Vol. 3: 59-83, 1987 | DISEASES OF AQUATIC ORGANISMS Dis. aquat. Org. | Published October 14

REVIEW

Diseases of Echinodermata. III. Agents metazoans (Annelida to Pisces)

Michel Jangoux

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

ABSTRACT· Parasitic myzostomids mostly infest crinoids but a few are known from asteroids and ophiuroids; they are either gallicole, cysticole or endoparasitic. Although many copepods have been said to be ectoparasitic on echinoderms, this has been proven for only a few species. Some copepods are known to induce gall formation in the spines of echinoids or in the body wall of ophiuroids; others have been found to infest either the bursae or gonads of ophiuroids. Ascothoracid cirripeds were reported either as ectoparasites on crinoids and ophiuroids or as endoparasites in the body cavity of asteroids and spatangoid echinoids. Echinoderm castration by copepods and ascothoracids was reported several times in the literature. Parasitic crabs mostly occur on or in echinoids. Ectoparasitic crabs often exert major effects and may kill their host; gut-inhabiting species may produce conspicuous host deformation. Some species of carapid fishes are known to live either temporarily or permanently in the body cavity of holothuroids and asteroids. Carapid infestations do not seem to seriously affect the echinoderms except for species permanently inhabiting the host's coelom. Parasitic associations between echinoderms and polychaetes, tardigrads, barnacles, amphipods, tanaidaceans, acarians, pycnogonids and insects have been casually reported in the literature.

INTRODUCTION

The present paper is the third of a series of 4 that review the diseases of Echinodermata. It considers the disease agents belonging to the Annelida (Polychaeta and Myzostomida), Tardigrada, Crustacea (Copepoda, Cirripedia and Malacostraca), Arachnida, Pycnogonida, Insecta and Pisces. (Other metazoan agents have been considered in Part II; Jangoux 1987b). As discussed in Part I (Jangoux 1987a), 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 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: Annelida, Polychaeta

Symbiotic polychaetes were reviewed by Paris (1955) and Clark (1956), both authors stating that these polychaetes rarely affect echinoderms. While numerous species are known to live ectocommensally on echinoderms, only 3 cases of parasitism have been reported with polychaetes. According to Monticelli (1892) the eunicid *Ophryotrocha puerilis* occurs in the coelomic cavity of the holothuroid *Ocnus planci* from Naples (Italy). Ganapati & Radhakrishna (1962) noted that 50% of the holothuroid *Molpadia* sp. investigated harbored the small hesionid *Ancistrocyllis* sp. either in the digestive tract or respiratory trees. The only case of unequivocal parasitism is that of the lumbrinereid *Ophiuricola cynips* which forms myzostomid-like galls at the base of the arms of the deep-sea ophiuroid *Ophioglypha tumulosa* (Ludwig 1905). According to Ludwig, the galls are rather large and partly protrude into the host's coelomic cavity.

Agents: Annelida, Myzostomida

The class Myzostomida (about 110 described species) occupies a peculiar place among echinoderm symbiotes. They are aberrant annelids with a small flattened body several mm in length. Their most extraordinary feature is their intimate association with echinoderms; in fact there are no known free-living

0177-5103/87/0003/0059/$ 03.00

Table 1. Parasitic myzostomids from echinoderms (compiled from the sources indicated). Myzostomid classification and species names according to Jägersten (1940). Hosts: A, asteroid; C, crinoid; O, ophiuroid. Records of conspicuous deformations caused by unidentified myzostomids were reported on several occasions (e.g. Carpenter 1889 for *Acitinometra notata)*. Speel & Dearborn (1983) noted that each of the 96 individuals of *Promochocrinus kerguelensis* they observed harbored 1 to 3 myzostomid cysts

Myzostomid	Host	Location on/in host	Remarks	Geographical area	Source
I. Proboscidea					
Myzostomum beardi	*Perissometra flexilis* (C)	Galls on arms	Only 1 worm gall^{-1}	NE Indian Ocean (Arafura Sea)	Graff (1887)
Myzostomum belli	*Endoxocrinus alternicirrus* (C)	Galls at base of arms	Only 1 worm gall^{-1}	NW Pacific (S Philippines)	Wheeler (1896)
Myzostomum cryptopodium	*Metacrinus interruptus* (C)	Galls on arms	–	Indian Ocean (Bay of Bengal?)	Wheeler (1896)
Myzostomum deformator	*Endoxocrinus alternicirrus* (C)	Galls in pinnules	2 worms (♂, ♀) gall^{-1}	NW Pacific (SE Philippines)	Graff (1884)
Myzostomum eremita	*Metacrinus moseleyi* (C)	Galls at base of arms and pinnules	Only 1 worms gall^{-1}	NW Pacific (SE Philippines)	Wheeler (1896)
Myzostomum pentacrini	*Endoxocrinus alternicirrus* (C)	Slight galls extending into 3 to 6 arm segments	1 to 3 worms gall^{-1}	NW Pacific (SE Philippines)	Graff (1884)
Myzostomum tenuispinum	*Pachylometra inaequalis, Perissometra flexilis, Charitometra basicurva, Charitometra incisa* (C)	Conspicuous galls extending into 2 to 3 arms segments	2 worms (♂, ♀) gall^{-1}; several galls on each infested host	Tropical W Pacific (SE Philippines, Fiji Islands and Kermadec Island)	Graff (1884)
Myzostomum willemoesi	*Pachylometra inaequalis, Perissometra flexilis, Charitometra basicurva* (C)	Galls in pinnules	2 worms (♂, ♀) gall^{-1})	Tropical W Pacific (Fiji and Kermadec Islands); NE Indian Ocean (Arafura Sea)	Graff (1884, 1887)
II. Pharyngidea					
Asteriomyzostomum asteriae	*Sclerasterias neglecta, Sclerasterias richardi* (A)	Hypertrophied pyloric caeca (proximal part of the caeca)	1 to 3 worms infested asteroid^{-1}	Mediterranean sea	Marenzeller (1895a, b), Stummer-Traunfels (1903)
Asteriomyzostomum fisheri	*Tosia leptoceramus* (A)	Coelomic cavity, loosely attached to body wall	–	Tropical E Pacific (off South California)	Wheeler (1904)
Cystimyzostomum clarki	*Metacrinus rotundus* (C)	Subcutaneous cysts on underside of arms	1 worm cyst^{-1}; up to 7 cysts host^{-1}	N. Pacific (Japan: Sagami Sea)	McClendon (1906)
Cystimyzostomum cysticolum	*Anthometra adriani, Amphimetra discoidea, Comactinia meridionalis* (C)	Subcutaneous calcified cysts on upper side of arms	2 worms (♂, ♀) cyst^{-1}; no more than 1 cyst on each host arm	Cosmopolitan (Caribbean; Red Sea; Aru Islands; Eastern coast of Japan)	Graff (1884), McClendon (1906), Remscheid (1916), Fishelson (1973, 1974)
Cystimyzostomum ijimai	*Tropiometra macrodiscus, Capillaster multiradiatus* (C)	Subcutaneous cyst on calyx (upper surface)	1 to 2 worms cyst^{-1}	Indo W Pacific (Sagami Sea, Japan; Red Sea)	Hara & Okada (1921), Fishelson (1973, 1974)
Cystimyzostomum inflator	*Neocomatella pulchella, Adelometra angus tiradia* (C)	Subcutaneous calcified cysts at arm base (upper surface)	2 worms (♂, ♀) cyst^{-1}	Circumtropical (Papua; Barbados)	Graff (1884)
Cystimyzostomum murrayi	*Horaeometra duplex, Stiremetra breviradia, Adelometra angustiradia* (C)	Subcutaneous stalked and calcified cysts on calyx (upper surface)	2 worms (♂, ♀) cyst^{-1}	Circumtropical (Papua; Kermadec Islands; Barbados)	Graff (1884)
Cystimyzostomum platypus	*Comanthina schlegeli* (C)	Subcutaneous cyst on calyx (upper surface)	1 worm cyst^{-1}	W Pacific (Philippines: off Samboangan)	Graff (1887)
Cystimyzostomum robustum	*Metacrinus rotundus* (C)	Cysts on arms	1 worm cyst^{-1}	NW Pacific (Japan: Sagami Sea)	Hara & Okada (1921)
Cystimyzostomum taeniatum	*Zygometra mertoni* (C)	Juvenile in cysts on pinnules, adults free-living	1 worm cyst^{-1}	NW Indian Ocean (Aru Islands)	Remscheid (1916)

Table 1 (continued)

Myzostomid	Host	Location on/in host	Remarks	Geographical area	Source
Mesomyzostoma katoi	*Comanthus japonicus* (C)	Gonads (genital pinnules)	–	Sea of Japan	Okada (1933)
Mesomyzostoma reichenspergi	*Amphimetra discoidea* (C)	Coelomic cavity of arms	Only 2 individuals known	NW Indian Ocean (Aru Islands)	Remscheid (1916)
Protomyzostomum astrocladi	*Astrocladus coniferus* (O)	Encysted in gonads	–	NW Pacific (Sagami Sea)	Fedotov (1925)
Protomyzostomum polynephris	*Gorgonocephalus arcticus, Gorgonocephalus eucnemis, Gorgonocephalus caput-medusae* (O)	Bursae and gonads	10 to 20 worms host^{-1}	North Sea (Scandinavian coast); Barents Sea	Fedotov (1912, 1914, 1916), Barel & Kramers (1977)
Protomyzostomum sagamiense	*Gorgonocephalus* sp. (O)	Bursae and gonads	–	NW Pacific (Sagami Sea)	Okada (1922)
Pulvinomyzostomum pulvinar	*Leptometra phalangium, Antedon bifida* (C)	Digestive tract	Infestation level: 10 to 20 % (Jägersten)	Mediterranean (Banyuls; Naples); NE Atlantic (Roscoff)	Prouho (1892), Wheeler (1896), Jägersten (1940), Barel & Kramers (1977)

myzostomids, nor is there any species associated with other phyla. Myzostomids mostly infest crinoids, but a few are known from asteroids and ophiuroids. Myzostomids are highly differentiated, both morphologically and ecologically. Their almost obligatory association with crinoids (they even infested now extinct crinoids; e.g. Meyer & Ausich 1983, Arendt 1985) suggests that they are an ancient group which evolved together with crinoids. Myzostomids may be considered a unique case of 'symbiogenesis' involving a whole class of organisms (e.g. Clark 1921, Stummer-Traunfels 1926, Prenant 1959).

About 25 species of myzostomids have been recorded as echinoderm parasites (Table 1), the remaining species being frequently referred to 'free-living'. However, these latter species are ectocommensals which generally live unattached on the echinoderm body surface. As pointed out by Stummer-Traunfels (1926), 3 types of parasitic myzostomids may be distinguished depending on whether they are gallicole, cysticole or endoparasitic. Endoparasitic species feed on the host's tissues, while cysticole and gallicole species are suspension feeders which divert the water current produced by the host's ambulacra (galls and cysts are most often located near the ambulacral grooves and always have 2 apertures allowing passage of directional water-currents) (Prenant 1959). With rather few exceptions (e.g. *Cystomyzostomum ijimai* and *Mesomyzostoma katoi*; respectively Fishelson 1974, Okada 1933), parasitic myzostomids mostly infest bathyal echinoderms (in 200 to 1200 m water depth; Stummer-Traunfels 1926). This fact explains why these parasitoses have been so anecdotically documented.

Gallicole species belong to the genus *Myzostomum*. They dig into the dermal tissue of crinoids arms or pinnules (Fig. 1A, B) and build more or less spacious intradermal cavities, always located under skeletal ossicles. The cavities sometimes are very complicated, with internal partitions (e.g. in *Myzostomum tenuispinum*; Graff 1884). Myzostomid galls often harbor a pair of individuals. Gallicole species were termed 'deformative Arten' by Stummer-Traunfels (1926); they induce conspicuous deformation of the host's ossicles which considerably enlarge and adjust their shape to that of the myzostomid's shelter (Graff 1884, Wheeler 1896, Stummer-Traunfels 1926). Cysticole species belong to the genus *Cystimyzostomum*; they behave differently in that they build remarkable stalked or unstalked cysts which are always subcutaneous (i.e. located outside the host's skeleton) and protrude into the external medium (Fig. 1C). In many cases the cyst wall is reinforced by a pavement of minute skeletal plates (Graff 1884, Stummer-Traunfels 1926). Both gallicole and cysticole myzostomids induce major host reactions affecting the crinoid skeleton either by modifying size and shape of skeletal ossicles or by inducing the formation of additional skeletal plates. Such host reactions invite further investigations.

Among the 8 species of endoparasitic myzosotomids, 4 infest ophiuroid or crinoid gonads (respectively *Protomyzostomum* spp. and *Mesomyzostoma katoi*). Gonad-infesting myzostomids cause at least partial castration of their host. Fedotov (1916) reported that *P. polynephris* infests the gonads of its ophiuroid host by rupturing the wall of the bursae. Infestation may be very intense (up to 119 myzostomids per host) and the

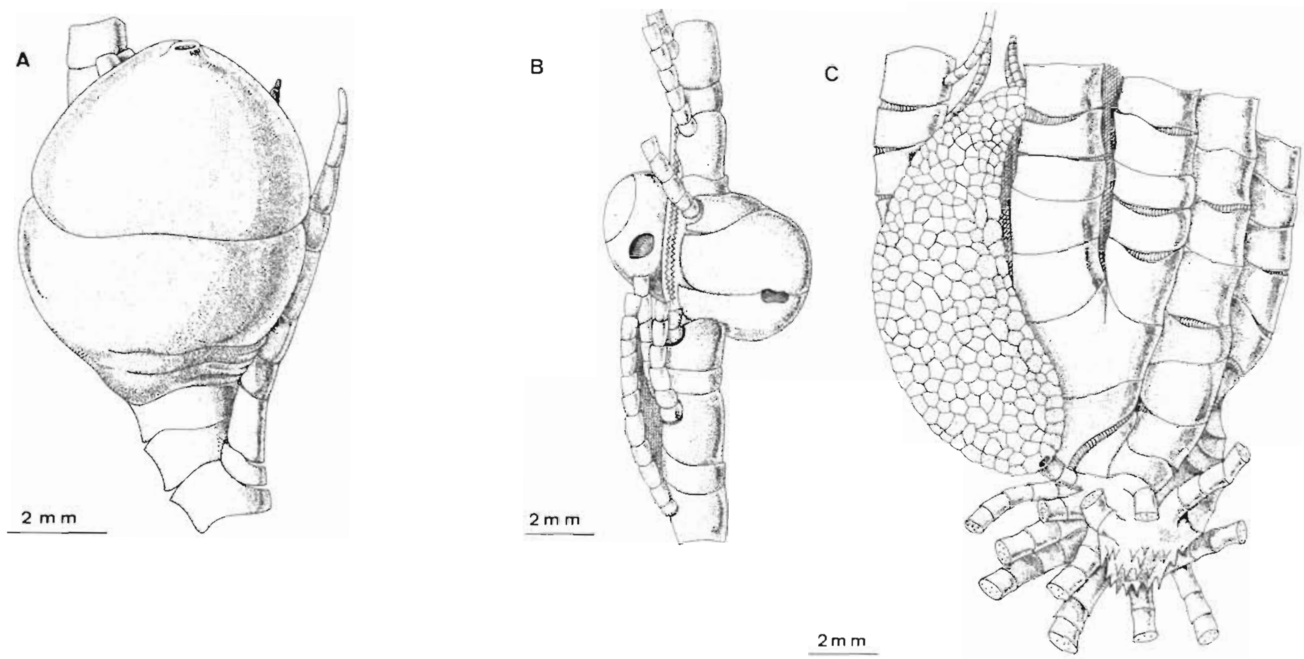

Fig. 1 Gallicole and cysticole myzostomids of crinoids. (A) *Myzostomum deformator.* Gall in the pinnules of *Endoxocrinus alternicirrus;* (B) *Myzostomum tenuispinum.* Gall in the arms of *Pachylometra inaequalis;* (C) *Cystomyzostomum murrayi.* Cyst on the arms of *Stiremetra breviradiata.* (Redrawn from Graff 1884)

parasites ingest germ cells causing direct castration of the gonads. The host reacts by progressively encysting each parasite by a thick layer of dense connective tissue in which minute calcareous ossicles are seen. Fedotov suggested moreover that germ cell dedifferentiation may also occur.

According to Remscheid (1916), *Mesomyzostoma reichenspergi* infests gonads, while according to Prenant (1959) it affects only the arm coelom of its crinoid host and feeds on coelomocytes. *Asteriomyzostomum asteriae* (Fig. 2) is said to feed on the host's digestive contents; its occurrence supposedly increases the propensity of asteroids to shed their arms (Marenzeller 1895a, b). *Pulvinomyzostomum pulvinar* might be more properly classified as 'semi-parasitic'. It inhabits the crinoid's digestive tract (anterior part) living intimately attached to the host's digestive epithelium without causing injury but diverting the flow of food particles entering the crinoid's mouth (Prenant 1959, West & West 1976).

