigated)	E Pacific (Southern California: Santa Catalina Island)	Pearse & Timm (1971)
Marimermis kerguelensi	*Hippasteria hyadesi* (A)	Coelomic cavity	–	Antarctic seas (off Kerguelen Islands)	Rubstov & Platonova (1974)
Onchaleimus echini	*Echinus esculentus* (E)	Digestive tract	–	–	Leydig (1854)
Philometra grayi	*Echinus esculentus* (E)	Coelomic cavity	1 to 4 nematodes echinoid^{-1}; infestation relatively rare	Around British Isles	Gemmil (1901), Gemmil & von Linstow (1902), Irving (1910), Ritchie (1910, see also Barel & Kramers 1977)
Philometra sp.	*Strongylocentrotus droebachiensis* (E)	Coelomic cavity	Infestation level: 20 30 %	North Sea (Vestfjorden, Norway)	Hagen (1983, 1985)
Thalassonema ephiacanthis	*Ophiacantha antaretica* (O)	Coelomic cavity	–	Antarctic Seas	Rubstov (1985)
Thalassonema ophioctinis	*Ophiocten amitium* (O)	Coelomic cavity	1 to 5 juvenile nematodes ophiuroid^{-1} (4 infested/37 investigated)	SW Indian Ocean (South Africa: Glendower Beacon)	Ward (1933)

the proboscis of *Melanella comatulicola* reaches the coelomic canal of its crinoid host's arm and sucks up coelomic fluid. Cabioch et al. (1978) found that *Balcis alba* – a temporary holothuroid ectoparasite – penetrates the host's body wall via its proboscis. Aquarium observations have shown that the proboscis does not seek out a specific organ or tissue. It moves actively within the holothuroid coelomic cavity and pumps off coelomic fluid. Aquarium observations further revealed that the point of penetration of the proboscis is not restricted to any part of the body surface. In the field however, it was invariably located immediately below the buccal tentacles. Smith (1984) observed that the proboscis of *B. alba* is unfolded when penetrating the holothuroid integument, and that the proboscis epithelium releases secretory material which appears to bring about a rapid loosening of the host's connective tissue. Fluid-feeding was inferred also with *Echineulima* spp., *Ophieulima minima* and *Peastilifer edulis*, as the proboscis of individuals of these species was observed inserted into the host's body cavity

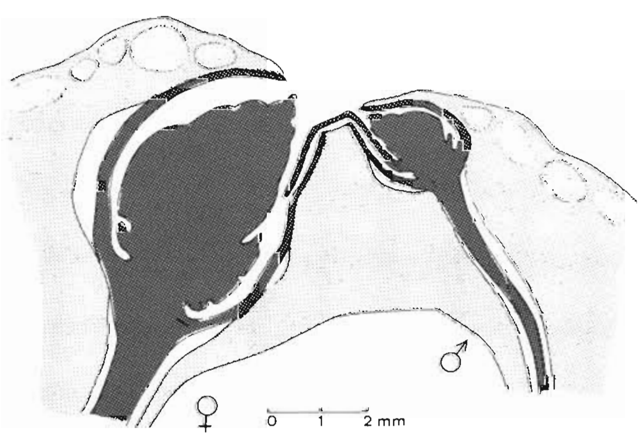

Fig. 9. *Stilifer linckiae*. Position of 2 specimens of a parasitic gastropod in a gall in the arm of the asteroid *Linckia laevigata*. (After Lützen 1972a)

(respectively Lützen & Nielsen 1975, Warén & Sibuet 1981, Hoskin & Warén 1983). Egloff (1966) and Warén (1980a) reported that the proboscis of adult *Thyca crys-*

Table 4. Parasitic gastropods from echinoderms (compiled from the sources indicated). Species names of gastropods according to Warén (1984)