Agents: Tardigrada

The tardigrade *Tetrakentron synaptae* lives attached to the body surface of the synaptid a holothuroid *Leptosynapta galliennei* (Cuénot 1892, 1912, Van der Land 1975, Kristensen 1980). This symbiosis has been reported only from Brittany, France (Roscoff and adjoining areas) where it is common. Very high infestation rates occur in various populations, *viz.* 45, 80 and even 100% (respectively Barel & Kramers 1970, Kristensen 1980, Cuénot 1912). The number of *T. synaptae* per holothuroid is highly variable; it ranges from 2 to 3 up to 270 individuals (respectively Cuénot 1912, Kristensen 1980). The latter author noted that infestation occurs only from May to October (eggs and juveniles are seen in June and July). Kristensen presented photographic evidence that *T. synaptae* punctures the epidermal cells of *L. galliennei* and sucks out their contents; such behavior indicates a parasitic nature of the tardigrade-holothuroid association. Another tardigrade, *Actinarchus doryphorus,* occurs on the body surface of the small European clypeasteroid echinoid *Echinocyamus pusillus.* According to Schulz (1935), *A. doryphorus* is a facultative parasite.

Agents: Crustacea, Copepoda

There is little information regarding the relations between echinoderms and closely associated copepods. This is paradoxical given the high numbers of copepods recorded as echinoderm symbiotes (e.g. Humes 1980a, 1986, Stock 1968b). Table 2 lists species demonstrated or presumed to be parasites. Although many ectoparasitic copepods of echinoderms have been reported in the literature, the parasitic nature of these associations has been proven for only 4 species, *viz. Cancerilla tubulata, Scottomyzon gibberum, Asterocheres lilljeborgi,* and *Ophiopsyllus reductus* (respectively Carton 1968, Röttger 1969, Röttger et al. 1972, Emson et al. 1985). *A. lilljeborgi* is not particularly adaptated to parasitic life. It is a motile copepod which uses its siphon-shaped mouth to feed on the skin of the asteroid *Henricia sanguinolenta. S. gibberum* mainly lives on or near the pedicellarial rosettes of *Asterias rubens* where it seems to feed more deeply in the host tissues (Fig. 3). *O. reductus* lives firmly attached to its ophiuroid host and feeds on surface tissues. As for endoparasitic species, Pyefinch (1940) concluded that *Ophioica asymmetrica* found in the genital bursae of ophiuroids does not feed on the host's tissues, and Changeux (1961) reported – based on casual observations – that the intracoelomic species *Allantogynus delamarei* 'browses' on the holothuroid's mesothelium.

Host reactions against several species of parasitic copepods have been documented. Parasitism by *Scottomyzon gibberum* induces the infested asteroid to produce dermal outgrowths which progressively embed the copepods (Röttger 1969). Ophiuroid hosts tend to produce a fibrous, sometimes calcified cyst around symbiotes which live in their bursae (Pyefinch 1940, Heegard 1951). However, encystment does not occur with all bursal-infesting species (Stephensen 1935a). Mortensen (1933) recorded unidentified copepods inducing gall formation in the dorsal wall of both *Ophiomitrella corynephora* and *O. hamata.* Paterson (1958) reported that cysts, presumably produced by the host, form around the intracoelomic copepod *Cucumaricola notabilis.* According to him, small spherical or oval cysts contain juvenile parasites. These cysts are attached to the coelomic wall either near the circumpharyngeal calcareous ring or on the cloaca near the insertion of the respiratory trees; large amorphous cysts containing mature copepods lie detached in the coelomic cavity. Jungersen (1914) reported that the ophiuroid *Asteronyx loveni* produces cysts around intracoelomic copepods. These cysts are attached on the ophiuroid's coelomic wall. Other intracoelomic copepods have been noted to live often 'free in the coelomic cavity' without seemingly inducing any host reaction (e.g. intracoelomic copepods of holothuroids). However, some bursal- or coelom-infesting copepods may produce conspicuous swellings of the body wall of ophiuroids. These swellings follow the outline of the parasite and do not result from a particular host reaction (Mortensen & Stephensen 1918, Stephensen 1933, Goudey-Perrière 1979).

Copepods have been found to induce gall formation in the spines of echinothurid echinoids by Hansen (1902), Stephensen (1935b) and Stock (1968a). According to Stock, the galls consist of loose calcareous material and always occur in the middle part of the spines. Galls contain a pigmented ampula in which lives a single copepod. Another gallicole copepod, *Pionodesmotes phormosomae,* occurs inside the echinoid *Hygrosoma petersi* (Bonnier 1898, Koehler 1898, see also Mortensen 1935) (Fig. 4). *P. phormosomae* lives in conspicuous inner galls located in the oral part of the host's coelomic cavity. The spherical, calcified galls correspond morphologically to intracoelomic outgrowths of the echinoid body wall. Each gall opens on the host's outer body surface by a slit measuring 1 to 2 mm in length. The slit is protected by the spines of the echinoid. At least 1 large female copepod was found in each gall. According to Bonnier (1898) the copepod does not prey on host tissues and obtains its food mostly from the outside through the slit in the gall. Mortensen (1935) reported that empty galls progressively disappear: the slit enlarges, then the gall wall normalizes, and finally new outer appendages develop.

The way in which intracoelomic copepods infest their host has been considered only for holothuroids and asteroids. According to Paterson (1958) and Changeux (1961), holothuroids are infested by larval copepods which cross the digestive wall either at the level of the esophagus or at the level of the cloaca and respiratory trees. In asteroids, Carton (1974) showed that male *Botulosoma endoarrhenum* penetrate the coelom of *Echinaster purpureus* through the respiratory papulae. Female *B. endoarrhenum* actually settle and grow in papulae, living in a kind of integumental cavity.

The effects of parasitic copepods on the biology of echinoderms have been considered practically only for *Amphiurophilus amphiurae* which parasitizes the genital bursae of a brooding ophiuroid *Amphipholis squamata* (e.g Goudey-Perrière 1979, 1980). The author reported that the occurrence of the parasite does not affect the host's gonads but decreases the host's fecundity by inhibiting the development of embryos incubated in the ophiuroid genital bursae. Such inhibition could result from competition for food between parasite and embryos. Gonad destruction occurred, however, in the ophiuroids *Ophiomitrella clavigera* and *O. corynephora* parasitized by an unidentified copepod (Mortensen 1933). According to Emson et al. (1985), parasitic copepods on the ophiuroid *Ophiocomella ophiactoides* may decrease the tendency of the host to undergo fission (cross-disc division).

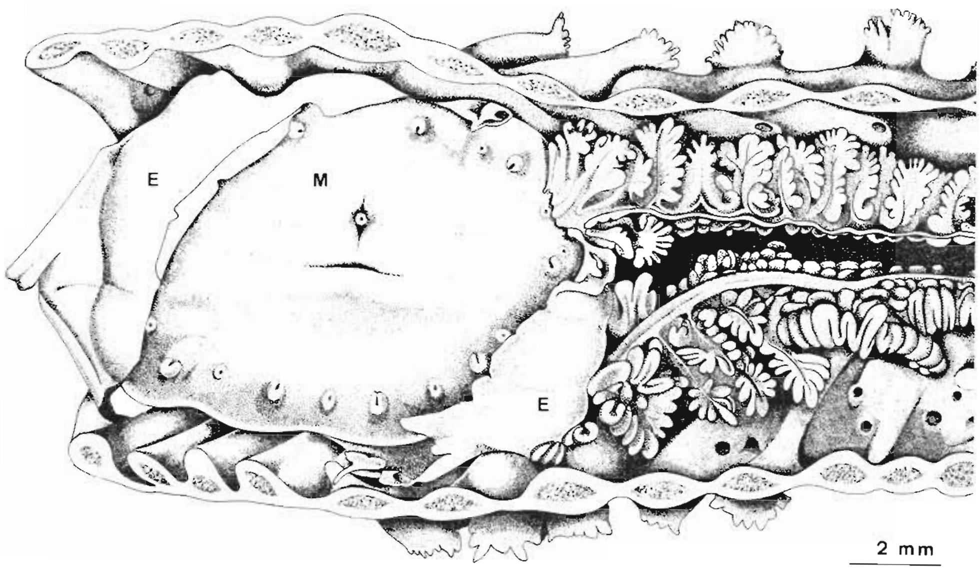

Fig. 2. *Asteriomyzostomum asteriae*, a myzostomid parasite of the pyloric caeca of the asteroid *Sclerasterias neglecta*. E: enlarged and deformed part of pyloric caeca harboring the parasite; M: myzostomid. (Redrawn from Stummer-Traunfels 1903; slightly modified)

Agents: Crustacea, Cirripedia

Thoracid cirripeds (i.e. barnacles) sometimes attach to the outer body surface of some species of regular echinoids (*Lytechninus anamesus, Tetrapygus niger, Stomopneustes variolaris, Strongylocentrotus* spp.) and clypeasteroids *(Dendraster excentricus, Rotula orbiculus)*. Either of 2 situations may occur: (1) the barnacle attaches only loosely to the host's body wall overlaping an intact cutaneous epithelium (Moore & McPherson 1963); (2) the barnacle is strongly attached to the echninoid test, the epidermis being destroyed (Giltay 1934, Dartevelle 1940, Boolootian 1958, 1964, Strachan 1970, Ganapati & Sastry 1972, Hurley 1973, Bay-Schmith & Jana 1977). Barnacles *Balanus* spp. have been noticed on echinoderms mainly by casual observations, except for the association between *D. excentricus* and *Balanus concavus pacificus* detailed by Boolootian (1964). There appears to be general agreement that the activity of pedicellariae and spines would avoid settlement of barnacle cyprids on the echinoid body wall (e.g Campbell & Rainbow 1977) However, the reviewer believes that the failure of cyprids to settle results basically from the occurrence of a cutaneous epithelium which prevents larval fixation. Presumably cyprid settlement can occur only when the echinoderm body wall is wounded, or when the epiderm is eroded for some mechanical or pathological reasons (such as bald-sea-urchin disease; Jangoux 1987a). Barnacles of the genera *Pachylasma, Scalpellum* and *Verruca* have been noticed firmly attached to the stem or cirri of several species of stalked crinoids (Clark 1921).

Ascothoracida are 'naked barnacles' that parasitize octorallian corals and echinoderms, except holothuroids. They have been found either as ectoparasites on crinoids and ophiuroids (genera *Ascothorax, Parascothorax, Waginella*) or as endoparasites in the coelomic cavity of asteroids and spatangoid echinoids (genera *Ctenosculum, Dendrogaster, Ulophysema*) (Table 3). *Waginella metacrinicola* lives attached to the crinoid calyx where it forms a conspicuous depression. It feeds on the 'fluids' of the host by piercing the body wall with its oral appendages (Okada 1926). Ophiuroid-associated ascothoracids infest the genital bursae producing marked swellings of part of the host disc (Fig. 5). According to Wagin (1946) *Ascothorax ophioctenis* feeds on the cells of the bursal wall and probably also on the coelomic fluid of the host. As for intracoelomic ascothoracids, Brattström (1947) concluded that *Ulophysema oeresundense* directly absorbs nutrients from the echinoid's coelomic fluid, while Wagin (1976) believed that coelomocytes form the bulk of the diet of *Dendrogaster* spp. (Fig. 6).

Echinoderms react against intracoelomic ascothoracids by forming a host envelope that surrounds the mantle of the parasite. According to Wagin (1946), this envelope consists of coelomocytes and covers even the mantle opening which consequently is continually cleaned and smoothed by the ascothoracid's anterior appendages; Wagin claimed that such appendage activity actually corresponds to the normal way of obtaining food by intracoelomic *Dendrogaster* species. However, investigations by Bresciani & Jespersen (1985) on *Ulophysema oeresundense*, parasitic in the coelom of *Echinocardium cordatum*, showed that the envelope is made of choanocyte-like cells and that consequently it should originate from host mesothelium. A conspicuous host reaction also occurs in *Parascothorax sinagodoides* which lives attached in the bursal cavity near the bursal slit of

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

Copepod	Host	Location in host	Remarks	Geographical area	Source
I. Harpacticoida					
Metis holothuriae	*Actinopyga agassizi* (H)	Coelomic cavity	–	Tropical Atlantic (Bahamas)	Edwards (1891), Humes (1980a)
Tisbe furcata	*Ocnus planci* (H)	Coelomic cavity	Almost 100 % of holothuroids investigated were infested (Monticelli)	Mediterranean Sea (Naples)	Monticelli (1892); Humes (1980a)
Tisbe holothuriae	*Holothuria stellati* (H)	Digestive tract (anterior part)	–	Mediterranean Sea (Banyuls)	Humes (1957)
II. Cyclopodia					
Allantogynus delamarei	*Holothuria tubulosa, Holothuria poli, Holothuria stellati* (H)	Anterior part of coelomic cavity fixed on mesothelium (occur also in wall of pharynx, gonads, tentacular ampullae, or Polian vesicles)	*H. tubulosa* and *H. stellati*: about 2 copepods holothuroid^{-1} (82 infested/117 investigated); *H. poli* is only occasional host	Mediterranean Sea (Banyuls, Villefranche)	Changeux (1958, 1961), Stock & Kleeton (1963, Humes (1980a)
Amphiurophilus amphiurae	*Amphipholis squamata* (O)	Bursae	About 12 % infested ophiuroids in Roscoff (Goudey-Perrière)	NE Atlantic (Roscoff); North Sea (Bergen); NW Atlantic (Woods Hole region)	Fewkes (1887, 1888), Hérouard (1906), Bocquet (1952), Masson (1965), Goudey-Perrière (1979, 1980)
Asterocheres lilljeborgi	*Henricia sanguinolenta* (A)	Free on outer body surface	Up to 24 copepods asteroid^{-1}	NE Atlantic (Swedish coast: Gullmarfjord)	Röttger et al. (1972), Brun (1976)
Botulosoma endoarrhenum	*Echinaster purpureus* (A)	Respiratory papulae (♀ copepod); coelomic cavity (♂ copepod)	Several dozen copepods asteroid^{-1}	SW Indian Ocean (Madagascar: Tuléar)	Carton (1974)
Calvocheres engeli	*Hygrosoma hoplacantha* (E)	Galls on spine at adoral side	Two infested echinoids with 6 and 3 copepods, respectively	NE Indian Ocean (off Celebes, Timor Sea)	Stock (1968a)
Calvocheres globosus	*Calveriosoma gracile, Sperosoma quincunciale* (E)	Galls on secondary spines or on spines of adoral side	Not more than 1 ♀ copepod gall^{-1} (2 and 5 galls observed on 2 infested hosts)	N Indo-Pacific (off Philippines; in Halmaheira Sea; off SE Japan)	Hansen (1902), Stephensen (1935b), Stock (1968a)
Calvocheres oblongus	*Hygrosoma petersi* (E)	Galls on spines	–	N Pacific (SE of Japan)	Stephensen (1935b)
Calypsarion carinatum	*Stichopus monotuberculatus* (H)	Internal	1 ♂ copepod ejected from host upon collection	NW Indian Ocean (Ethiopia: Dahlak Archipelago)	Stock (1968b), Humes (1980a)
Calypsarion leprum	*Actinopyga mauritania, Actinopyga miliaris, Actinopyga lecanora* (H)	Internal	*A. miliaris* is most common host (76 copepods – 43 ♂ and 33 ♀ – collected from 726 hosts)	SW Indian Ocean (Madagascar: Nossy-Bé)	Humes & Ho (1969), Humes (1980a)
Calypsarion sentosum	*Bohadschia marmorata* (H)	Internal	8 copepods (5 ♂, 3 ♀) collected from 8 hosts	SW Indian Ocean (Madagascar: Nossy-Bé)	Humes & Ho (1969), Humes (1980a)
Calypsina changeuxi	*Holothuria tubulosa, Holothuria stellati* (H)	Esophagus and gonoduct	–	Mediterranean (Banyuls)	Changeux (1961), Stock & Kleeton (1963), Humes (1980a)
Cancerilla tubulata	*Amphipholis squamata* (O)	Attached to outer body surface	Infestation rate ca 10 % (Giard)	NE Atlantic (Brittany; North Sea)	Giard (1887), Carton (1968)

Table 2 (continued)