Gastropod	Host	Location in host	Remarks	Geographical area	Source
I. Parasites of crinoids					
Annulobalcis marshalli	*Crotalometra rustica*	Attached between arm ossicles	2 specimens known from single host	New Zealand (off Mayor Island)	Warén (1981a)
Balcis devians	*Antedon bifida*	Attached to base of pinnule	Only 1 specimen found	North Sea (Plymouth)	Fretter (1955)
Eulima ptilocrinida	*Ptilocrinus pinnatus*	Proboscis deeply inserted in side of the crinoid calix	–	NE Pacific (off British Columbia)	Bartsch (1907)
Goodingia varicosa	*Capillaster multiradiatus*	Attached to aboral side of arms	4 specimens known from 2 hosts	NE Indian Ocean (New Guinea)	Lützen (1972b)
Melanella comatulicola	*Antedon mediterraneas*	Attached to pinnules, also to calyx or anal cone	1 to 18 gastropods crinoid^{-1} (27 infested/65 investigated)	Mediterranean Sea (Naples, Banyuls)	Graff (1874); Bacci (1948); Changeux (1956)
Mucronalia capillastericola	*Capillaster multiradiatus*	Attached to the oral side of arms	–	Indian Ocean (Red Sea, Singapore)	Bartsch (1909), Fishelson (1973, 1974)
Tropiometricola sphaeroconchus	*Tropiometra afra macrodiscus*	Galls on arms	–	Japan Sea (Honshu)	Habe (1974, 1976), Warén (1981b)
II. Parasites of holothuroids					
Balcis acicula	*Stichopus chloronotus*	Body surface or coelomic cavity	–	Tropical W Pacific (Fiji, Hawaii, Palao)	Habe (1952)
Balcis alba	*Neopentadactyla mixta*	Body surface, near tentacles	Up to 6 gastropods on single host (aquarium observation)	NE Atlantic (Irish coast)	Cabioch et al. (1978)
Balcis catalinensis	*Holothuria arenicola*	Body surface or stomach	Stomach of infested hosts harbors 9 to 26 gastropods according to holothuroid size; percentage of infestation 66 to 100 % depending on locality	Tropical E Pacific (Mexico: Bay of La Paz)	Brand & Ley (1980)
Balcis intermedia	*Holothuria glaberrima*	Firmly attached to outer body surface	1 to 3 gastropods holothuroid^{-1} (12 infested/35 investigated)	Tropical E Pacific (Mexico: Vera Cruz)	Caso (1968)
Diacolax cucumariae	*Cucumaria mendax*	Parasite protrudes outside host body with its rostrum deeply inserted into the holothuroid's coelomic cavity	Only 1 specimen known	Southern Atlantic (51> 10'S, 64> 15'W)	Mandahl-Barth (1945)
Enteroxenos bouvieri	*Holothuria atra*	Coelomic cavity	–	Tropical W Pacific (New Caledonia)	Risbec (1953)
Enteroxenos oestergeni	*Parastichopus tremulus*	Mostly hanging in coelomic cavity, attached to esophagus, rarely to stomach or intestine. Some live free in coelomic cavity	5 gastropods holothuroid^{-1} (average number) (537 infested/1515 investigated) (Lützen)	North Sea (Scandinavian coast)	Bonnevie (1902), Oestergren (1938), Lützen (1979)
Enteroxenos parastichopoli	*Parastichopus californicus*	Hanging in coelomic cavity, attached to esophagus	Ca 3 gastropods holothuroid^{-1} (average number) (37 infested/244 investigated) (Lutzen)	NE Pacific (Washington: Puget Sound)	Tikasingh (1961, 1962), Kincaid (1964), Lützen (1979)
Entocolax chirodotae	*Chirodata pellucida*	Hanging in coelomic cavity, attached to body wall (anterior part)	–	Sea of Japan	Skarlato (1951)
Entocolax ludwigi	*Myriotrochus rinki*	Hanging in coelomic cavity, attached to body wall (anterior part)	–	Behring Sea (Lorenz Bay)	Voigt (1888)

Table 4 (continued)

Gastropod	Host	Location in host	Remarks	Geographical area	Source
Entocolax rimskykorsacovi	*Myriotrochus mitsukurii*	Hanging in coelomic cavity, attached to intestine	–	Sea of Japan	Ivanov (1945a; quoted from Lützen 1979)
Entocolax schiemenzi	*Chirodota pisani*	Hanging in coelomic cavity, attached to body wall	2 infested holothuroids observed (1 gastropod holothuroid^{-1})	SE Pacific (Chile: Calbuco)	Ludwig (1897, 1898), Voigt (1901)
Entocolax schwanwitschi	*Myriotrochus eurycyclus*	Hanging in coelomic cavity, attached to intestine	1 to 22 gastropods holothuroid^{-1} (10 % of investigated hosts infested; Heding & Mandahl-Barth)	Barents sea (Kola Bay)	Schwanwitsch (1914), Heding & Mandahl-Barth (1938), Andersen (1971)
Entocolax trochodotae	*Trochodota purpurea*	Hanging in coelomic cavity, attached to body wall (anterior part)	–	SW Atlantic (Falkland Islands)	Heding (1934)
Entoconcha mirabilis	*Oestergrenia digitata*	Hanging in coelomic cavity, attached to ventral hemal vessel of intestine	–	Mediterranean Sea	Baur (1864) (see also Koehler 1895, Lützen 1979)
Peastilifer edulis	*Holothuria edulis*	Attached to body surface	–	Tropical W Pacific (Great Barrier Reef)	Hoskin & Warén (1983)
Peastilifer nitidula	*Holothuria atra*	Free on body surface	1 to 5 gastropods holothuroid^{-1} (200 infested/400 investigated)	Tropical W Pacific (Hawaii, NE Australia, New Caledonia)	Hoskin & Cheng (1970); Hoskin & Warén (1983)
Pisolamia brychius	*Oneirophanta mutabilis*	Attached to body surface	26 gastropods collected from 17 infested holothuroids (111 investigated)	NE Atlantic (Bay of Biscay, deep sea)	Bouchet & Lützen (1976, 1980)
Prostifer subpellucida	*Bohadschia argus*, *Holothuria* sp.	Galls in body wall	–	NE Indian Ocean (N Australia: Yonge Reef)	Warén (1980b)
Scalaribalcis angulata	*Holothuria cinerascens*	Galls in body wall	–	SE Pacific (Easter Island)	Mandahl-Barth (1949), Warén (1980b)
Thyonicola americana	*Eupentacta quinquesemita*, *Eupentacta pseudoquinquesemita*	Hanging in coelomic cavity, attached to posterior intestine	Overall incidence of infestation: 41 % (1 to several hundred parasites host^{-1}, Wright; infestation highly variable according to the host populations, Byrne)	NE Pacific (US and Canadian coasts)	Tikasing (1961), Wright (1974), Byrne (1985)
Thyonicola dogieli	*Cucumaria miniata*, *Cucumaria japonica*, *Cucumaria obunca*	Hanging in coelomic cavity, attached to posterior intestine	–	NE Pacific (?)	Ivanov (1945b; quoted from Lützen 1979)
Thyonicola mortenseni	*Thyone serrata*	Hanging in coelomic cavity, attached to posterior intestine	About 40 gastropods in a single holothuroid	SE Indian Ocean (off Cape of Good Hope)	Mandahl-Barth (1941)
Gasterosiphon deimatis	*Deima blackei*	In coelomic cavity; proboscis penetrates the intestine hemal system while siphon opens to outer medium across the host's body wall	Only 2 specimens known from a single host	NE Indian Ocean (Bay of Bengal)	Koehler & Vaney (1903, 1905)
Megadenus cantharelloides	*Stichopus chloronotus*	Presumably attached to digestive wall or body wall	Only 2 specimens known from a single host	Tropical Indian Ocean (Aldabra)	Humphreys & Lützen (1972)
Megadenus holothuricola	*Holothuria mexicana*	Attached to wall of respiratory trees	Only 2 specimens known from a single host	Tropical Atlantic (Bahamas)	Rosén (1910)
Megadenus oneirophantae	*Oneirophanta mutabilis*	Swellings in intestine	The 2 hosts investigated had 3 and 9 gastropods	North Atlantic (deep sea)	Bouchet & Lützen (1980)