Copepod	Host	Location in host	Remarks	Geographical area	Source
Chauliolobion bulbosum	*Actinopyga echinites*, *Actinopyga obesa* (H)	Internal	*A. echinites*: 11 copepods (4 ♀, 7 ♂) from 72 hosts; *A. obesa*: 21 copepods (4 ♀, 17 ♂) from 1 host	Tropical W Pacific (New Caledonia: Nouméa)	Humes (1975, 1980a)
Chauliolobion foliaceum	*Holothuria atra* (H)	Coelomic cavity	11 copepods (5 ♂, 6 ♀) collected	N Indian Ocean (Gulf of Mannar)	Ummerkutty (1970)
Clavisodalis dilatatus	*Diadema setosum* (E)	Esophagus	43 copepods collected from 65 echinoids	New Caledonia	Dojiri & Humes (1982)
Clavisodalis salmacidis	*Salmacis belli* (E)	Mouth and esophagus	4 copepods	Moreton Bay (Queensland)	Humes (1980b), Dojiri & Humes (1982)
Clavisodalis sentifer	*Diadema setosum* (E)	Esophagus	4 copepods collected from 17 echinoids	Moreton Bay (Queensland), Ambon	Dojiri & Humes (1982)
Collocheres elegans	*Ophiocomina nigra* (O)	Attached to arm base	Up to 5 copepods per ophiuroid (infestation increases with host size)	Firth of Clyde (Scotland)	Gorzula (1978)
Collocherides astroboae	*Astroboa nuda*, *Astroboa albatrossi* (O)	Stomach	*A. nuda*: 2 infested individuals with respectively 29 (23 ♀, 6 ♂) and more than 100 copepods; *A. albatrossi*: 1 infested individual with 25 copepods (16 ♀, 6 ♂)	Red Sea (Eilat; Dahlate Archipelago); SE Indian Ocean (Java Sea)	Stock (1971)
Cucumariocola notabilis	*Cucumaria frauenfeldi* (H)	Coelomic cavity (free cysts lying in the cavity)	Of 337 investigated holothuroids, 63 were infested by 1 to 4 cysts	SW Indian Ocean (Cape Town Province)	Paterson (1958)
Dichelina phormosomae	*Phormosoma bursarium*, *Phormosoma verticillatum*, *Paraphormosoma alternans* (E)	Digestive tract	2 copepods (1 ♂, 1 ♀) taken from 1 individual of each host species	NW Pacific (Philippines: off Mindanao)	Stephensen (1933, 1935b)
Dichelina seticauda	*Hygrosoma hoplacantha* (E)	Internal	5 ♀ copepods taken from 1 echinoid	NE Indian Ocean (Celebes: off Menado)	Stock (1968c)
Diogenella deichmannae	*Holothuria arenicola* (H)	Internal	43 copepods (4 ♂, 39 ♀) collected from 88 individuals	Tropical Atlantic (Barbados)	Humes & Ho (1970), Humes (1980a)
Diogenella seticauda	*Holothuria surinamensis*, *Holothuria impatiens*, *Holothuria arenicola* (H)	Internal	23 copepods from 2 holothuroids (Stock 1968); 5 copepods (1 ♂, 4 ♀) from 47 holothuroids	Tropical Atlantic (Puerto Rico)	Stock (1968b), Humes & Ho (1970), Humes (1980a)

Table 2 (continued)

Copepod	Host	Location in host	Remarks	Geographical area	Source
Diogenella spinicauda	*Holothuria mexicana, Actinopyga agassizi* (H)	Internal (ejected from *H. mexicana*; Stock)	2 copepods (1 ♂, 1 ♀) from *H. mexicana* (Stock); 46 copepods (22 ♂, 24 ♀) from 119 *H. mexicana*, 50 copepods (32 ♂, 18 ♀) from 62 *A. agassizi* (Humes & Ho)	Tropical Atlantic (Curaçao, Bahamas, Jamaica, Puerto Rico)	Stock (1968b), Humes & Ho (1970), Humes (1980a)
Diogenidium deforme	*Holothuria glaberrima, Holothuria arenicola, Holothuria mexicana* (H)	Internal (ejected from *H. glaberrima*; Stock)	2 copepods (1 ♂, 1 ♀) from 1 *H. glaberrima* (Stock); 7 copepods (1 ♂, 6 ♀) from 87 *H. arenicola*, and 5 copepods (2 ♂, 3 ♀) from 24 *H. mexicana*	Tropical Atlantic (Puerto Rico, Barbados, Bahamas)	Stock (1968b), Humes & Ho (1971), Humes (1980a)
Diogenidium nasutum	*Actinopyga agassizi, Holothuria mexicana, Holothuria grisea* (H)	Coelomic cavity	9 copepods (5 ♂, 4 ♀) from 3 *H. mexicana* (Stock); 9 copepods (4 ♂, 5 ♀) from 69 *A. agassizi*, 10 copepods (4 ♂, 6 ♀) from 29 *H. mexicana*, and 6 copepods (4 ♂, 2 ♀) from 11 *H. grisea* (Humes & Ho)	Tropical Atlantic (Bahamas, Curaçao, Jamaica, Puerto Rico)	Edwards (1891), Stock (1968b), Humes & Ho (1971), Humes (1980a)
Diogenidium spinulosum	*Isostichopus badionotus* (H)	Internal (ejected from host; Stock)	1 ♂ copepod from 1 holothuroid (Stock); 4 copepods (2 ♂, 2 ♀) from 17 holothuroids (Humes)	Tropical Atlantic (Puerto Rico, Jamaica)	Stock (1968b), Humes & Ho (1971), Humes (1980a)
Diogenidium tectum	*Actinopyga agassizi* (H)	Internal	3 ♂ copepods from 64 holothuroids	Tropical Atlantic (Jamaica, Bahamas)	Humes & Ho (1971), Humes (1980a)
Echinosocius gulicolus	*Diadema setosum* (E)	Esophagus	85 copepods collected from 65 echinoids	New Caledonia	Dojiri & Humes (1982)
Enterognathus comatulae	*Antedon mediterranea, Antedon bifida* (C)	Digestive tract, rarely in coelomic cavity	11 copepods, (2 ♂, 9 ♀) from 12 *A. mediterranea* (Changeux & Delamare Deboutteville)	Mediterranean Sea (Banyuls, Naples); NE Atlantic (Dublin, Plymouth)	Giesbrecht (1900), Grainger (1950), Changeux & Delamare-Deboutteville (1956), Stock (1959)
Enterognathus lateripes	*Decametra chadwicki, Heterometra savignyi, Oligometra serripinna* (C)	Digestive tract	Not more than 4 copepods found	Indian Ocean (Red Sea)	Stock (1966)
Lecanurius intestinalis	*Actinopyga lecanora* (H)	Digestive tract	–	NW Pacific, (Philippines: Bohol Island)	Kossmann (1877, quoted by Stock 1968b)
Lecanurius kossmannianus	*Actinopyga lecanora, Actinopyga mulleri* (H)	Internal	14 copepods (7 ♂, 7 ♀) from 11 *A. lecanora* and 8 copepods (4 ♂, 4 ♀) from 205 *A. mulleri*	SW Indian Ocean (Madagascar: Nossy-Bé)	Humes (1968)
Lecanurius planifrontalis	*Actinopyga echinites, Actinopyga miliaris* (H)	Digestive tract (posterior part)	3 copepods (2 ♂, 1 ♀) from 3 *A. echinites*	Tropical W Pacific (New Caledonia; Great Barrier Reef)	Humes (1980a)
Lernaeosaccus ophiacanthae	*Ophiacantha disjuncta* (O)	Coelomic cavity (presumably)	Only 1 individual found	Antarctic seas (Palmer Archipelago)	Heegard (1951)

Table 2 (continued)

Copepod	Host	Location in host	Remarks	Geographical area	Source
Lichothuria mandibularis	*Holothuria atra, Holothuria scabra, Holothuria nobilis, Holothuria fuscopunctata* (H)	Internal (ejected from host; Stock)	4 copepods (2 ♂, 2 ♀) from 12 *H. atra* (Stock); 188 copepods (54 ♂, 134 ♀) from 470 *H. scabra*, 19 copepods (6 ♂, 13 ♀) from 24 *H. nobilis*, 139 copepods (34 ♂, 105 ♀) from 345 *H. atra*, and 1 ♂ copepod from *H. fuscopunctata* (Humes & Ho)	W Indian Ocean (Red Sea: Eilat; Madagascar Nossy-Bé)	Stock (1968b), Humes & Ho (1969), Humes 1980a
Ophioika appendiculata	*Ophiomitrella calvigera, Ophiacantha bidentata* (O)	Bursae, forming swelling of host's tissue	1 to 3 copepods host^{-1} (no more than 1 bursa infested host^{-1})	N Atlantic (S of Greenland, S of Iceland, W of Hebrides)	Stephensen (1935b, 1940)
Ophioika asymmetrica	*Ophiacantha imago* (O)	Bursae, forming slight swelling of host disc	Each of the 2 infested ophiuroids investigated had a pair (♂, ♀) of copepods encysted in 1 of their bursae	Antarctic seas	Pyefinch (1940)
Ophioika ophiacanthae	*Ophiacantha severa* (O)	Bursae, forming swelling of host disc	Only 1 ♀ copepod found	SE Indian Ocean (Bali Sea)	Stephensen (1933)
Ophioika tenuibrachia	*Ophiacantha vivipara, Ophiacantha disjuncta* (O)	Bursae (presumably)	8 copepods found	Antarctic seas (South Georgia; Adelaide Land)	Heegaard (1951)
Ophiopsyllus reductus	*Ophiocomella ophiactoides* (O)	Oral and lateral parts of arm base	40 to 65 % of host population parasitized depending on period of year. Usually 1 to 3 copepods ophiuroid^{-1}	Jamaica	Emson et al. (1985)
Pinnodesmotes phormosomae	*Hygrosoma petersi*[1] (E)	Intracoelomic galls	1 or 2 (♂, ♀) copepods gall^{-1}	NE Atlantic (Azores)	Koehler (1898), Bonnier (1898)
Scottomyzon gibberum	*Asterias rubens* (A)	Galls in rosettes of pedicellariae	Most asteroids are infested; 4 to 175 copepods asteroid^{-1}	North Sea (off Helgoland; Kattegat)	Röttger (1969, see also Barel & Kramers (1977)
Synapticola teres	*Polyplectana kefersteini, Synapta maculata* (H)	Coelomic cavity, digestive tract (posterior part)	5 copepods (2 ♂, 3 ♀) free in coelomic cavity (Voigt)	Indian Ocean (Amboina); W Pacific (Queensland)	Voigt (1892), Humes (1979)
III. Monstrilloida					
Thespesiopsyllus paradoxus	*Ophiothrix fragilis, Ophiopholis aculeata* (O)	Stomach folds	About 50 % of *O. aculeata* infested	North Sea (Gullmarfjord)	Bresciani & Lützen (1962)
IV. Incertae sedis					
Arthrochordeumium appendiculosum	*Astrocharis gracilis* (O)	Galls at arm base	At least 2 copepods (♂, ♀) found	NW Pacific (Philippines: Mindanao)	Mortensen & Stephensen (1918)
Arthrochordeumium asteromorphae	*Asteromorpha koehleri* (O)	Galls at arm base	Only 1 copepod found	NE Indian Ocean (Amboina)	Stephensen (1933)
Codoba discoveryi	*Ophiura meridionalis* (O)	Calcified cysts inside bursa	3 infested ophiuroids were found	Antarctic Sea (South Georgia)	Heegard (1951)
Chordeumium obesum	*Asteronyx loveni* (O)	Cysts within coelomic cavity (attached cysts)	Almost 100 % infestation; no more than 1 copepod gall^{-1}	North Sea (Skagerrak)	Mortensen (1912), Jungersen (1912, 1914)
Parachordeumium tetraceros	*Amphipholis squamata* (O)	Coelomic cavity	Only 1 copepod observed	Mediterranean (Villefranche)	Le Calvez (1938), Bocquet (1952)

[1] Indentified *Phormosoma uranus* by Koehler (1898)

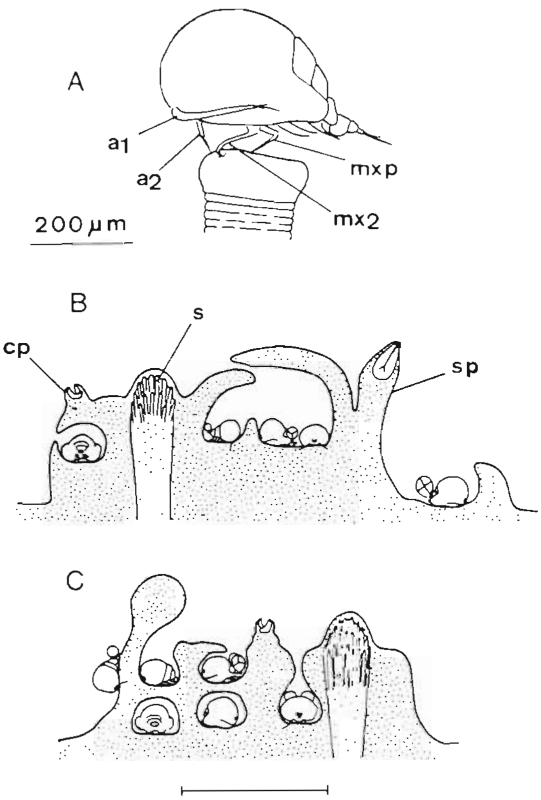

Fig. 3. *Scottomyzon gibberum*, an ectoparasitic copepod of the asteroid *Asterias rubens*. (A) Female on tube-foot tip. (B & C) Copepods embedded in dermal tissue of a pedicellarial rosette. a1 & a2: antennae; cp: crossed pedicellaria; mxp: maxilliped; mx2: maxilla; s: spine; sp: straight pedicellaria. (After Röttger 1969)

Ophiura quadrispina (Wagin 1964, 1976). The ophiuroid first encysts the parasite with its own tissues; then both cyst and parasite grow into the bursal cavity. The cyst is gradually ejected from the cavity through the bursal slit. *P. sinagodoides* apparently has adapted its life cycle to the reaction of its host, as rejected cysts as a rule include infesting ascothoracid larvae. According to Grygier (1985b) the asteroid-associated ascothoracid *Endaster hamatosculum* lives in conspicuous inner galls located in the arm coelom of its host. Galls are calcified and correspond morphologically to intracoelomic outgrowths of the asteroid body wall; each gall opens on the host's outer body surface by a slit-like hole.

Ascothoracids may castrate their host. Thus *Ascothorax ophioctenis* causes complete castration of *Ophiocten sericerum*, even though it does not feed on the host's gonads. Wagin (1946) found a single juvenile *A. ophioctenis* to inhibit the activity of the germinal epithelium leading to a regression of the whole gonad. Similar castration occurs in spatangoids infested with large-sized *Ulophysema oeresundense*. According to Brattström (1947), castration results from competition for food between gonads and ascothoracid. Casual observations of host castration have been made also by Yosii (1928b), Fisher (1930) and Korschelt (1933). Heavy infestation of *Ophionotus victoriae* by *Ascothorax gigas* (up to 7 genital bursae infested) causes occlusion of the ophiuroid mouth opening and reduces the development of the gonads (Grygier & Fratt 1984). The gonads do not completely regress, however. The stomach volume is reduced, but there is no demonstrable reduction in the volume of stomach contents.

According to Brattström (1947) infesting larvae of *Ulophysema oeresundense* usually penetrate their host through the genital apertures and also through the ambulacral pores. Infesting larvae thus reach either the gonadal lumen or the axial sinus. They must cross the wall of the gonad or of the axial sinus in order to reach the general coelomic cavity where they normally grow and reproduce. When mature, *Ulophysema* spp. most frequently attach to the apical part of the host's body wall in which they bore holes up to 1 mm in diameter. These holes are used by the larvae to escape from the host. Grygier (1981) suggested that the release of larvae from a female *Dendrogaster antarcticus* into the asteroid coelom is produced by rupturing of the mantle of the female. Larvae of *Dendrogaster tasmaniensis* penetrate the asteroid *Allostichaster polyplax* through respiratory papulae; they infest the coelom and escape by crossing the asteroid's stomach wall and passing to the outside through its mouth (Hickman 1959).

Agents: Crustacea, Malacostraca

Associations between amphipods and echinoderms were reviewed by Vader (1978). A parasitic relation has been inferred by Shoemaker (1919) for *Laphystiopsis iridometra* which lives embedded in the calyx of the crinoid *Iridometra melpomene*. Typical ectoparasitism occurs with the North Sea species *Epimeria parasitica* which feed on the outer tissues of the holothuroid *Stichopus tremulus* and the asteroid *Porania pulvillus* (Vader 1978). According to Ruffo (1957), the amphipods *Jassia ocia* and *Aristias negletus* occur at Banyuls (France, Mediterranean Sea) in the coelomic cavity of the holothuroid *Stichopus regalis* and the crinoid *Antedon mediterranea*, respectively.

An unexpected association between the tanaidacean *Exspina typica* and 3 species of deep-sea holothuroids has been reported by Thurston et al. (1987). *E. typica* should be considered a facultative parasite; it occurs either in the intestine or body cavity of its host.

Crabs associated with and potentially harmful to echinoderms belong to 3 distinct families:

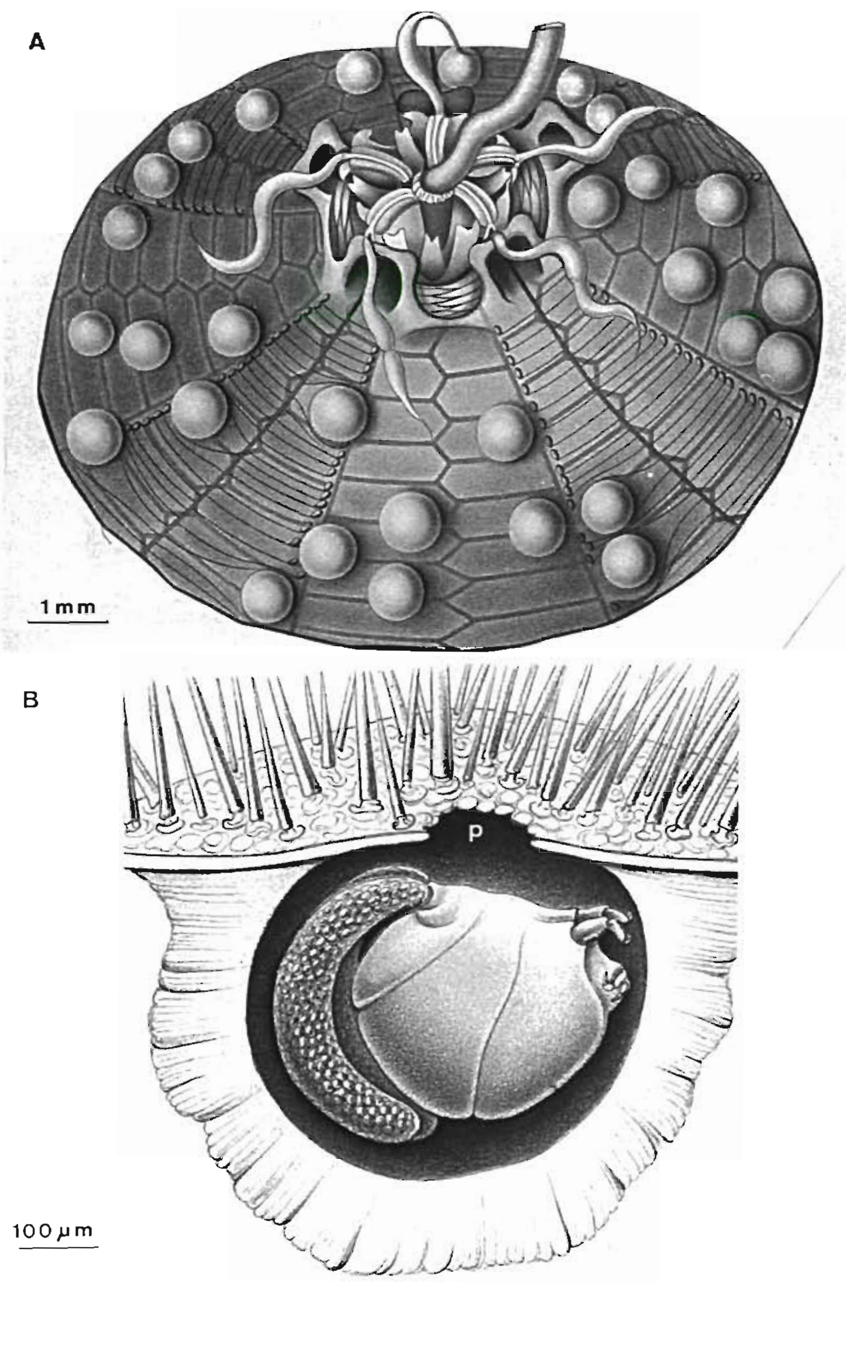

Fig. 4. *Pionodesmotes phormosomae*, a gallicole copepode parasite of the echinoid *Hygrosoma petersi*. (A) Inner view of the oral part of a dissected echinoid showing the location of calcified galls. (B) Section through gall containing an ovigerous female. p: outer pore of the gall. (A after Koehler 1898; B after Bonnier 1898)

Pinnotheridae (genera *Dissodactylus, Ophisthopus, Pinnaxodes, Pinnixa, Pinnotheres*), Parthenopidae (genera *Echinoecus, Zebrida*), and Portunidae (genus *Lissocarcinus*) (Table 4). Feeding habits of associated species of *Ophisthopus, Pinnixa, Pinnotheres* and *Lissocarcinus* have not been reported. Presumably these forms do not feed on host tissues, nor cause any other detrimental effects, except to slightly wound the wall of the respiratory trees or of the cloaca (Tao 1930, Jones & Mahadevan 1965). Species inhabiting the posterior part of the echinoid digestive tract *(Echinoecus convictor, E. pentagonus, E. rathbunae* and *Pinnaxodes chilensis)* are generally said to feed on host fecal pellets (e.g. Miyake 1939, Fenucci 1967). Trophic relations between *E. pentagonus* and the echinoid *Echinothrix calamaris* were studied carefully by Castro (1971) (see also Suzuki & Takeda 1974). Males and small immature females inhabit the peristomeal region where they feed on epithelial tissue and tube feet, damage being in equilibrium with the regenerating capacities of the host. Large mature females live in the rectum and ingest material from fecal pellets and aggregates of pigmented coelomocytes that migrate across the rectal wall.

Table 3. Parasitic ascothoracid cirripeds (compiled from the sources indicated). Ascothoracid species names according to Wagin (1976) and Grygier (1981 to 1983). Hosts: A, asteroids; C, crinoids, E, echinoids; O, ophiuroids. Unidentified species of ascothoracids were reported from asteroids by Fisher (1940; *Diplasterias meridionalis*) and from ophiuroids by Bartsch (1982; *Ophiurolepis inornata*)

Ascothoracid	Host	Location on/in host	Remarks	Geographical area	Source
Ascothorax bulbosus	*Amphiura belgicae, Amphiura microplax* (O)	Bursae	1 ascothoracid host^{-1}	Southern Atlantic (off South Georgia)	Heegard (1951)
Ascothorax gigas	*Ophinotus victoriae* (O)	Bursae	Up to 27 parasites host^{-1} (Grygier & Fratt)	South Sandwich Islands	Wagin (1968), Grygier (1983c), Grygier & Fratt (1984)
Ascothorax mortenseni	*Amphiura microplax* (O)	Bursae	–	South Georgia	Grygier (1983c)
Ascothoras ophioctenis	*Ophiocten sericeum* (O)	Bursae	Infestation rate: 0.7 to 3.4 % (Wagin)	Barents Sea; Kara Sea; North Atlantic (around Iceland and Faroë Islands)	Djakonov (1914), Stephensen (1935a), Wagin (1946)
Ascothorax pilocaudatus	*Ophiosphalma armigerum* (O)	Bursae	–	NE Atlantic	Grygier (1983c)
Ctenosculum hawaiiense[1]	*Brisinga evermanni* (A)	Coelomic cavity	–	Tropical W Pacific (Hawaii)	Heath (1910), Warén (1981)
Dendrogaster antarcticus	*Acodontaster conspicuus* (A)	Coelomic cavity	Infestation level ca 2 %	Antarctic seas (off Ross Island)	Fisher (1930), Grygier (1981)
Dendrogaster arborescens	*Dipsacaster sladeni, Coscinasterias calamaria* (A)	Coelomic cavity	1 to 3 ascothoracids host^{-1} (infestation not uncommon) (Okada)	Southern Indian Ocean (off Cape Town); Misaki (Japan)	Le Roi (1905, 1907), Okada (1925)
Dendrogaster arbusculus	*Hippasteria californica* (A)	Coelomic cavity	1 observation	NE Pacific (off California)	Fisher (1911), Grygier (1982)
Dendrogaster arctica	*Leptasterias groenlandica* (A)	Coelomic cavity	–	N Pacific (Bering Sea)	Fisher (1930), Korschelt (1933), Wagin (1950), Grygier (1986)
Dendrogaster argentinensis	*Anasterias minuta* (A)	Coelomic cavity	5 asteroids infested (326 investigated)	SW Atlantic	Grygier & Salvat (1984)
Dendrogaster astericola	*Henricia sanguinolenta* (A)	Coelomic cavity	3 infested *H. sanguinolenta* (500 investigated)	Barents Sea (White Sea)	Knipowitsch (1891)
Dendrogaster asterinae	*Asterina burtoni* (A)	Coelomic cavity	1 to 10 ascothoracids asteroid^{-1}	Red Sea (Gulf of Aqaba)	Achituv (1971)
Dendrogaster astropectinis	*Astropecten scoparius* (A)	Coelomic cavity	5 infested asteroids (250 investigated)	Misaki (Japan)	Yosii (1928b)
Dendrogaster beringensis	*Eremicaster tenebrarius, Hyphalaster inermis* (A)	Coelomic cavity	–	Bering Sea	Wagin (1957), Madsen (1961), Grygier (1985a)
Dendrogaster dichotomus	*Crossaster papposus* (A)	Coelomic cavity	3 infested asteroids (13 investigated)	NE Pacific	Wagin (1950)
Dendorgaster dogieli	*Pteraster obscurus* (A)	Coelomic cavity	–	Bering Sea	Wagin (1950)
Dendrogaster elegans	*Leptasterias polaris* (A)	Coelomic cavity	–	Bering Sea; Gulf of St Lawrence	Wagin (1950), Grygier (1986)
Dendorgaster fisheri	*Pedicellaster magister megalabis* (A)	Coelomic cavity	–	NE Pacific (off California)	Fisher (1928), Grygier (1982)
Dendrogaster iwanowi	*Leptasterias fisheri* (A)	Coelomic cavity	–	Bering Sea	Wagin (1950)
Dendrogaster leptasteriae	*Leptasterias fisheri* (A)	Coelomic cavity	–	Bering Sea	Wagin (1950)
Dendrogaster ludwigi	*Echinaster luzonicus, Certonardoa semiregularis, Nepanthia belcheri* (A)	Coelomic cavity	–	W. Pacific (Philippines, Japan Sea; Tasmania)	Le Roi (1905, 1907), Yosii (1928b), Kenny (1959)
Dendrogaster murmanensis	*Crossaster papposus, Solaster endeca* (A)	Coelomic cavity	–	Barents Sea; N Pacific (Okhotsk Sea)	Korschelt (1933), Wagin (1950)
Dendrogaster okadai	*Coscinasterias calamaria* (A)	Coelomic cavity	–	Misaki (Japan)	Yosii (1928b)

Table 3 (continued)

Ascothoracid	Host	Location on/in host	Remarks	Geographical area	Source
Dendrogaster orientalis	*Leptasterias polaris* (A)	Coelomic cavity	–	Bering Sea	Wagin (1950)
Dendrogaster punctata	*Poraniopsis inflata* (A)	Coelomic cavity	–	NE Pacific (off California)	Grygier (1982)
Dendrogaster ramosus	*Leptasterias fisheri* (A)	Coelomic cavity	–	Bering Sea	Wagin (1950)
Dendrogaster rimskykorsakowi	*Ctenodiscus crispatus*, *Hippasteria leiopelta* (A)	Coelomic cavity	–	NW Pacific (Okhotsk Sea)	Wagin (1950)
Dendrogaster sagittaria	*Sidonaster vaneyi* (A)	Coelomic cavity	2 individuals in a single asteroid	Philippine Seas	Fisher (1919), Grygier (1985a)
Dendrogaster tasmaniae	*Allostichaster polyplax* (A)	Coelomic cavity	1 ascothoracid asteroid^{-1} (26 infested/116 investigated)	Around Tasmania	Hickman (1959)
Endaster hamatosculum	*Zeroaster carinatus* (A)	Intracoelomic galls	1 to 2 ascothoracids asteroid^{-1}	Philippines Sea	Grygier (1985b)
Parascothorax synagodoides	*Ophiura quadrispina* (O)	In cysts in bursae	1 to 9 ascothoracids ophiuroid^{-1}	Okhotsk Sea	Wagin (1964)
Ulophysema oeresundense	*Echinocardium cordatum*, *Echinocardium flavescens*, *Brissopsis lyrifera* (E)	Coelomic cavity; more rarely gonads, ambulacral ampullae or axial sinus	1 to 9 (mostly 1) ascothoracids echinoid^{-1} (all stations together: 814 infested/42 874 investigated) (Brattström 1947); infestation rate: 20 to 25 % (Bresciani & Jespersen)	North Sea (Scandinavian coast)	Brattström (1936, 1938, 1946, 1947), Bresciani & Jespersen (1985)
Ulophysema pourtalesiae	*Pourtalesia jeffreysi* (E)	Coelomic cavity	1 or 2 ascothoricids echinoid^{-1}	N Atlantic (between Norway, Spitzberg, Greenland and the Faroes)	Brattström (1937)
Waginella metacrinicola	*Metacrinus rotundus* (O)	On stalk	–	Sea of Japan	Okada (1926, 1938), Grygier (1983b)
Waginella axotremata	*Metacrinus acutus*, *Metacrinus angulatus*, *Metacrinus cingulatus* (C)	On cirri	–	Indonesia; China Sea	Grygier (1983b)

[1] Waren (1981) showed that *Ctenosculum hawaiiense* (Heath 1910) is better interpreted as an ascothoracid than as a mollusc; Grygier (1983a) confirmed this opinion from direct examination of *C. hawaiiense*

According to Mortensen (1943a) and Suzuki & Takeda (1974) an obvious parasitic relation occurs between the parthenopid crab *Zebrida adamsi* and several echinoid species (Table 4). the crab feeds on appendages, skin and peripheral dermal tissue of echinoids, producing conspicuous naked test areas. Similar parasitic behavior also occurs with some species of *Dissodactylus* living on clypeasteroid and spatangoid echinoids (Dexter 1977, Telford 1982, Bell & Stancyk 1983). Telford (1982) reported that, depending on the species studied, the associated *Dissodactylus* take 50 to 100% of their diet from host tissues. According to him differences in feeding habits can be attributed partly to the structure of host spines, *viz.* larger test areas are denuded if the spines of the echinoid host are more porous (Fig. 7).

Gut-inhabiting species may produce deformations that are sometimes very conspicuous. Verrill (1867) reported that *Pinnotheres chilensis* considerably distends the rectal wall of the echinoid *Coenocentrotus gibbosus* to form a membranous cyst. The cyst attaches aborally to the echinoid body wall and extends near the mouth into the coelomic cavity. The anal area of the host is depressed and distorded, and the echinoid test is usually swollen on the side over the cyst (Fenucci 1967). *P. chilensis* parasitizes both *C. gibbosus* and *Loxechinus albus.* According to Mortensen (1943b) the crab does not induce major test deformation when infesting *L. albus.* Similar but less conspicuous deformations are caused also by *Echinoecus convictor*, *E. pentagonus* and *E. rathbunae* (respectively Bouvier & Seurat 1905, Castro 1971, Miyake 1939), all of them producing

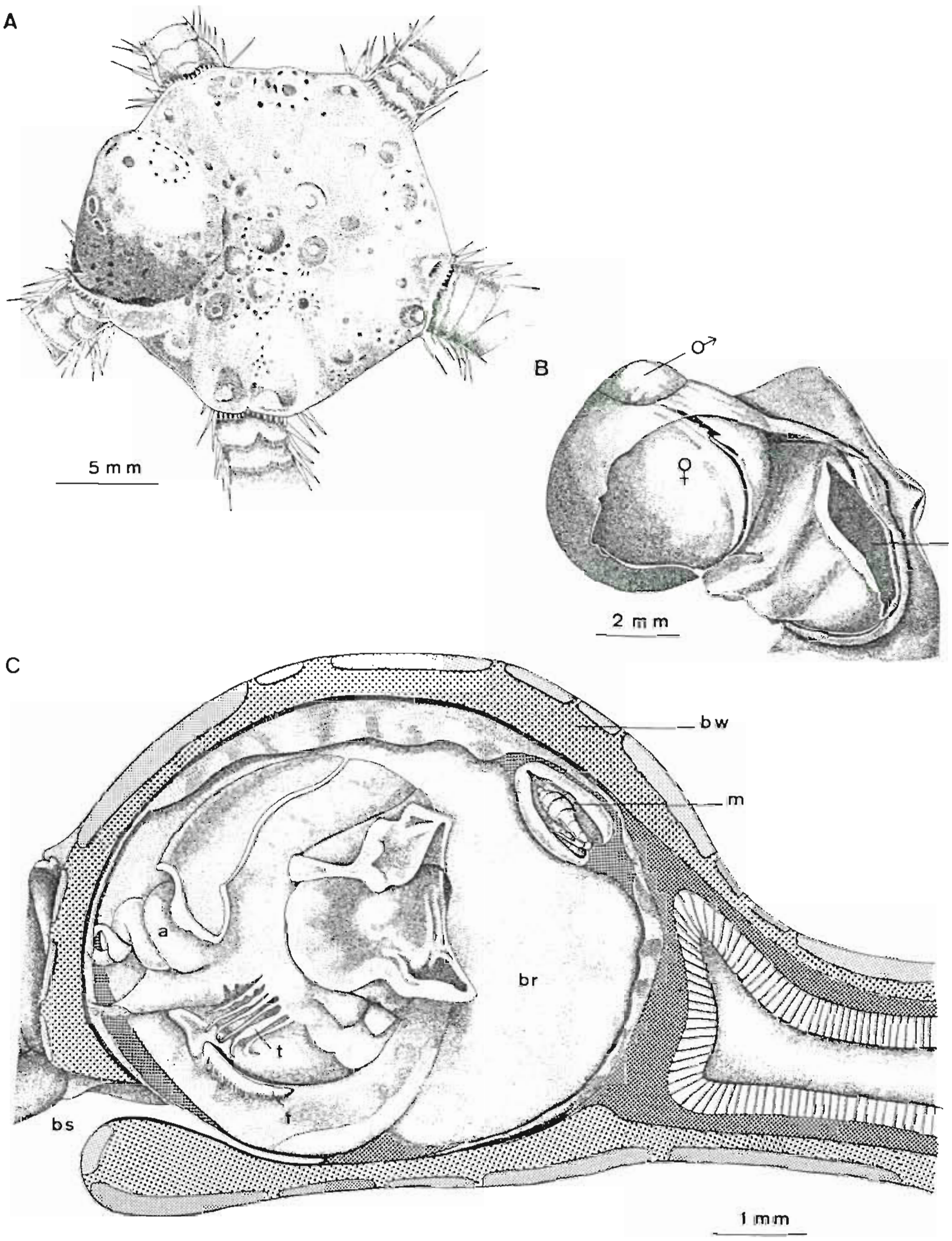

Fig. 5. *Ascothorax ophioctenis*, an ascothoracid parasite of the genital bursae of the ophiuroid *Ophiocten sericeum* (A) Aboral view of disc of an infested ophiuroid. (B) Dissected genital bursa containing a pair of *A. ophioctenis* (C) Diagramatic drawing of parasites *in situ*. a: antennule; br: brood pouch. bs: bursal slit, bw ophiuroid body-wall, f furca, m dwarf male; t thoracic limbs (Redrawn from Wagin 1946; slightly modified)

swellings of anal tube and periproct of their host.