Table 4 (continued)

Gastropod	Host	Location in host	Remarks	Geographical area	Source
Megadenus voeltzkowi	*Holothuria pardalis*	Attached to peri-esophagial ring (presumably water-vascular ring)	Only 1 specimen known	Tropical W Indian Ocean (Zanzibar)	Schepman & Nierstrasz (1914)
Megadenus sp.	*Holothuria atra*	Cloaca	1 to 3 gastropods holothuroid^{-1} (8 infested/1359 investigated)	NE Indian Ocean	Jones & James (1970)
Melanella muelleriae	*Actinopyga mauritiana, Holothuria pervicax, Holothuria cinarescens, Holothuria arenicola*	Projecting from body wall	Some individuals infested	Central Indian Ocean (Aldabra)	Sloan et al. (1979)
Molpadicola orientalis	*Molpadia* sp.	Coelomic cavity	–	Okhotsk Sea (deep sea)	Grusov (1957)
Mucronalia variabilis	*Synapta ooplax*	Free on host body surface, or in host digestive tract	–	SW Indian Ocean (Zanzibar)	Vaney (1913), Schepman & Nierstrasz (1914)
Paedophorus dicoelobius	*Eupyrgus pacificus*	In Polian vesicles or respiratory trees	12 gastropods collected from 3 infested holothuroids (80 investigated)	NW Pacific (Peter the Great Bay)	Ivanov (1933, 1937)
III. Parasites of echinoids					
Euchineulima eburnea	*Chaetodiadema granulatum, Astropyga radiata, Astropyga pulvinata, Heterocentrotus mammillatus, Heterocentrotus trigonaria*	Attached to oral side of body surface	1 to 4 gastropods echinoid^{-1}	Tropical Indo-Pacific	Lützen & Nielsen (1975)
Euchineulima mittrei	*Echinothrix diadema, Echinothrix calamaris, Diadema setosum, Diadema mexicanum, Diadema savignyi*	Attached to oral side of body surface	1 to 6 gastropods echinoid^{-1}	Circumtropical	Lützen & Nielsen (1975)
Euchineulima ponderi	*Parasalenia gratiosa*	Attached to peristome	Only 2 specimens from single host	Tropical W Pacific (Great Barrier Reef: Lizard Island)	Warén (1980a)
Luetzenia asthenosoma	*Asthenosoma* sp.	Attached to peristome	Only 2 specimens from single host	SW Pacific (Australia: New South Wales)	Warén (1980b)
Megadenus cysticola[1]	*Stylocidaris tiara*	Galls in primary spines	1 to 7 gastropods echinoid^{-1}	E Indian Ocean (off Ceylon)	Koehler (1924, 1927); Koehler & Vaney (1925)
Monogamus entopodia	*Echinometra mathaei*	Tube feet wall	21 gastropods from 10 infested echinoids	Red Sea (Gulf of Aqaba)	Lützen (1976)
Monogamus interspinea	*Echinometra mathaei*	Buried in skin	2 gastropods from 2 infested echinoids (55 investigated)	SW Indian Ocean (Amboina)	Lützen (1976)
Monogamus parasaleniae	*Parasalenia gratiosa*	Galls in spines	2 gastropods from single host	Tropical Pacific (Tonga Islands)	Warén (1980b)
'*Mucronalia*' sp.	*Stylocidaris tiara, Stereocidaris indica*	Attached to body surface, producing conspicuous test deformations	–	E Indian Ocean (Ceylon, Bay of Bengal)	Koehler (1927)
Pelseenaria media	*Echinus affinis*	Attached to body surface	–	NE Atlantic (off Azores: deep sea)	Koehler & Vaney (1908)
Pelseenaria minor	*Echinus affinis*	Attached to body surface	–	North Sea (Banc de Seine)	Koehler & Vaney (1908)
Pelseenaria profunda	*Genocidaris maculata*	Attached to body surface	11 echinoids infested (several hundred investigated)	NE Atlantic (off Azores: deep sea)	Koehler & Vaney (1908)

Table 4 (continued)

Gastropod	Host	Location in host	Remarks	Geographical area	Source
Pelseenaria stilifera	*Strongylocentrotus droebachiensis, Echinus esculentus*	Attached to body surface	4 gastropods from single host (Ankel)	Baltic Sea (Kristinenberg)	Ankel (1938), Montensen (1940)
Pulicochlea calamaris	*Echinothrix calamaris*	Free on body surface	Rather frequent infestation	Tropical W Pacific (Hawaii, Papua New Guinea, New Caledonia)	Ponder & Gooding (1978)
Pulicochlea fusca	*Diadema setosum*	Free on body surface	Numerous gastropods collected	Tropical W Pacific (Papua New Guinea and adjacent islands)	Ponder & Gooding (1978)
Robillardia cernica	*Echinometra mathaei, Echinometra insularis*	Attached to wall of rectum	1 to 2 gastropods echinoid^{-1} (54 infested/185 investigated)	Indian Ocean (Red Sea, Mauritius, Amboina); SW Pacific (Easter Island)	Gooding & Lützen (1973)
Sabinella infrapatula	*Ogmocidaris benhami*	Attached to body surface, close to periproct	Only 1 individual found	SW Pacific (New Zealand: off Major Island)	Warén (1981a)
Sabinella troglodytes[2]	*Eucidaris tribuloides*	Galls in primary spines	Infestation relatively rare (33 infested/1467 investigated) (McPherson)	Tropical Atlantic (Cape Verde Islands, Florida)	Thiele (1925), Pilsbry (1956), McPherson (1968)
Trochostilifer mortenseni	*Prionocidaris australis*	Galls in primary spines	1 gall with 2 gastropods in each infested echinoid	Tropical W Pacific (New Caledonia)	Warén (1980b)
Vitreobalcis temnopleuricola	*Temnopleurus toreumaticus*	Attached to body surface	Infestation rate varied from 5.3 to 50 % depending on host population and season	Inland Sea (Japan)	Fujioka & Habe (1983), Fujioka (1984, 1985)
IV. Parasites of asteroids					
Apicalia palmipedis	*Palmipes rosaceus*	Attached to body surface (oral side)	1 to 2 gastropods per infested asteroid	NW Indian Ocean (Ceylan, Singapore)	Koehler (1910), Koehler & Vaney (1912), Warén (1981b)
Asterolamia cingulatus	*Craspidaster hesperus*	Attached to side of body (marginal plates)	–	NW Pacific (Hong Kong)	Warén (1980b)
Asterolamia hians	*Astropecten indicus*	Attached to aboral body surface, among paxillae	–	Tropical Pacific (Great Barrier Reef)	Warén (1980b)
Asterophila japonica	*Pedicellaster magister, Ctenodiscus crispatus, Leptasterias polaris, Leptasterias arctica*	Coelomic cavity attached to the body wall	10 to 29 % asteroids infested depending on locality (Hoberg et al.)	N Pacific (off Japan, Asiatic coast, Alaska)	Randall & Heath (1911), Grusov (1965), Hoberg et al (1980)
Paramegadenus arrhynchus	*Anthenoides rugulosus*	Open gall on body surface (aboral side)	–	Tropical W Pacific (Philippines: near Cebu)	Kanazawa & Habe (1979), Warén (1980b)
Paramegadenus scutellicola	*Stellaster incei*	On tube feet	–	Tropical W Pacific (Great Barrier Reef)	Warén (1980b)
Parvioris equestris	*Stellaster incei*	Attached to body surface (marginal plates)	–	Indo-West Pacific (Andaman Islands, Java Sea, Great Barrier Reef)	Koehler (1910), Koehler & Vaney (1912), Warén (1981b)
Parvioris mortoni[3]	*Archaster typicus*	Attached to body surface (aboral or lateral side)	1 to 4 gastropods asteroid^{-1} (75 infested/396 investigated)	NW Pacific (Hong Kong)	Morton (1976), Warén (1981b)
Stilifer astericola	*Heliaster cumingi*	Gall in body wall	Up to 5 gastropods asteroid^{-1}	E Pacific (Galapagos)	Lützen (1972a)
Stilifer inflatus	*Linckia laevigata*	Gall in body wall	Only 1 specimen known	Tropical W Pacific (Great Barrier Reef)	Warén (1980a)
Stilifer linckiae	*Linckia multifora*	Gall in body wall	1 to 2 galls asteroid^{-1} (54 infested/665 investigated) (Davis)	Tropical Indo-West Pacific (Oman Sea, Ceylan, Great Barrier Reef, Hawaii)	Sarasin & Sarasin (1887), Davis (1967), Tullis & Cheng (1971), Lützen (1972a), Warén (1980a)

Table 4 (continued)