According to Suzuki & Takeda (1974) and Dexter (1977), infestations by ectoparasitic crabs often exert major effects and may kill echinoids. The crabs select a particular site on the host's body surface and clear away the spines of the region (see also Telford 1982). This produces an obvious decrease in movements and spine activities of infested regular echinoids (Suzuki & Takeda 1974). Dexter (1977) observed a reduction in spine activity which decreased the ability of clypeasteroids to feed and to move about in aquaria, resulting in a substantial increase in mortality.

Agents: Arachnida; Pycnogonida; Insecta

The only arachnid reported to be an echinoderm parasite is the acarian *Enterohalacarus minutipalpus*

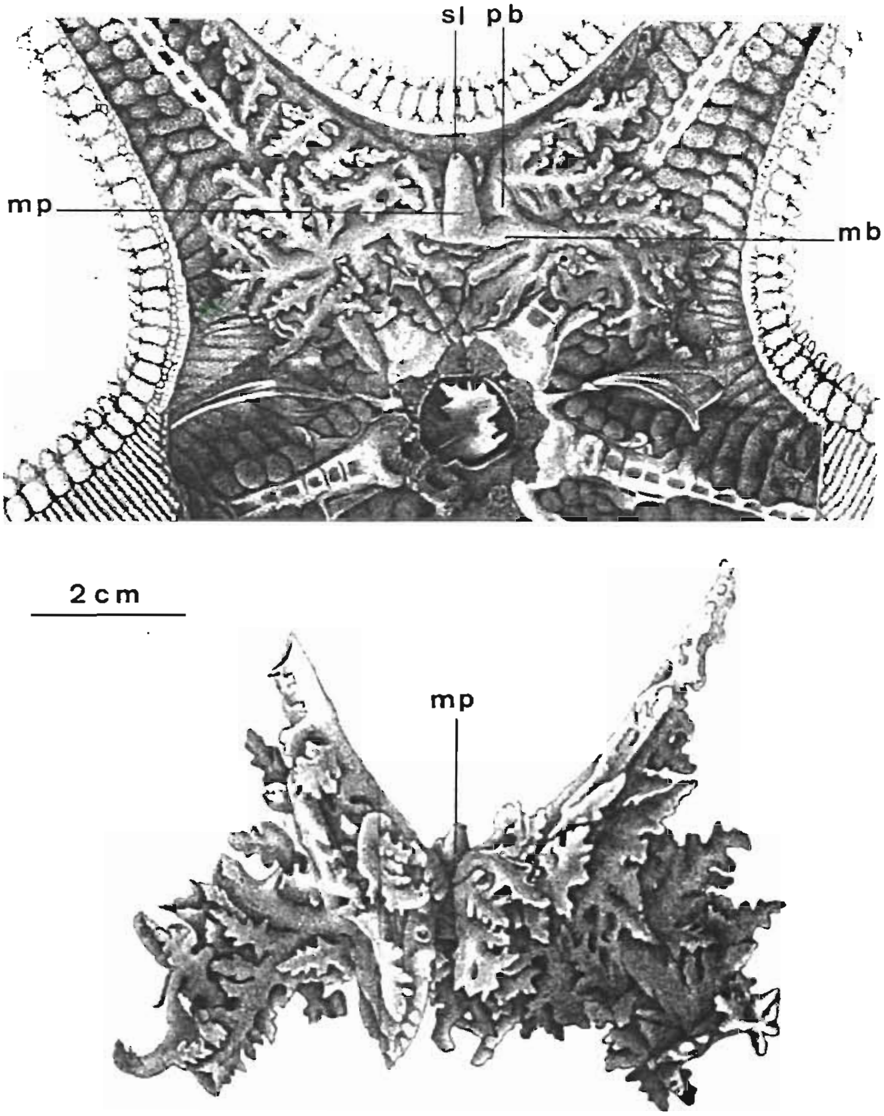

Fig. 6. *Dendrogaster arborescens*, an ascothoracid parasite of the coelomic cavity of the asteroid *Dipsacaster sladeni*. mb: main branch; mp: middle piece; pb: primary branch; sl: distal slit. (After Le Roi 1907)

found in the gut of the echinoid *Plesiodiadema indicum* (Viets 1939). Three specimens were collected in echinoid material dredged by the *Albatross* off North Moluccas, Indonesia. Northing is known about host-associate relations.

Pycnogonid-echinoderm associations have been noticed by several authors who generally suggested an ectoparasitic relation. Associations with holothuroids were observed by Prell (1910; *Pycnogonum littorale/Cucumaria frondosa*) and Ohshima (1927; *Lecythrorhynchus hilgendorfi/Holothuria lubrica*). According to Ohshima, a single host may carry up to 30 pycnogonids which supposedly absorb the blood or 'body juice' of the holothuroid. An obvious pycnogonid-ophiuroid association occurs at Aldabra (Indian Ocean) with 3 species of *Ophioderma* and the sea-spider, *Anoplodactylus ophiurophilus* (Sloan 1979, Sloan et al. 1979, Stock 1979). Sloan reported various infestation levels – from 3.6 to 83.7% – depending on the host species. He presented evidence that *A. ophiurophilus* has the potential to feed on the host's tube feet. The occurrence of pycnogonids on echinoids and asteroids has also been reported casually (Stock 1981).

An unexpected association between the marine trichopter *Philanisus plebeius* and the asteroids *Patiriella exigua* and *Patiriella regularis* was reported by Anderson et al. (1976) and by Winterbourn & Anderson (1980). Caddis fly eggs were found in the asteroid coelomic cavity. Singly or in small clumps, eggs occur loose within the coelom close to the peristome or enveloped in stomach folds. The authors presumed that eggs are deposited through the respiratory papulae and that newly hatched intracoelomic larvae leave the host either via the same route or through the stomach wall. According to Winterbourn & Anderson (1980),

Table 4. Parasitic decapods (Reptantia) of echinoderms (compiled from the sources indicated). Hosts: E, echinoid; H, holothuroid

Reptant	Host	Location on/in host	Remarks	Geographical area	Source
Dissodactylus calmani	*Clypeaster rosaceus* (E)	Outer body surface (oral surface)	Infestation level 25 to 50 %	Tropical W Atlantic (Florida, Jamaica)	Telford (1982)
Dissodactylus crinitichelis	*Mellita sexiesperforata* (E)	Outer body surface	Infestation level 30 to 60 %	Tropical W Atlantic (Barbados)	Telford (1978, 1982)
Dissodactylus encopei	*Encope emarginata* (E)	Outer body surface	–	Tropical W Atlantic (Florida to N Brazil)	Rathbun (1918)
Dissodactylus glasselli	*Mellita longifissa* (E)	Outer body surface	–	Tropical E Pacific (Mexican coast)	Rioja (1944)
Dissodactylus lockingtoni	*Mellita longifissa, Encope micropora, Encope grandis, Encope californica* (E)	Outer body surface (proximal portion of posterior interambulacral lunule)	–	Tropical E Pacific (Northern Mexico)	Glassell (1935)
Dissodactylus mellitae	*Mellita quinquiesperforata, Echinarachnius parma* (E)	Outer body surface	13 crabs collected from 50 *M. quinquiesperforata* (Pearse); almost 100 % infestation (Johnson)	NW Atlantic (Massachusetts to Florida)	Rathbun (1918), Pearse (1947), Johnson (1952), Gray et al. (1968), Telford (1982)
Dissodactylus nitidus	*Encope stokesi, Encope micropora* (E)	Outer body surface (near lunule or marginal slits)	1 to 2 crabs host^{-1}; infest mostly large echinoids (diameter > 30 mm)	Tropical E Pacific (Panama)	Dexter (1977)
Dissodactylus primitivus	*Meoma ventricosa, Plagiobrissus grandis* (E)	Outer body surface (mostly on oral surface)	Infestation level 79 to 100 %	Tropical W Atlantic (Barbados, Jamaica)	Telford (1978, 1982)
Dissodactylus smithi	*Mellita longifissa* (E)	Outer body surface	–	Tropical E Pacific (Mexican coast)	Rioja (1944)
Dissodactylus xantusi	*Encope stokesi, Encope micropora* (E)	Outer body surface (near lunule or marginal slits)	More often on *E. micropora*	Tropical E Pacific (Panama)	Dexter (1977)
Echinoecus convictor	*Echinothrix diadema* (E)	Internal swelling of anal tube	–	Tropical Indo-West Pacific (Gambier Island; Mauritius)	Bouvier & Seurar (1905), Mortensen (1940)
Echinoecus pentagonus	*Pseudocentrotus depressus, Anthocidaris crassispina, Echinothrix calamaris, Echinothrix diadema* (E)	Outer body surface (near peristome)	10 crabs collected on 48 *P. depressus* (Suzuki & Takeda)	Tropical Indo-W Pacific (Andaman, Hawaii, Japan: coast of Uchida)	Castro (1971, 1978), Suzuki & Takeda (1974), Sastry (1977, 1981)
Echineocus rathbunae	*Echinothrix calamaris, Phyllacanthus dubius* (E)	Internal swelling of the anal tubes	–	NW Pacific (Ogasawara Islands)	Miyake (1939)
Lissocarcinus orbiculatus	*Bohadschia argus* (H)	Mainly respiratory trees, also cloaca	11 holothuroids infested (61 investigated)	NW Pacific (Philippines: Puerto Galera)	Trott & Garth (1970)
Lissocarcinus ornatus	*Holothuria* sp. (H)	Cloaca	–	N Indian Ocean (Andaman Sea)	Chopra (1931)
Ophisthopus transversus	*Parastichopus californicus* (H)	Cloaca	Occur also in other invertebrates (e.g., bivalve molluscs)	NE Pacific (California)	Rathbun (1918)
Pinnaxodes chilensis[1]	*Loxechinus albus, Coenocentrotus gibbosus* (E)	Partly embedded in rectum wall	1 to 2 crabs echinoid^{-1}. Infestation generally very high (90 to 100 %) (Verrill, Clark, Rathbun, Schwabe)	SE Pacific (Ecuador to Patagonia)	Verrill (1867), Ortmann (1894), Meissner (1896), Clark (1910), Rathbun (1918), Schwabe (1936), Mortensen (1943b), Fenucci (1967)
Pinnixa barnharti	*Molpadia arenicola* (H)	Cloaca	–	NE Pacific (California)	Rathbun (1918)
Pinnixa timida	*Caudina chilensis* (H)	Cloaca	Infestation level 75 %	NW Pacific (Japan: Mutsu Bay)	Tao (1930)
Pinnotheres decanus	*Holothuria scabra* (H)	Cloaca and respiratory trees; rarely in the coelomic cavity	10 holothuroids infested (25 investigated)	N Indian Ocean (Indian coast)	Chopra (1931), Jones & Mahadevan (1965), Adithiya (1969)

Table 4 (continued)

Reptant	Host	Location on/in host	Remarks	Geographical area	Source
Pinnotheres setnai	Unidentified holothuroid	Respiratory trees	–	NW Indian Ocean (Andaman Sea)	Chopra (1931)
Pinnotheres villosissimus	*Actinopyga mauritiana, Actinopyga lecanora* (H)	Cloaca	–	NW Indian Ocean (Andaman Sea; west coast of Sumatra)	Doflein (1904), Chopra (1931)
Zebrida adamsi	*Diadema setosum, Tripneustes gratilla, Toxopneustes pileolus, Toxopneustes elegans, Asthenosoma ijimai, Salmacis sphaeroides* (E)	Outer body surface (near ambitus)	As a rule 1 crab echinoid^{-1} (11 crabs collected) (Suzuki & Takeda)	NW Pacific (Japan: Suruga Bay; coast of Thailand)	Rathbun (1910), Mortensen (1943a), Suzuki & Takeda (1974), Daniel & Krishnan (1978)

[1] Often identified *Fabia chilensis*

eggs are found in the coelom during most of the year, the infestation level being about 10%.

Agents: Pisces

Associations between echinoderms and carapid fishes (pearlfishes) are of particular interest as they concern – at least in a few cases – typical parasitic relations between an invertebrate host and a vertebrate associate. The systematics, general biology, and ecology of pearlfishes are documented satisfactorily, and some species have been studied in detail (e.g. Zankert 1940, Arnold 1956, Trott 1970, Van Meter & Ache 1974, Smith et al. 1981, Trott 1981). Pearlfish species associate with holothuroids and asteroids are listed in Table 5.