Gastropod	Host	Location in host	Remarks	Geographical area	Source
Stilifer ophidiastericola	*Ophidiaster cribrarius, Ophidiaster lorioli, Ophidiaster confestus, Ophidiaster granifer*	Gall in body wall	–	Tropical Indo-Pacific (Indonesia to SW Japan)	Habe (1976)
Stilifer ovoideus[4]	*Certonardoa semiregularis, Ophidiaster granifer, Tamaria dubiosa*	Gall in body wall	–	Tropical Indo-Pacific (Indonesia to SW Japan)	Hirase (1927, 1932), Lützen (1972a), Habe (1976)
Stilifer utinomi	*Linckia guildingi, Linckia laevigata*	Gall in body wall	–	Tropical W Pacific (Great Barier Reef, SW Japan)	Habe (1952), Lützen (1972a)
Stilifer sp.	*Ophidiaster granifer*	Gall in body wall	Up to 4 gastropods asteroid^{-1} (26 investigated/8 infested)	Tropical W Pacific (Guam)	Yamaguchi & Lucas (1984)
Thyca callista	*Phataria unifascialis, Pharia pyramidata*	Attached to body surface	1 to 3 gastropods asteroid^{-1}, infestation rather rare	Tropical E Pacific (coast of Mexico and central America)	Berry (1959), Shasky (1961), Bertsch (1975)
Thyca cristallina	*Linckia multifora, Linckia laevigata*	Attached to body surface	Infestation rate variable: from 14 to 62 % depending on localities	Tropical Indo-West Pacific (Indonesia, Papua New Guinea, Great Barrier Reet, Fiji)	Egloff (1966), Elder (1979), Warén (1980a), Bouillon & Jangoux (1984)
Thyca ectoconcha	*Linckia multifora, Linckia guildingi*	Attached to body surface	Infestation rate ca 3 % (MacNae & Kalk)	Indian Ocean (Ceylon, Mozambique coast)	Sarasin & Sarasin (1887), MacNae & Kalk (1962)
Thyca stellasteris	*Stellaster equestris*	Attached to body surface	–	Indian Ocean (Andaman Islands, West Australia, Red Sea)	Koehler (1910), Koehler & Vaney (1912), Warén (1980a)
V. Parasites of ophiuroids					
Fuscapex ophiocanthicola	*Ophiocantha* sp.	Attached to body surface (oral side), covering bursal slits	3 gastropods from single host	SW Pacific (off Kermadec Islands, deep sea)	Warén (1981a)
Ophieulima armigeri	*Ophiomusium armigerum*	Attached to body surface (oral side), near bursal slits	Up to 5 gastropods ophiuroid^{-1} (23 infested/more than 3000 investigated)	NW Atlantic (off Virginia)	Warén & Carney (1981)
Ophieulima fuscoapicata	*Ophiactis profundi*	Attached to body surface (radial shields)	2 gastropods from single host	SW Pacific (off Kermadec Islands, deep sea)	Warén (1981a)
Ophieulima minima	*Ophiactis abyssicola*	Attached to body surface (aboral side)	–	N Atlantic (deep-sea: off Ireland, off Iceland, Bay of Biscay)	Warén & Sibuet (1981)
Ophioarachnicola biformis	*Ophioarachna incrassata*	Attached to body surface (oral side of arm)	Only 1 gastropod found	Tropical W Pacific (Salomon Islands)	Warén (1980b)
Punctifera ophiomoerae	*Ophiomoeris projecta*	Open galls (aboral side of the disc)	2 gastropods from single host	SW Pacific (off Kermadec Islands: deep sea)	Warén (1981a)

[1] Generic position unclear (see Warén 1980b)
[2] Identified as *Mucronalia nidorum* by Pilsbry (1956) and McPherson (1968) (see Warén 1980b)
[3] Identified as *Eulima shoplandi* by Morton (1976) (see Warén 1981b)
[4] Identified as *Stilifer celebensis* by Hirase (1927, 1932) (see Warén 1980a)

tallina passes through the asteroid's body wall to reach the radial (water-vascular) canal. One may wonder, however, if the ambulacral or coelomic fluids together with coelomocytes can ensure sufficient nutrients for parasites. As noted by Lützen & Nielsen (1975), additional predation upon internal organs presumably occurs. Other fluid-feeding eulimids insert their proboscis into the hemal lacunae of holothuroids (their hemal system has energy-rich contents). Such a symbiosis has been documented by Bouchet & Lützen (1976, 1980) who studied relations between *Pisolamia brychius* and the deep-sea holothuroid *Oneirophanta mutabilis* (Fig. 11). Ectoparasitic gastropods may also feed directly on internal organs (i.e. digestive organs);

Fig. 10. *Monogamus entopodia.* Male and female (with 3 egg capsules) of a parasitic gastropod in a transformed tube foot of the echinoid *Echinometra mathaei.* (After Lützen 1976)