Most authors report that the stomach contents of *Carapus* spp. from echinoderm coelomic cavities do not show remains of host tissue (e.g. Trott 1970, Smith et al. 1981). *Carapus* spp. are predators. Basically, they use the host's coelom as shelter (Fig. 8). They leave it in order to catch prey, feeding primarily on crustaceans. Casual observations of feeding by *Carapus* on the host's gonad have been reported however (Hipeau-

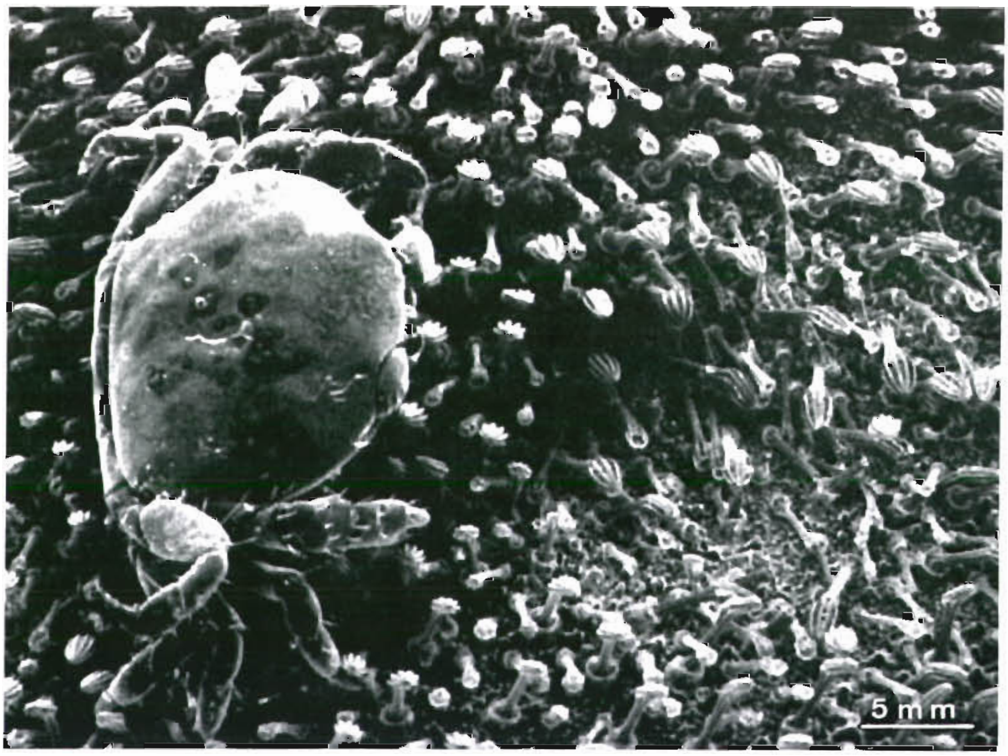

Fig. 7 *Dissodactylus crinitichelis*, an ectoparasitic crab of the clypeastroid echinoid *Mellita sexiesperforata*. The crab is seen beside the devastated area where it had been feeding. (After Telford 1982)

Table 5. Fishes endosymbiotic in echinoderms (compiled from the sources indicated). Hosts: A, asteroid; H, holothuroid

Fish	Host	Location in host	Remarks	Geographical area	Source
Carapus acus	*Holothuria tubulosa, Stichopus regalis* (H)	Mostly coelomic cavity; sometimes respiratory trees or cloaca	29 infested holothuroids (89 investigated) (Arnold)	Mediterranean Sea (mostly western part)	Emery (1880), Zanker (1940), Arnold (1953, 1956), Gustato (1977)
Carapus bermudensis	*Actinopyga agassizi* (usual host); also *Astichopus multifidus, Holothuria glaberrima, Holothuria lentiginosa, Holothuria princeps, Isostichopus badionotus, Thyone* sp. (H)	Coelomic cavity; sometimes respiratory trees	1 to 10 fishes holothuroid $^{-1}$ (mostly 1); infestation level may reach 50 % (Smith et al.)	W Atlantic from Brazil to North to Bermuda	Linton (1907), Parker (1926), Ancona-Lopez (1956), Smith & Tyler (1969), Trott (1970), Dawson (1971), Koster & Caycedo (1979), Smith et al. (1981)
Carapus dubius	Unidentified holothuroid	Internal	–	Tropical W Atlantic (Caribbeans)	Putnam (1874)
Carapus homei	*Stichopus chloronotus* and *Bohadschia argus* (usual host); also in *Actionpyga mauritiana, Holothuria atra, Thelonota ananas, Stichopus tropicalis* (H)	Mostly coelomic cavity, also respiratory trees	Infestation level 16 to 88 % according to period of year (Smith)	Tropical Indo-W Pacific	Bedford (1899), Fisher (1907), Sivickis & Domantay (1928), Mukerji (1932), Smith (1964), Hipeau-Jacquotte (1967), Trott (1970, 1981), Trott & Trott (1972)
Carapus mourlani[1]	*Culcita schmideliana* and *Culcita novaeguineae* (usual hosts); also *Acanthaster planci, Choriaster granulosus, Protoreaster lincki, Thromidia seychellensis*[2] (A) *Bohadschia argus* (H)	Coelomic cavity of asteroids; coelomic cavity and respiratory trees of holothuroids	1 to 2 fishes asteroid^{-1} Infestation level may reach about 100 % (Mortensen; Trott 1970). A single *B. argus* contained 15 fishes (Meyer-Rochow 1977)	Tropical Indo-W Pacific	Putnam (1874), Simpson & Brown (1910), Mortensen (1923), Mukerji (1932), Strasburg (1961), Smith (1964), Hipeau-Jacquotte (1967), Trott (1970), Trott & Trott (1972), Cheney (1973), Jangoux (1974), Meyer-Rochow (1977, 1979)
Jordanicus gracilis	*Bohadschia argus* (usual host); also *Holothuria atra, Holothuria scabra, Stichopus chloronotus, Thelonota ananas* (H) *Culcita novaeguinea, Acanthaster planci* (A)	Coelomic cavity	Infestation level may reach 30 % (Trott & Trott)	Tropical Indo-W Pacific	Doleschall (1861), Arnold (1956), Strasburg (1961), Smith (1964), Trott (1970), Trott & Trott (1972), Cheney (1973)
Jordanicus sagamianus	*Holothuria monacaria* (H) *Certonardoa semiregularis* (A)	Intestine (?) of holothuroid; coelomic cavity of asteroid	Infestation common in *H. monacaria* (Tanaka)	NW Pacific (Japan: Sagami, Misaki)	Tanaka (1908), Yosii (1928a)

[1] Identified *Carapus homei* by many authors
[2] Previously identified *Mithrodia fisheri* (Jangoux 1974)

Jacquotte 1967), and some authors suggested that juvenile individuals could depend on their host for food (Jangoux 1974, Meyer-Rochow 1979). In contrast, *Encheliophis* spp. are considered true parasites which stay permanently in the echinoderm coelom feeding on host viscera (Strasburg 1961, Smith 1964).

Effects of pearlfish infestations are said to be practically non-existent except for *Encheliophis* spp. which

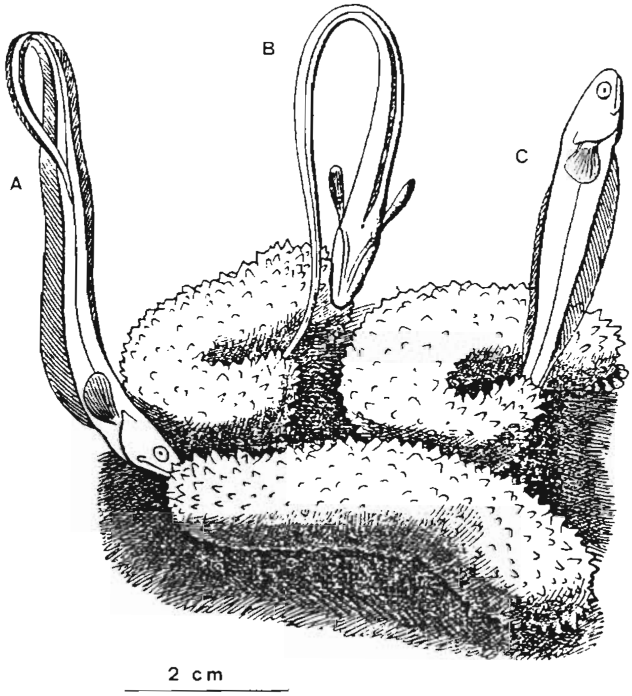

Fig. 8. *Carapus acus* penetrating the holothuroid *Holothuria tubulosa*. (A) Recognition. (B) Twisting. (C) Penetration. (After Emery 1880)

presumably cause castration by consuming the host's gonads. *Carapus* spp. cause only slight injury by piercing the host's digestive wall when entering or leaving the coelomic cavity. At low infestation levels the effect on the host should be negligible as pearlfishes do not always infest the same host, but shelter in the nearest suitable host found. However, in a higher infested echinoderm population (high infestation levels were, for example, recorded by Mortensen [1923] and Trott [1970] for *Carapus mourlani* inhabiting *Culcita novaeguineae*) chances increase that a given host is infested regularly; hence repeated loss of coelomic fluid and successive wound repairs have to be considered.

Acknowledgements. I thank Drs M. J. Grygier, O. Kinne and J. M. Lawrence for information and criticism; Dr C. Massin for helping with literature research; N. Biot, Dr G. Coppois, M. Doizé and M. Klinkert for assisting in the preparation of the manuscript and illustrations.

LITERATURE CITED

Achituv, Y. (1971). *Dendrogaster asterinae* n. sp., an ascothoracid (Cirripedia) parasite of the starfish *Asterina burtoni* of the Gulf of Eilat. Crustaceana 21: 1–4

Adithiya, L. (1969). Some notes on the anatomy of *Holothuria*. Loris 11: 385–388

Ancona-Lopez, A. A. (1956). Occorrência de *Carapus* Raf. (= *Fierasfer* Oken) no Brasil. Pap. Avuls. Dpto Zool. (S. Paulo) 12: 389–397

Anderson, D. T., Fletcher, M. J., Lawson-Kerr, C. (1976). A marine caddis fly, *Philanius plebeius*, ovipositing in a starfish *Patiriella exigua*. Search 7: 483–484

Arendt, Y. A. (1985). Biotic relations of crinoids. Paleontol. Zh. USSR 1982(2): 69–76. (Russian; English summary)

Arnold, D. C. (1953). Observations on *Carapus acus* (Brünnich), (Jugulares, Carapidae). Pubbl. Staz. zool. Napoli 24: 152–166

Arnold, D. C. (1956). A systematic revision of the fishes of the teleost family Carapidae (Percomorphi, Blennioidea), with descriptions of two new species. Bull. Br. Mus. nat. Hist. 4: 247–307

Barel, C. D., Kramers, P. G. (1970). Notes on associates of echinoderms from Plymouth and the coast of Brittany. Proc. K. ned. Akad. Wet. (C)73: 159–170

Barel, C. D., Kramers, P. G. (1977). A survey of the echinoderm associates of the north-east Atlantic area. Zool. Verh., Leiden 156: 1–159

Bartsch, I. (1982). Ophiuroidea (Echinodermata) from the Patagonian shelf. Mitt. zool. Mus. Hamb. 79: 211–250

Bay-Schmith, E., Jana, C. (1977). *Balanus tintinabulum concinnus* Darwin, 1854, epibionte poco comun del erizo negro, *Tetrapygus niger* (Molina, 1782). Boln Soc. Biol. Concepción 51: 59–61

Bedford, F. P. (1899). Holothurians. A. Willey's Zool. Results (London) 2: 141–150

Bell, J. L., Stancyk, S. E. (1983). Population dynamics and reproduction of *Dissodactylus mellitae* (Brachyura: innotheridae) on its sand dollar host, *Mellita quinquiesperforata* (Echinodermata). Mar. Ecol. Prog. Ser. 13: 141–149

Bocquet, T. (1952). Copépodes semi-parasites et parasites des échinodermes de la région de Roscoff. Bull. Soc. zool. Fr. 77: 495–504

Bonnier, J. (1898). Note sur le *Pionodesmotes phormosomae*, copépode parasite du *Phormosoma uranus*. Rés. Camp. scient. Albert I Monaco 12 (Appendice): 61–66

Boolootian, R. A. (1958). Notes on an unexpected association between a common barnacle and an echinoid. Bull. Sth. Calif. Acad. Sci. 57: 91–92

Boolootian, R. A. (1964). The occurrence of *Balanus concavus* on the test of *Dendraster excentricus*. Bull. Sth. Calif. Acad. Sci. 63: 185–191

Bouvier, E. L., Seurat, G. (1905). *Eumedon convictor* crabe commensal d'un oursin. C.r. hebd. Séanc. Acad. Sci., Paris 140: 629–631

Brattström, H. (1936). *Ulophysema oeresundense* n. gen. et sp. eine neue Art der Ordnung Cirripedia Ascothoracida. Ark. Zool. 28A(23): 1–10

Brattström, H. (1937). On the genus *Ulophysema* Brattström with description of a new species from east Greenland. Meddr Grønland 118(7): 1–23

Brattström, H. (1938). Ascothoracica, eine für die norwegische Fauna neue Ordnung parasitischer Crustaceen. Det. Kong. Norske Vidensk. Selsk. Forh. 11(6): 22–25

Brattström, H. (1946). Observations on *Brissopsis lyrifera* (Forbes) in the Gullmar Fjord. Ark. Zool. 37A(18): 1–25

Brattström, H. (1947). On the ecology of the ascothoracid *Ulophysema oeresundense* Brattström. Lunds Univ. Arsskr. (N.F. 2) 43(7): 1–75

Bresciani, J., Jespersen, A. (1985). The ultrastructure of the integument of *Ulophysema oeresundense* Brattström, 1936 (Crustacea, Ascothoracida). J. crust. Biol. 5: 146–159

Bresciani, J., Lützen, J. (1962). Parasitic copepods from the west coast of Sweden including some new or little known species. Vidensk Meddr dansk. naturh. Foren. 124: 367–408

Brun, E. (1976). Ecology and taxonomic position of *Henricia* *oculata* Pennant. Thalassia jugosl. 12: 51–64

Campbell, A. C., Rainbow, P.S. (1977). The role of the pedicellariae in preventive barnacle settlement on the sea-urchin test. Mar Behav. Physiol. 4: 253–260

Carpenter, P. H. (1889). Report on the Comatulae of the Mergui Archipelago, collected for the trustees of the Indian Museum, Calcutta, by Dr John Anderson, F.R.S., superintendent of the Museum. J. Linn. Soc., Zool. 21. 304–316

Carton, Y (1968). Etude expérimentale de l'infestation d'*Amphipholis squamata* Delle Chiajei (ophiuride) par *Cancerilla tubulata* Dalyell (copépode cycloïde). Cah. Biol. mar 9: 269–284

Carton, Y (1974). Copépodes parasites de Madagascar II. Description de *Botulosoma endoarrhenum* n. gen., n. sp. (Lichomolgidae) parasite d'*Othilia purpurea* (Echinodermata, Asteridae); étude de ses relations anatomiques avec l'hôte. Crustaceana 26: 65–79

Castro, P. (1971). Nutritional aspects of the symbiosis between *Echinoecus pentagonus* and its host in Hawaii, *Echinothrix calmaris*. In: Cheng, T C. (ed.) Aspects of the biology of symbiosis. Univ. Press, Baltimore, p. 229–247

Castro, P. (1978). Settlement and habitat selection in the larvae of *Echinoecus pentagonus* (A. Milne Edwards), a brachyuran crab symbiotic with sea urchins. J. exp. mar Biol. Ecol. 34: 259–270

Changeux, J. P. (1958). Quelques caractères biologiques d'un copépode parasite d'holothuries: *Allantogymus delamarei* n. g. n. sp. C. r. hebd. Séanc. Acad. Sci., Paris 247: 961–964

Changeux, J. P. (1961). Contribution à l'étude des animaux associés aux holothurides. Vie Milieu 10 (Suppl.): 1–124

Changeux, J. P., Delamare-Deboutteville, C. (1956). *Enterognathus comatulae* Giesbrecht, 1900. Vie Milieu 7: 106–107

Cheney, D. P. (1973). Pearlfish (Carapidae) in *Acanthaster planci* (L.). Micronesica 9: 159

Chopra, B. (1931). On some decapod Crustacea found in the cloaca of holothurians. Rec. Indian Mus. 33: 303–324

Clark, A. H. (1921). A monograph of the existing crinoids. I. The comatulids (Part 2). Bull. U.S. natn. Mus. 82: 1–795

Clark, H. L. (1910). The echinoderms of Peru. Bull. Mus. comp. Zool. Harv. 52: 321–358

Clark, R. B. (1959). *Capitella capitata* as a commensal, with a bibliography of parasitism and commensalism in the polychaetes. Ann. Mag. nat. Hist. (12) 2: 433–438

Cuénot, L. (1892). Commensaux et parasites des échinodermes (deuxième note). Rev. biol. Nord France 5: 1–22

Cuénot, L. (1912). Contribution à la faune du Bassin d'Arcachon. V Echinodermes. Bull. Stn biol. Arcachon 14: 17–116

Daniel, A., Krishnan, S. (1978). A parthenopid crab, *Zebrida adamsii* White, 1847, inhabiting interspaces of spines of the sea urchin, *Salmacis virgulata* L. Agassiz, 1846. Bull. zool. Surv. India 1: 171–175

Dartevelle, E. (1940). Les 'rotules' de la côte occidentale d'Afrique. Bull. Inst. r colon. Belge 11: 175–198

Dawson, C. E. (1971). Records of the pearlfish, *Carapus bermudensis* in the northern Gulf of Mexico and of a new host species. Copeia 1971. 730–731

Dexter, D. M. (1977). A natural history of the sand dollar *Encope stokesi* L. Agassiz in Panama. Bull. mar. Sci. 27: 544–551

Djakonov, M. D. (1914). *Ascothorax ophioctenis* n. g. et n. sp., a new endoparasite belonging to the Ascothoracida. Trudy imp. S. Petersb. Obshch. Estest. 45: 158–164. (Russian; German summary)

Doflein, F. (1904). Brachyura. Deutsche Tiefsee-Expedition 6: 1–314

Dojiri, M., Humes, A. J. (1982). Copepods (Poecilostomatoidea: Taeniacanthidae) from sea urchins (Echinoidea) in the southwest Pacific. Zool. J. Linn. Soc. 74: 381–436

Doleschall, C. L. (1861). On *Oxybeles gracilis* Bleeker. Ann. Mag. nat. Hist. (3) 7: 340–342

Edwards, C. L. (1891). Beschreibung einiger neuen Copepoden und eines neuen copepoden ähnlichen Krebses, *Leukkartella paradoxa*. Arch. Naturgesch. 57: 75–104