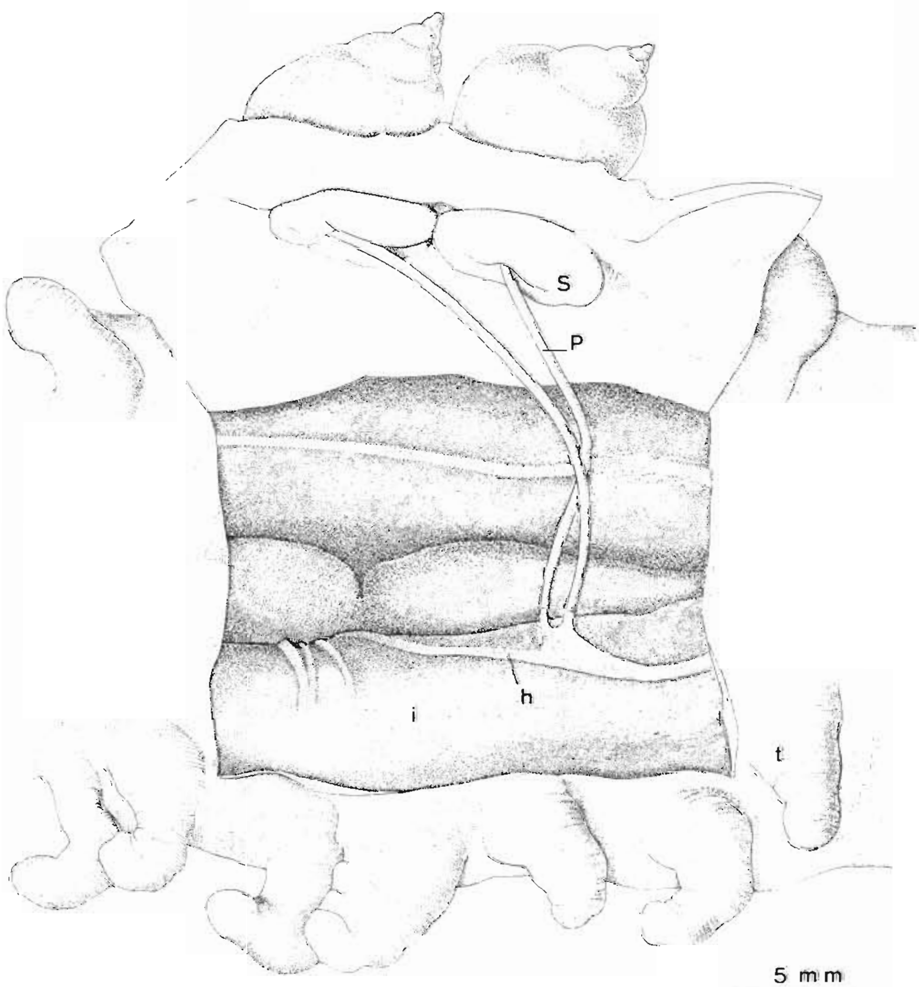

Fig. 11. *Pisolamia brychius,* a blood-sucking gastropod parasite of the deep-sea holothuroid *Oneirophanta mutabilis.* i: intestine of holothuroid; h: hemal vessel of holothuroid; P: proboscis; S: snout; t: tube-foot. (After Bouchet & Lützen 1976)

this has been suggested by Warén (1980b) for 2 species of *Asterolamia*.

Little information is available on the feeding biology of intradigestive eulimids. An unusual feeding habit was reported for 2 unattached species of holothuroid-associated snails, *Mucronalia variabilis* and *Balcis catalinensis*, symbiotic with *Synapta ooplax* and *Holothuria arenicola* (respectively Vaney 1913, Brand & Ley 1980). The snails move freely on the body surface of their host but may enter the host's digestive tract in order to feed by puncturing the digestive wall. The presence of several individuals of *B. catalinensis* in the stomach of *H. arenicola* does not cause significant effects on the absorption efficiency of the host (Brand & Ley 1980). Gooding & Lützen (1973) provide evidence that *Robillardia cernica*, which inhabits the rectum of the echinoid *Echinometra insularis*, feeds on host gonads, using its elongated proboscis. *Megadenus oneirophantae* lives in cyst-like swellings in the digestive wall of a deep-sea holothuroid. According to Bouchet & Lützen (1980), it supposedly feeds on content of the digestive hemal lacunae. A most unusual feeding habit is that of *Megadenus cantharelloides*: it attaches to the digestive wall of *Stichopus chloronotus* – the visceral mass of the parasite protruding into the digestive cavity – with its proboscis crossing both digestive wall and coelomic cavity and penetrating the host's body wall, in order to feed on dermal tissue (Humphreys & Lützen 1972).

Oral feeding by intracoelomic eulimids has been inferred only for *Gasterosiphon deimatis* which inserts its proboscis into digestive hemal lacunae (Koehler & Vaney 1903). Other intracoelomic forms (*viz.* the aberrant *Entocolax* and allied genera, i.e., the former Entoconchidae; e.g. Tikasingh & Pratt 1961, Lützen 1968, 1979, Byrne 1985) are believed to derive their energy from the host's coelomic fluid by direct absorption of nutrients through their body wall. Intracoelomic parasitic gastropods occur only in asteroids (eulimid genus *Asterophila*) and in holothuroids (eulimid genera *Diacolax, Enteroxenox, Entoconcha, Gasterosiphon, Molpadicola, Paedophorus, Thyonicola*) (Table 4; Fig. 12 & 13). Most of them are attached to the coelomic side of either digestive tract or body wall of their host by a hollow stalk or by a siphon. Although some authors have suggested that feeding could take place through that duct (Heath 1910, Tikasingh 1962), such a hypothesis has not been accepted generally.

Harmful effects of parasitic gastropods are not restricted to their feeding activities. Ectoparasitic eulimids may produce clearly definable attachment lesions (Lützen & Nielsen 1975, Lützen 1976, Elder 1979). Host reactions produce conspicuous soft swellings of the dermal tissue in parasitized echinoid tube feet (Lützen 1976) and in infested crinoid pinnules

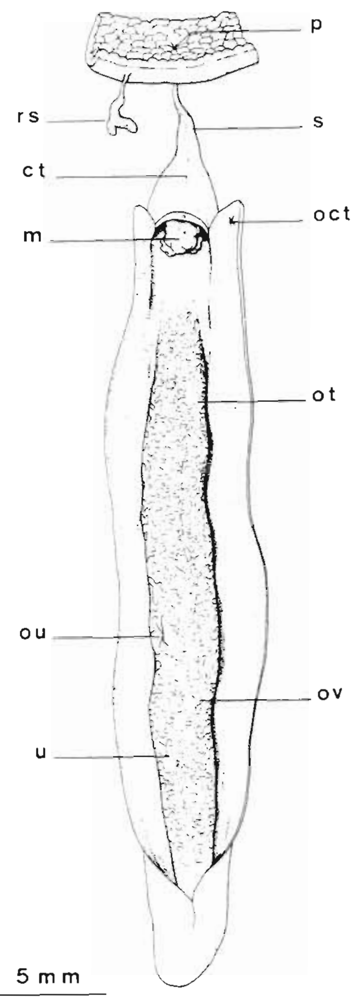

Fig. 12. *Enteroxenos oestergreni*, an intracoelomic gastropod parasite of the holothuroid *Stichopus tremulus*. ct: ciliated tubule; m: modified male implanted in receptaculum masculinum; p: pit in the wall of host's esophagus; rs: remains of stalk of another individual; s: stalk; oct: opening of ciliated tubule; ot: ovarian tubules; ou: opening of uterus; ov: oviduct; u: uterus. (After Lützen 1979)

(Bacci 1948, Fretter 1955). Gallicole eulimids (e.g. *Stilifer* spp., *Puctifera ophiomoerae, Tropiometricola sphaeroconchus*; Table 4) produce spectacular hard swellings or galls in the body wall of asteroids, ophiuroids and crinoids. These galls resemble those induced by myzostomids on crinoid arms. Whether or not they involve particular modifications of host skeleton has not been investigated. According to Davis (1967) *S. linckiae* suppresses the autotomizing capability of the asteroid arm in which it is located. Other gallicole species modify primary spines of cidaroid echinoids (Koehler & Vaney 1925, Koehler 1927, Pilsbry 1956, Warén 1980b). In most cases the snails bore into the distal part of spines which then enlarges. Sometimes spine-dwelling gastropods appear to

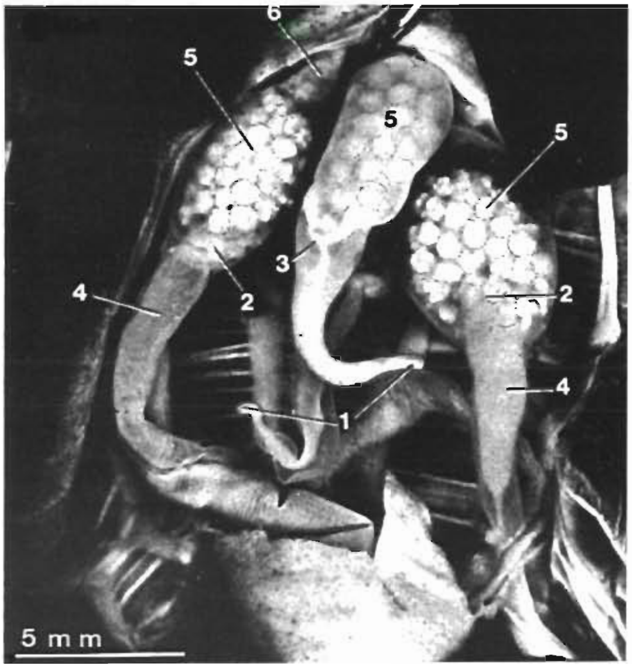

Fig. 13. *Myriotrochus rinki*. Holothuroid parasitized by 3 ovigerous specimens of the intracoelomic gastropod *Entocolax ludwigi*. 1: oral end; 2: ovary; 3: oviduct; 4: part of the body containing intestine; 5: pseudopallium with egg capsules; 6: siphon. (After Lützen 1979)

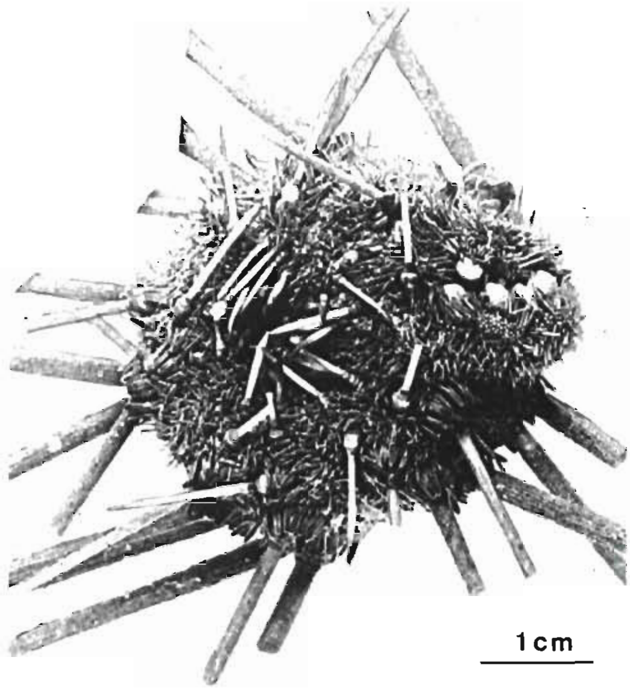

Fig. 14. *Stereocidaris tricarinata*. Oral view of cidaroid echinoid showing test deformations produced by parasitic gastropods (*Stilifer* sp.). (After Döderlein 1906)