Emery, C. (1880). Le specie del genere *Fierasfer* nel Golfo di Napoli e regione limitrofe. Fauna Flora Golfes Neapel 2: 1–76

Emson, R. H., Mladenov, P. V., Wilkie, I. C. (1985). Studies of the biology of the West Indian copepod *Ophiopsyllus reductus* (Siphonostomatoidea: Cancerillidae) parasitic upon the brittlestar *Ophiocomella ophiactoides*. J. nat. Hist. 19: 151–171

Fedotov, D. M. (1912). *Protomyzostomum polynephris*, eine neue Myzostomidenart. Zool. Anz. 39: 649–653

Fedotov, D. M. (1914). Die Anatomie von *Protomyzostomum polynephris* Fedotov. Z. wiss. Zool. 109: 631–696

Fedotov, D. M. (1916). On the parasitism of *Protomyzostomum* in *Gorgonocephalus eucnemis* M. Tr. Zool. Zh. SSSR 1: 161–218. (Russian; English summary)

Fedotov, D. M. (1925). Über eine neue Art von *Protomyzostomum (Pr. astrocladi*, sp. n.) aus *Astrocladus*. Zool. Anz. 63: 183–194

Fenucci, J. L. (1967). Contribucion al conocimiento del crustacea decapodo braquiuro *Pinnaxodes chilensis* (M. Edwards), comensal de *Loxechinus albus* (Molina) (Echinodermata, Echinoidea). Physis, B. Aires 27· 125–133

Fewkes, J. W. (1887). A troublesome parasite of brittle starfish *(Amphiura squamata)*. Nature, Lond. 37: 274–275

Fewkes, J. W. (1888). On a new parasite of *Amphiura*. Proc. Boston Soc. nat. Hist. 24: 31–33

Fishelson, L. (1973). Ecology of the crinoids of the northern Red Sea with emphasis on epi- and endozoic fauna associated with them. J. mar. biol. Ass. India 15: 461–473

Fishelson, L. (1974). Ecology of the northern Red Sea crinoids and their epi- and endozoic fauna. Mar. Biol. 26: 183–192

Fisher, W. K. (1907). The holothurians of the Hawaiian Islands. Proc. U.S. natn. Mus. 32: 637–744

Fisher, W. K. (1911). Asteroidea of the North Pacific and adjacent waters. Part I. Phanerozonia and Spinulosa. Bull. U.S. natn. Mus. 76(1): 1–419

Fisher, W. K. (1919). Starfishes of the Philippines seas and adjacent waters. Bull. U.S. natn. Mus. 100(3): 1–712

Fisher, W K. (1928). Asteroidea of the North Pacific and adjacent waters. Part II. Forcipulata (pars). Bull. U.S. natn. Mus. 76(2): 1–245

Fisher, W. K. (1930). Asteroidea of the North Pacific and adjacent waters. Part III. Forcipulata (concluded). Bull. U.S. natn. Mus. 76(3): 1–356

Fisher, W. K. (1940). Asteroidea. 'Discovery' Rep. 20: 69–306

Ganapati, P. N., Radhakrishna, Y. (1962). Inquilinism between a new hesionid polychaete and a holothurian *Molpadia* sp. Curr. Sci. 31: 382–383

Ganapati, P. N., Sastry, D. R. (1972). Record of *Athanas indicus* (Coutière) (Decapoda: Alpheidae) associated with *Stomopneustes variolaris* (Lamarck) (Echinodermata: Echinoidea) from Visakhapatnam coast. Proc. Indian Acad. Sci. (B)38: 367–372

Giard, A. (1887). Sur un copépode (*Cancerilla tubulata* Dalyell), parasite de l'*Amphiura squamata* Delle Chiaje. C.r. hebd. Séanc. Acad. Sci., Paris 104: 1189–1192

Giesbrecht, W (1900). Mitteilungen über Copepoden. Mitt. zool. Stn Neapel 14: 61–79

Giltay, L. (1934). Note sur l'association de *Balanus concavus pacificus* Pilsbry (Cirripède) et *Dendraster excentricus* (Eschscholtz) (échinoderme). Bull. Mus. r Hist. nat. Belg. 10(5): 1–7

Glassell, S. A. (1935). New or little known crabs from the Pacific coast of northern Mexico. Trans. San Diego Soc. nat. Hist. 8: 91–106

Gorzula, S. (1978). *Collocheres elegans*, a cyclostome copepod infesting *Ophiocomina nigra* in the Firth of Clyde. Western Natur. 7: 67–77

Goudey-Perrière, F. (1979). *Amphiurophilus amphiurae* (Hérouard), crustacé copépode parasite des bourses génitales de l'ophiure *Amphipholis squamata* Delle Chiaje, échinoderme: morphologie des adultes et études des stades juvéniles. Cah. Biol. mar. 20: 201–230

Goudey-Perrière, F. (1980). Modalités de l'infestation de l'ophiure *Amphipholis squamata* Della Chiaje, échinoderme, par le crustacé copépode *Amphiurophilus amphiurae* (Hérouard) et influence du parasite sur l'état de gravidité de l'hôte. C.r. hebd. Séanc. Acad. Sci., Paris 291. 697–700

Graff, L. von (1884). Report on the Myzostomida. Challenger Rep. Zool. 10: 1–82

Graff, L. von (1887). Report on the Myzostoma. Supplement. Challenger Rep. Zool. 20: 1–16

Grainger, J. N. (1950). Notes on parasitic Crustacea. Ann. Mag. nat. Hist (12) 3: 635–638

Gray, I. E., McCloskey, L. R., Weihe, S. T (1968). The commensal crab *Dissodactylus mellitae* and its reaction to sand dollar host-factor. J. Elisha Mitchell scient. Soc. 84: 472–481

Grygier, M. J. (1981). A representative of the genus *Dendrogaster* (Cirripedia: Ascothoracida) parasitic in an Antarctic starfish. Antarct. Res. Ser. 32: 1–15

Grygier, M. J. (1982). *Dendrogaster* (Crustacea: Ascothoracida) from California: sea-star parasites collected by the Albatross. Proc. Calif. Acad. Sci. 42: 443–454

Grygier, M. J. (1983a). *Ctenosculum hawaiiense* Heath: confirmation of its affinities (Crustacea: Ascothoracida – *Ex* Mollusca: Gastropoda) J. crust. Biol. 3: 257–265

Grygier, M. J. (1983b). Revision of *Synagoga*. (Crustacea: Maxillopoda: Ascothoracida). J. nat. Hist. 17: 213–239

Grygier, M. J. (1983c). *Ascothorax*, a review with descriptions of new species and remarks on larval development, biogeography, and ecology (Crustacea: Ascothoracida). Sarsia 68: 103–126

Grygier, M. J. (1985a). Two species of *Dendrogaster* (Crustacea: Ascothoracida) parasitic in porcellanasterid starfishes. Galathea Rep. 16: 113–120

Grygier, M. J. (1985b). Résultats des campagnes Musorstom. Crustacea Ascothoracida. Mém. Mus. natn. Hist. nat., Paris (A) Zool. 133: 417–426

Grygier, M. J. (1986). *Dendrogaster* (Crustacea: Ascothoracida) parasitic in Alaskan and eastern Canadian *Leptasterias* (Asteroidea). Can. J. Zool. 64: 1249–1253

Grygier, M. J., Fratt, D. B. (1984). The ascothoracid crustacean *Ascothorax gigas*: redescription, larval development, and notes on its infestation of the Antarctic ophiuroid *Ophionotus victoriae*. Biol. Antarct. Seas 41 43–58

Grygier, M. J., Salvat, M. B. (1984). *Dendrogaster argentinas* sp. nov., a South American sea-star parasite. Proc. biol. Soc. Wash. 97: 43–48

Gustato, G. (1977). Osservazioni sulla biologia e sul comportamento di *Carapus acus* (Ophidioidea – Percomorphi). Boll. Soc. Nat. Napoli 85: 505–536

Hansen, H. J. (1902). *Echinocheres globosus*, n. gen., n. sp., a copepod parasitic in spines of an echinothurid. Vidensk. Meddr dansk naturh. Foren. 1902: 437–499

Hara, J., Okada, Y (1921). Two new species of *Myzostoma*. Annotnes zool. jap. 10: 33–39

Heath, H. (1910). A new genus of parasitic gastropods. Biol. Bull. mar. biol. Lab., Woods Hole 18: 99–108

Heegard, P. (1951). Antarctic parasitic copepods and an ascothoracid cirriped from brittle-star Vidensk. Meddr dansk naturh. Foren. 113: 171–190

Hérouard, E. (1906). Sur un nouveau copépode parasite d'*Amphiura squamata*. C.r hebd. Séanc. Acad. Sci., Paris 142: 1287–1289

Hickmann, J. L. (1959). *Dendrogaster tasmaniensis* sp. nov. (Ascothoracida) from the sea-star *Allostichaster polyplax* (Müller and Troschel). Parasitology 49: 316–329

Hipeau-Jacquotte, R. (1967). Observations sur le comportement du poisson Carapidae *Carapus homei* (Richardson, 1884) de Madagascar Recl Trav. Stn mar. Endoume 6 (Fasc. suppl.): 141–151

Humes, A. G. (1957). Deux copépodes harpacticoïdes nouveaux du genre *Tisbe*, parasite des holothuries de la Méditerranée. Vie Milieu 8: 9–22

Humes, A. C. (1968). *Lecanarius kossmannianus*, a new cyclopoid copepod parasitic in holothurians in Madagascar. Proc. biol. Soc. Wash. 81. 179–190

Humes, A. G. (1975). Cyclopoid copepods (Nanaspididae and Sabelliphilidae) associate with holothurians in New Caledonia. Smithson. Contr. Zool. 202: 1–41

Humes, A. G. (1979). *Synapticola teres* Voigt, 1892 (Copepoda, Cyclopoida, Sabelliphilidae) from a holothurian in northeastern Australia. Crustaceana 36: 249–256

Humes, A. G. (1980a). A review of the copepods associated with holothurians, including new species from the Indo-Pacific. Beaufortia 30: 31–123

Humes, A. G. (1980b). A new taeniacanthid copepod from the esophagus of a sea urchin in Queensland. Mem. Qd Mus. 20: 171–179

Humes, A. G. (1986). Synopsis of copepods associated with asteroid echinoderms, including new species from the Moluccas. J. nat. Hist. 20: 981–1020

Humes, A. G., Ho, J. S. (1969). Cyclopoid copepods parasitic in holothurians in Madagascar. J. Parasit. 55: 877–894

Humes, A. G., Ho, J. S. (1970). The genus *Diogenella* (Copepoda, Cyclopoida) parasitic in holothurians in the West Indies. Crustaceana 19: 15–36

Humes, A. G., Ho, J. S. (1971). The genus *Diogenidium* (Copepoda, Cyclopoida) parasitic in holothurians in the West Indies. Crustaceana 20: 171–191

Hurley, A. C. (1973). Larval settling behaviour of the acorn barnacle (*Balanus pacificus* Pilsbry) and its relation to distribution. J. Anim. Ecol. 42: 599–609

Jägersten, G. (1940). Zur Kenntnis der Morphologie, Entwicklung und Taxonomie der Myzostoma. Nova Acta R. Soc. Scient. upsal. (4)11(8): 1–84

Jangouy, M. (1974). Sur l''association' entre certaines astéries (Echinodermata) et des poissons Carapidae. Rev. Zool. afr. 88: 789–796

Jangoux, M. (1987a). Diseases of Echinodermata. I. Agents microorganisms and protistans. Dis. aquat. Org. 2: 147–162

Jangoux, M. (1987b). Diseases of Echinodermata. II. Agents metazoans (Mesozoa to Bryozoa). Dis. aquat. Org. 2: 205–234

Johnson, I. S. (1952). The demonstration of a 'host-factor' in commensal crabs. Trans. Kans. Acad. Sci. 55: 458–464

Jones, S., Mahadevan, S. (1965). Notes on animal associations. 5. The pea crab *Pinnotheres deccanensis* Chopra inside the respiratory tree of the sea cucumber, *Holothuria scabra* Jäger. J. mar. biol. Ass. India 7: 377–380

Jungersen, H. F. (1912). *Chordeuma obesum*, a new parasitic copepod endoparasite in *Asteronyx loveni*. Rep. Brit. Ass. Adv. Sci. 1912: 505–506

Jungersen, H. F. (1914). *Chordeuma obesum*, a new parasitic copepod endoparasitic in *Asteronyx loveni* M.Tr. Mindeskrift J. Steenstrup 1914(16): 1–19

Kenny, R. (1959). A new Australian record of an ascothoracid parasite. Aust. J. Sci. 21: 221

Kinne, O. (1980). Diseases of marine animals: general aspects. In: Kinne, O. (ed.) Diseases of marine animals, Vol. I. General aspects, Protozoa to Gastropoda. Wiley, Chicester, p. 13–73

Knipowitsch, N. (1891). *Dendrogaster astericola* nov. gen. et sp., eine neue Form aus der Gruppe Ascothoracida. Biol. Zbl. 100: 707–711

Koehler, R. (1898). Echinides et ophiures provenant des campagnes du yacht l'Hirondelle (Golfe de Gascogne, Açores, Terre-Neuve). Rés. Camp. scient. Albert I Monaco 12: 1–78

Kossmann, R. (1877). Entomostracea (I. Theil: Lichomolgidae). Zool. Ergebn. Reise Kunstgeb. Roten Meeres (K. Acad. Wiss. Berlin) (1)4: 1–24

Korschelt, E. (1933). Über zwei parasitäre Cirripedien, *Chelonibia* und *Dendrogaster*, nebst Angaben über die Beziehungen der Balanomorphen zu ihrer Unterlage. Zool. Jb. (Abt. Syst.) 64: 1–40

Koster, F., Caycedo, I. E. (1979). Primer hallazgo de *Astichopus multifidus* (Echinodermata: Holothurioidea, Stichopodidae) y *Carapus bermudensis* (Pisces: Gadiformes, Carapidae) en el Caribe Columbiano, con notas sobre esta nueva associacion. Bol. Mus. Mar Bogota 9: 1–47

Kristensen, R. M. (1980). Zur Biologie des marinen Heterotardigraden *Tetrakentron synaptae*. Helgoländer Meeresunters. 34: 165–177

Le Calvez, J. (1938). *Parachordeumium tetraceros* n. gen. n. sp., copépode gallicole parasite d'une ophiure de Villefanche-sur-mer. C.r. Congr. Socs sav. Paris, Sect. Sci. 71: 259–263

Le Roi, O. (1905). Zwei neue parasitische Cirripedien aus der Gruppe der Ascothoracida. Zool. Anz. 29: 399–401

Le Roi, O. (1907). *Dendrogaster arborescens* und *Dendrogaster ludwigi*, zwei entoparasitische Ascothoraciden. Z. wiss. Zool. 86: 100–133

Linton, E. (1907). Note on the habits of *Fierasfer affinis*. Am. Nat. 41 1–4

Ludwig, H. (1905). Ein entoparasitischer Chaetopod in einer Tiefsee-Ophiure. Zool. Anz. 29: 397–399

Madsen, E. J. (1961). The Porcellanasteridae. A monographic revision of an abyssal group of sea-stars. Galathea Rep. 4: 33–174

Marenzeller, E. von (1895a). *Myzostoma asteriae* n. sp., ein Endoparasit von *Asterias* Arten. Anz. Akad. Wiss. Wien 18: 192–193

Marenzeller, E. von (1895b). Zoologische Ergebnisse. V. Echinodermen gesammelt 1893, 1894 (im östlichen Mittelmeere). K. Akad. Wiss. Wien (Math. Naturw. Cl.) 62: 123–148

Masson, C. (1965). Description morphologique de la femelle de *Amphiurophilus*, copépode parasite interne de *Amphipholis squamata* Chiaje. Proc. First intern. Congr. Parasitol. 2: 1078–1079

McClendon, J. F. (1906). The myzostomes of the Albatross expedition to Japan. Bull. Am. Mus. nat. Hist. 22: 119–130

Meissner, M. (1896). Die von Herrn Dr. Plate aus Chile heimgebrachten See-Igel. Arch. Naturgesch. 62: 84–90

Meyer, D. L., Ausich, W. I. (1983). Biotic interactions among recent and among fossil crinoids. In: Tevesz, M. J. S., McCall, P. L. (ed.) Biotic interactions in recent and fossil benthic communities. Plenum Press, New York, p. 377–427

Meyer-Rochow, V B. (1977). Comparison between 15 *Carapus mourlani* in a single holothurian and 19 *C. mourlani* from starfish. Copeia 1977: 582–584

Meyer-Rochow, V B. (1979) Stomach and gut content of *Carapus mourlani* from starfish and a holothurian. Annls. Zool. fenn. 16: 287–289