induce a conspicuous regression of the host skeleton, the spine being reduced to its swollen basal part (Koehler & Vaney 1925). Nothing is known of the feeding habits of these spine-associated eulimids. The host skeleton is also affected by non-gallicole species. Fishelson (1973, 1974) reported that *Mucronalia capillastericola* attaches to crinoid arms and causes a prononced twist and degeneration of the arm skeleton above the place of attachment. Koehler & Vaney (1912) and Vaney (1913) drew attention to the particular gaps occurring in the marginal skeleton of asteroids infested by *Parvioris equestris*. According to them, the absence of marginal plates is the consequence of the early attachment of parasitic snails which had inhibited skeletal growth. Eulimids parasitizing cidaroid echinoids may induce conspicuous test swellings implying deformations of the test skeleton (Döderlein 1906, Koehler 1927) (Fig. 14). Pyriform test deformations caused by a *Mucronalia*-like species were reported by Mortensen (1943) for the echinoid *Salmacis bicolor*. According to Byrne (1985) the intracoelomic eulimid *Thyonicola americana* for the most part did not appear to affect its holothuroid host *Eupentacta quinquesemita*. She noted, however, that heavily parasitized hosts could be detected by their apparent inability to keep their tentacles fully retracted and that, in some cases of mass infestation, the parasites may interfere with the use of the holothuroid's tentacles for suspension feeding.

That parasitic eulimids may produce partial castration of the host was considered by Gooding & Lützen (1973). They found the size of the gonads in echinoids infested by *Robillardia cernica* to be usually smaller than in uninfested echinoids. According to Heding & Mandahl-Barth (1938), intracoelomic *Entocolax* spp. may castrate their host; in contrast Lützen (1979) reported that *Enteroxenox oestergreni* is not likely to influence the fecundity of the holothuroid *Parastichopus tremulus*.

Few host reactions have been reported from echinoderms parasitized by gastropods, except the induction of dermal swellings and galls. This does not imply of course that echinoderms do not react to snail infestations. A particular host-parasite relation must be noted, namely the constant presence of a host envelope surrounding the intracoelomic entoconchid eulimids from holothuroids (Vaney 1913, Tikasingh 1962, Wright 1974). This envelope consists of an outer mesothelial layer and of an inner connective tissue layer. Considering the unsolved question of entoconchid nutrition, it would be worth investigating whether or not host hemal lacunae occur within the inner layer of the envelope. A similar envelope was found around individuals of *Asterophila japonica*, an intracoelomic entoconchid from asteroids (Hoberg et al. 1980). The mesothelial cover surrounding intracoelomic gastropods should occur presumably around any part of the parasitic snail which permanently crosses the coelomic cavity (a mesothelial covering of the parasite proboscis has been noticed by Warén [1980b] for *Asterolamia hians*).

So far there are practically no data indicating that parasitism by eulimids can seriously alter the echinoderm life cycle. Eulimids do not – or only exceptionally – produce host castration, nor do they have any measurable effect on the biology of their host, not even when mass infestations occur. (It may be presumed, however, that eulimids involving skeletal deformations are rather constraining for the echinoderms.) All these facts suggest that the ecological consequences of parasitism due to eulimid gastropods may be quite limited for the echinoderms involved.

Agents: Mollusca, Bivalvia

Bivalves associated with echinoderms have been recorded almost exclusively from echinoids and holothuroids (Boss 1965). Most echinoid-associated bivalves are simply attached to the host's spines through byssal threads (e.g. Gage 1966, Barel & Kramers 1977). However, Bernard (1895, 1896) described a species *(Scioberetia australis)* which lives in the brood pouches of the Antarctic spatangoid *Abatus cavernosus*. According to Bernard, only females of *A. cavernosus* without *S. australis* had developing embryos in their brood pouches. This might imply that the bivalves inhibit the development of embryos or prevent their settlement in brood pouches.

A few bivalve species live ectosymbiotically on synaptid holothuroids. They attach to the synaptid body surface through their spade-shaped creeping foot. It is generally agreed that creeping bivalves do not affect their host, except that they may slightly erode its skin (Anthony 1916, Popham 1940). Three species of endosymbiotic bivalves have been reported from holothuroids. There is almost no information on the relations between *Holothuria fuscocineria* and *Entovalva major* which is said to supposedly live in the holothuroid cloaca (Bruun 1938). *Entovalva mirabilis* and *Cycladoconcha amboinensis* inhabit small pouches dug into the digestive wall of synaptid holothuroids (respectively Voeltzkow 1890, Schepman & Nierstrasz 1914; Spärck 1931). These 3 species are presumably typical suspension feeders.

Agents: Entoprocta

A few Loxosomatidae appear to be relatively common symbiotes of crinoids and ophiuroids, especially in polar and subpolar areas. Mortensen (1910, 1911) reported the occurrence of *Loxosomella antedonis* on cirri of *Poliometra prolixa* and *Heliometra glacialis*. *L. antedonis* appears to secrete a cement on the surface of the crinoid cirri and then attach to its host. The ophiuroid *Amphiocnida pilosa* often supports individuals of *Loxosoma* sp. attached to various places of the oral side of its disc and arms (Mortensen 1924). According to Moyano & Wendt (1981) the entoproct *Barentsia discreta* may attach to the bivium of the Antarctic holothuroid *Psolus charcoti*.

Agents: Bryozoa

Bryozoans may be found firmly attached to the body surface of comatulid crinoids, mostly to their arms or cirri. They were recorded by Mortensen (1910) on *Poliometra prolixa*, and by Gautier (1959) on *Leptometra phalangium*. According to Gautier, about 25 % of the crinoid population was infested (6 different species of bryozoans were associated with *L. phalangium*). Moyano & Wendt (1981) report that up to 4 different species of Bryozoa were seen attached to the outer body surface of the Antarctic holothuroid *Psolus charcoti*.

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