Miyake, S. (1939). Note on crabs of the genus *Echinoecus* Rathbun living commensally with echinoids. (Parthenopidae, Eumedoniidae). Annotnes zool. jap. 18: 83–94

Monticelli, F. S. (1892). Notizia preliminare intorno ad alcuni inquilini degli Holothuroidea del Golfo di Napoli. Monitore zool. ital. 3: 249–256

Moore, H. B., McPherson, B. F. (1963). Colonization of the Miami area by the barnacle *Balanus trigonus* Darwin and a note on its occurrence on the test of an echinoid. Bull. mar. Sci. 13: 418–421

Mortensen, T (1912). Über *Asteronyx loveni* M. Tr Z. wiss. Zool. 101: 264–289

Mortensen, T (1923). The Danish expedition to the Kei Islands 1922. Vidensk. Meddr dansk naturh. Foren. 76: 55–100

Mortensen, T (1933). Echinoderms of South Africa (Asteroidea and Ophiuroidea). Vidensk. Meddr dansk naturh. Foren. 93: 215–400

Mortensen, T (1935). A Monograph of the Echinoidea. Part II. C. A. Reitzel, Copenhagen

Mortensen, T (1940). A Monograph of the Echinoidea. Part III(1) Aulodonta. C. A. Reitzel, Copenhagen

Mortensen, T. (1943a). A Monograph of the Echinoidea. Part III(2) Camarodonta I. C. A. Reitzel, Copenhagen

Mortensen, T (1943b). A Monograph of the Echinoidea. Part III(3) Camaradonta II. C. A. Reitzel, Copenhagen

Mortensen, T., Stephensen, K. (1918). On a gall-producing parasitic copepod, infesting an ophiurid. Vidensk. Meddr dansk naturh. Foren. 69: 261–275

Mukerji, D. D. (1932). Biological observations on and instances of commensalism of an ophioid fish with echinoderms of the Andaman Islands. Rec. Indian Mus. 34: 567–570

Ohshima, H. (1927). Notes on some pycnogons living semiparasitic on holothurians. Proc. imp. Acad. Japan 3: 610–613

Okada, Y. (1922). On a new *Protomyzostomum (P. sagamiense*, sp. nov.) from ovary of *Gorgonocephalus*. Annotnes zool. jap. 10: 165–169

Okada, Y (1925). Contribution à l'étude des cirripèdes ascothoraciques. I. Note sur le *Dendrogaster arborescens* Le Roi; établissement d'un nouveau genre. Bull. Mus. Hist. nat., Paris 31. 364–371

Okada, Y (1926). Contribution à l'étude des Cirripèdes ascothoraciques. II. Note sur l'organisation des *Synagoga*. Bull. Mus. Hist. nat., Paris 32: 69–73

Okada, Y. (1933). *Mesomyzostoma katoi*, n. sp., an interesting myzostome found in the gonad of *Comanthus japonicus*. Annotnes zool. jap. 14: 185–189

Okada, Y (1938). Les Cirripèdes ascothoraciques. Trav. Sta. zool. Wimereux 13: 489–514

Ortmann, A. (1894). Die Decapoden-Krebse des Strassburger Museums. Zool. Jb. 7: 683–772

Paris, J. (1955). Commensalisme et parasitisme chez les annélides polychètes. Vie Milieu 5: 525–536

Parker, G. M. (1926). The inquiline fish *Fierasfer* at Key West, Florida. Proc. natn. Acad. Sci. U.S.A. 12: 421–422

Paterson, N. F. (1958). External features and life cycle of *Cucumaricola notabilis* nov. gen. et sp., a copepod parasite of the holothurian, *Cucumaria*. Parasitology 48: 269–290

Pearse, A. S. (1947). On the occurrence of ectoconsortes on marine animals at Beaufort, N. C. J. Parasitol. 33: 453–458

Prell, H. (1910). Beiträge zur Kenntnis der Lebensweise

einiger Pantopoden. Bergens Mus. Årb. 1909(10): 1–30
Prenant, M. (1959). Classe des Mysostomides. In: Grassé, P. P. (ed.) Traité de Zoologie, 5(1). Masson, Paris, p. 714–784
Prouho, H. (1892). Sur deux myzostomes parasites de l'*Antedon phalangium* (Müller). C.r. hebd. Séanc. Acad. Sci., Paris 115: 846–849
Putnam, F. W (1874). Notes on Ophidiidae and Fierasferidae, with descriptions of new species from America and the Mediterranean. Proc. Boston Soc. nat. Hist. 16: 339–348
Pyefinch, K. A. (1940). The anatomy of *Ophioica asymmetrica*, sp. n., a copepod endoparasitic in an ophiuroid. J Linn. Soc. Lond. (Zool.) 41 1–19
Rathbun, M. J. (1910). The Danish expedition to Siam 1899–1900. V Brachyura. D. Kgl. Dansk Vidensk. Selsk. Skr. (7) 5: 301–368
Rathbun, M. J. (1918). The grapsoid crabs of America. Bull. U.S. natn. Mus. 97: 1–461
Remscheid, E. (1916). Beiträge zur Kenntnis der Myzostomiden. Abh. Senckenb. naturf. Ges. 35: 179–226
Rioja, E. (1944). Observaciones sobre algunas especies de cangrejas del genero *Dissodactylus* Smith (Braquiros, Pinnoteridos) en las costas mexicanas del Pacifico. Anls. Inst. Biol. Univ. Mexico 15: 147–160
Röttger, R. (1969). Ökologie und Postlarvalentwicklung von *Scottomyzon gibberum*, eines auf *Asterias rubens* parasitisch lebenden Copepoden (Cyclopoida, Siphonostoma). Mar. Biol. 2: 145–202
Röttger, R., Astheimer, H., Spindler, M., Steinborn, J. (1972). Ökologie von *Asterocheres lilljeborgi*, eines auf *Henricia sanguinolenta* parasitisch lebenden Copepoden. Mar. Biol. 13: 259–266
Ruffo, S. (1957). Studi sui corstacei anfipodi. 19. Osservazioni sopra alcune specie di anfipodi trovate a Banyuls su echinodermi. Vie Milieu 8: 312–318
Sastry, D. R. (1977). On some crustacean associated of sea-uchins of the Andaman and Nicobar Islands. Newsl. zool. Surv. India 3: 119–120
Sastry, D. R. (1981). On some crustacean associates of Echinodermata from the Bay of Bengal. Rec. zool. Surv. India 79: 19–30
Schulz, E. (1935). *Actinarctus doryphorus* nov. gen. nov. sp., ein merkwürdiger Tardigrad aus der Nordsee. Zool. Anz. 111: 285–288
Schwabe, G. H. (1936). Investigaciones sobre *Loxechinus albus* Mol. y *Pinnotheres chilensis* Edw. Boln Soc. Biol. Concepción 10: 125–137
Shoemaker, C. R. (1919). A new amphipod parasitic on a crinoid. Proc. biol. Soc. Wash. 32: 245–246
Simpson, J. J., Brown, R. N. (1910). Asteroidea of Portuguese East Africa, collected by Jas. J. Simpson. Proc. R. Soc. Edinb. 18: 45–60
Sivickis, P. B., Domantay, J. S. (1928). The morphology of a holothurian, *Stichopus chloronotus* Brandt. Philip. J. Sci. 37: 299–332
Sloan, N. A. (1979). A pycnogonid-ophiuroid association. Mar. Biol. 52: 171–176
Sloan, N. A., Clark, A. M., Taylor, J. D. (1979). The echinoderms of Aldabra and their habitats. Bull. Br. Mus. nat. Hist. (Zool.) 37(2): 81–128
Smith, C. L. (1964). Some pearlfishes from Guam, with notes on their ecology. Pacif. Sci 18: 34–40
Smith, C. L., Tyler, J. C. (1969). Observations on the commensal relationship of the western Atlantic pearlfish *Carapus bermudensis*, and holothurians. Copeia 1969: 206–208
Smith, C. L., Tyler, J. C., Feinberg, M. N. (1981). Population ecology and biology of the pearlfish *(Carapus bermudensis)* in the lagoon at Bimini, Bahamas. Bull. mar. Sci. 31: 876–902
Speel, J. A., Dearborn, J. H (1983). Comatulid crinoids from R/V Eltamin cruises in the Southern Ocean. Biol. Antarct. Seas 38: 1–60
Stephensen, K. (1933). Some new copepods, parasites of ophiuroids and echinids. Vidensk. Meddr dansk naturh. Foren. 93: 197–213
Stephensen, K. (1935a). Two crustaceans (a cirriped and a copepod) endoparasitic in ophiuroids. Danish Ingolf-Exped. 3(12): 1–18
Stephensen, K. (1935b). Some endoparasitic copepods found in echinids. Vidensk. Meddr dansk naturh. Foren. 98: 223–228
Stephensen, K. (1940). Parasitic and semiparasitic Copepoda. Zool. Iceland 3(34): 1–24
Stock, J. H. (1959). Copepoda associated with Neapolitan invertebrates. Pubbl. Staz. zool. Napoli 31: 59–75
Stock, J. H. (1966). Copepoda associated with invertebrates from the Gulf of Aquaba. 2. *Enterognathus lateripes* n. sp., a new endoparasite of Crinoidea (Cyclopoida, Ascidicolidae). Proc. K. ned. Akad. Wet (C)69: 211–216
Stock, J. H. (1968a). The Calvocheridae, a family of copepods inducing galls in sea-urchin spines. Bijdr. Dierk. 38: 84–90
Stock, J. H. (1968b). Copepods endoparasitic of tropical holothurians. Bull. zool. Mus. Univ. Amsterdam 1. 89–105
Stock, J. H. (1968c). *Dichelima seticauda* n. sp., a new copepod parasite of an indonesian abyssal echinid. Crustaceana 1 (Suppl.): 210–214
Stock, J. H. (1971). *Collocherides astroboae* n. gen., n. sp. a siphonostome cyclopoid copepod living in the stomach of basket stars. Bijdr. Dierk. 41: 19–22
Stock, J. H. (1979). *Anoplodactylus ophiurophilus* n. sp., a sea spider associated with brittle stars in the Seychelles. Bijdr. Dierk. 48: 156–160
Stock, J. H. (1981). *Pycnosomia asterophila*, a sea spider associated with the starfish *Calliaster* from the Philippines. Rés. Camp. MusOrstom Philippines 1 (Mém. Orstom n° 91): 309–312
Stock, J. H., Kleeton, G. (1963). Copépodes associés aux invertébrés des côtes du Roussillon. Vie Milieu 13: 681–702
Strachan, A. R. (1970). A white sea urchin-acorn barnacle enigma. Calif. Fish Game 56: 134–135
Strasburg, D. W (1961). Larval carapid fishes from Hawaii, with remarks on the ecology of adults. Copeia 1961. 478–480
Stummer-Traunfels, R. R. von (1903). Beiträge zur Anatomie und Histologie des Myzostoma. I. *Myzostoma asteriae* Marenz. Z. wiss. Zool. 75: 495–595
Stummer-Traunfels, R. R. von (1926). Myzostomida. In: Kükenthal, W. (ed.) Handbuch der Zoologie, 3(1), p. 132–210
Suzuki, K., Takeda, M. (1974). On a parthenopid crab, *Zebrida adamsii* on the sea urchins from Suruga Bay, with a special reference to their parasitic relations. Bull. natn. Sci. Mus. Tokyo 17: 287–296
Tanaka, S. (1908). Description of eight new species of fishes from Japan. Annotnes zool. jap 7: 27–46
Tao, L. (1930). Notes on the ecology and the physiology of *Caudina chilensis* (Müller) in Mutsu Bay. Proc. 4th Pacif. Sci. Congr., Java 1929, p. 7–11
Telford, M. (1978). Distribution of two species of *Dissodactylus* (Brachyura: Pinnotheridae) among their echinoid host populations in Barbados. Bull. mar. Sci. 28: 651–658
Telford, M. (1982). Echinoderm spine structure, feeding and host relationships of four species of *Dissodactylus* (Brachyura: Pinnotheridae). Bull. mar. Sci. 32: 584–594

Thurston, M. H., Billett, D. S. M., Hassack, E. (1987). An association between *Exspina typica* Lang (Tanaidacea) and deep-sea holothurians. J. mar. biol. Ass. U.K. 67: 11–15

Trott, L. B. (1970). Contributions to the biology of Carapid fishes (Paracanthopterygii: Gadiformes). Univ. Calif Publs Zool. 89: 1–41

Trott, L. B. (1981). A general review of the pearlfishes (Pisces, Carapidae). Bull. mar Sci. 31 623–629

Trott, L. B., Garth, J. S. (1970). *Lissocarcinus orbicularis* Dana (Portunidae, Caphyrinae) commensal with *Holothuria argus* Jaeger. A new host record; cohabition with the pearlfish, *Carapus homei* (Richardson). Crustaceana 19: 320–321

Trott, L. B., Trott, E. B. (1972). Pearlfishes (Carapidae: Gadiformes) collected from Puerto Galera, Mindoro, Philippines. Copeia 1972: 839–843

Ummerkutty, A. N. (1970). Description of *Sabelliphilus foliacea* sp. n. (Copepoda, Cyclopoidea) with notes on the affinities of the species. Rec. zool. Survey India 64: 101–105

Vader, W. (1978). Association between amphipods and echinoderms. Astarte 11· 123–134

Van der Land, J. (1975). The parasitic marine tardigrade *Tetrakentron synaptae*. Memorie Ist. ital. Idrobiol. 32 (Suppl.): 413–423

Van Meter, V B., Ache, B. W. (1974). Host location by the pearlfish, *Carapus bermudensis*. Mar Biol. 26: 379–383

Verrill, A. E. (1867). Remarkable instances of crustacean parasitism. Am. J. Sci. 44: 126

Viets, K. (1939). Eine merkwürdige, neue in Tiefsee-Echiniden schmarotzende Halacaridengattung und -art (Acari). Z. Parasitkde 10: 211–216

Voigt, W. (1892). *Synapticola teres* n. g., n. sp., ein parasitischer Copepode aus *Synapta keferteinii* Sel. Z. wiss. Zool. 5 (Suppl.): 31–42

Wagin, V L. (1946). *Ascothorax ophioctenis* and the position of Ascothoracida Wagin in the system of the Entomostracea. Acta zool. Stockh. 27: 155–267

Wagin, V L. (1950). On new parasitic crustaceans of the family Dendrogasteridae (order Ascothoracida). Trudy Leningr O-va. Estestvoispyt. 70(4): 3–98. (Russian)

Wagin, V L. (1957). Dendrogasteridae (Entomostraca, Ascothoracida) aus den Asteroidea der Beringsee. Trudy Leningr O-va. Estestvoispyt. 73(4): 58–63. (Russian; German summary)

Wagin, V L. (1964). On *Parascothorax sinagodoides* gen. n., sp. n. parasitizing an *Ophiura quadrispina* Clark and some remarks on geographical distibution of Ascothoracidae. Trudy Inst. Okeanol. 69: 271–284. (Russian; English summary)

Wagin, V L. (1968). *Ascothorax gigas* sp. nov. from the Antarctic ophiuroid *Ophionotus victoriae* and data on the distribution of the genus *Ascothorax*. Sbornik Kratkikh Soobshchenii Zoologia 2: 10–19. (Russian)

Wagin, V L. (1976). Ascothoracida. Kazan Univ. Press, Kazan. (Russian)

Warén, A. (1981). *Ctenosculum hawaiiense* Heath, an ascothoracican (Cirripedia) described as a mollusc. Crustaceana 40: 310–312

West, B., West, L. (1976). A note on the uptake of dissolved nutrients from sea water by the endoparasitic myzostome *Pulvinomyzostomum pulvinar*, in situ in its host *Leptometra phalangium*. Vie Milieu 26: 47–52

Wheeler, W. M. (1896). The sexual phases of *Myzostoma*. Mitt. zool. Stn Neapel 12: 227–302

Wheeler, W M. (1904). A new *Myzostoma*, parasitic in a starfish. Biol. Bull. mar biol. Lab., Woods Hole 8: 75–80

Winterbourn, M. J., Anderson, N. H. (1980). The life history of *Philanisus plebeius* Walker (Trichoptera: Chathamiidae), a caddisfly whose eggs were found in a starfish. Ecol. Entomol. 5: 293–303

Yosii, N. (1928a). Note on a *Carapus* in a starfish. Annotnes zool. jap. 2: 339–340

Yosii, N. (1928b). Note on *Myriocladus*. J. Fac. Sci. imp. Univ. Tokyo (4)2: 337–347

Zankert, A. (1940). Studien über das Verhalten von *Fierasfer acus* Brünn. beim Aufsuchen und Beziehen seines Wohntieres *Holothuria tubulosa* Gm. SBer. Ges. naturf. Fr 1940: 95–104

Editorial responsibility: Managing Editor; accepted for printing on June 3, 1987