

An Annotated List of Protozoan Parasites, Hyperparasites, and Commensals of Decapod Crustacea*

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SYNOPSIS. An approximately complete list of the known protozoan associates (exclusive of a few aberrant forms like *Amalocystis*) of decapods is presented. A few taxonomic changes are

suggested. Host, site of infection and geographic location are mentioned. Some comments on pathogenicity are made.

THIS is principally a taxonomic paper, intended to present in a systematic manner a complete list of the protozoa known to be associated with decapods and to deal with a few of the problems in classification and nomenclature found at the generic and specific levels. At the same time, such highly relevant matters as host and site of infection, locality and pathogenicity are mentioned.

At the higher levels of classification we followed "A revised classification of the phylum Protozoa" of the Honigberg Committee (78) as far as we could but were unable to follow it consistently because several specialists consider different parts of that system inadequate. In classifying the Amoebae we have followed Bovee and Jahn (20). Commenting on their difficulties, they stated very clearly the nature of some of the basic problems: "One reason these families are difficult to deal with is the consensus of taxonomists of protozoa (Honigberg et al., 1964) which still fails to recognize fully that protozoa are at least as evolutionally ancient and taxonomically diverse as are the metazoa. The protozoa probably should be considered at least a subkingdom (or kingdom) of organisms, containing several phyla and subphyla (Raabe, 1964). This idea was well presented by Raabe, and was discussed at length and strongly emphasized by Kozloff (1960) in a symposial address; and kingdoms were suggested—but not adopted—by Corliss (1962)." In the classification of the "sporozoa" we have followed Levine (128), who has given the most recent modification. However, the comment just quoted from Bovee and Jahn is applicable also to this, because the "Sporozoa" probably include at least 3 distinct phyla. We have followed the Honigberg Committee on classification of the ciliates, since that part, strongly influenced by the opinions of Corliss, has not been so controversial.

Altho we have listed most of the protozoa reported as associates of decapods, these are doubtless a small fraction of those which actually occur. Probably all decapods harbor protozoan parasites; few species are known because relatively few decapods have been examined.

The pathogenicity of protozoan infections in decapods is poorly understood but a few general statements may be made. The one known amoeba is highly pathogenic to its crab host. Gregarines do not seem to be very pathogenic, altho they cause some local damage and occlude passages

in the inhabited organ (9) with serious results. Microsporidia are notorious pathogens and generally kill the decapod host. A few ciliates are pathogenic in decapods but many are harmless commensals.

Even when we can state with confidence that a parasite is or is not particularly pathogenic to a decapod host, we know little about what this means in terms of the fluctuation of the host populations.

Subphylum SARCOMASTOGOPHORA Honigberg & Balamuth, 1963 (78).

Superclass SARCODINA Hertwig & Lesser, 1874 (78).

Class HYDRAULEA Jahn & Bovee, 1965 (85).

Order HYALPODIA Bovee & Jahn, 1966 (20).

Family PARAMOEBIDAE Poche, 1913 (153).

Genus *Paramoeba* Schaudinn, 1896 (169).

Paramoeba pernicioso Sprague, Beckett & Sawyer, 1969 (190).
Syn.: *Paramoeba* sp. Sprague & Beckett, 1968 (185). In hemolymph of blue crab *Callinectes sapidus* Rathbun, 1896. Chincoteague Bay, Virginia and Maryland, USA (165, 166, 167, 184, 185, 190); coast of North Carolina and Georgia, USA (129). Dr. Eugene E. Bovee (pers. com.) thinks *P. eithardi* Schaudinn, 1896, the type species, belongs to genus *Mayorella* and (in press) has rejected both genus *Paramoeba* Schaudinn and family Paramoebidae Poche. If Bovee's opinion is justified, which we see no reason to doubt, then *P. pernicioso* must be transferred to another genus. Since we hold no opinion as to the correct systematic position of this amoeba we have, for convenience, used the old classification here.

Subphylum APICOMPLEXA Levine, 1970 (128).

Class SPOROZOEAE Leuckart, 1879 (128).

Subclass GREGARINIA Dufour, 1828 (78).

Order EUGREGARINIDA Léger, 1900 (78).

Family CEPHALOIDOPHORIDAE Kamm, 1922 (90).

Genus *Cephaloidophora* Mavrodidi, 1908 (90).

Cephaloidophora bermudensis (Ball, 1951) n. comb. Syn.: *Carcinoecetes bermudensis* Ball, 1951 (10). In mid- and hindgut of the grapsid crab *Pachygrapsus transversus* (Gibbs), Bermuda. The generic name *Carcinoecetes* Ball, 1938 (7), is a junior synonym of *Nematopsis* (210). The present species does not seem to have any of the essential characters of *Nematopsis* but is much like *Cephaloidophora*, to which genus it is here provisionally transferred.

Cephaloidophora carpilodei Ball, 1963 (13). In the gut of the xanthid crab *Carpilodes rugatus*. Coconut Island, Hawaii, USA.

Cephaloidophora conformis (Diesing, 1951) Léger & Duboscq, 1911 (122). Syn.: *Gregarina conformis* Diesing, 1851 (90); *Aggregata conformis* (Diesing, 1851) Labbé, 1899 (107); *Frenzelina conformis* (Diesing, 1851) Léger & Duboscq, 1907 (116); *Carcinoecetes conformis* (Diesing, 1851) Ball, 1938 (7). In the

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ceca the gut lumen of the grapsid crab *Pochygrapsus marmoratus* Fabricius. Mediterranean coast of France; coast of Tunisia (214); northeast coast of Spain (213). Tuzet and Ormières (210) declared the name *Carcinoecetes* Ball, 1938, a junior synonym of *Nematopsis* Schneider and returned this species to genus *Cephaloidophora*.

Cephaloidophora drachi Théodoridès, 1962 (201). Syn.: *Cephaloidophora* sp. Tuzet & Ormières, 1961 (210). In the gastric ceca of the xanthid crab *Xantho rivulosus* (Risso). Banyuls, France.

Cephaloidophora dromiae (Frenzel, 1885) Vivarès & Rubió, 1969 (213). Syn.: *Gregarina dromiae* Frenzel, 1885 (61). In gut of the crab *Dromia personata* (= *vulgaris*) (61, 214). Gulf of Naples (61), Blanes, Spain (213); and coast of Tunisia (214). Altho Théodoridès (201) suggested that this gregarine probably should be placed in genus *Cephaloidophora*, the new combination is here attributed to Vivarès and Rubió (213), who first used it.

Cephaloidophora duboscqi Poisson, 1924 (154). In the gut of the alpheid shrimp *Athanas nitescens* Leach. Luc-sur-Mer (Calvados) (154) and Roscoff (211), France.

Cephaloidophora etisi (Ball, 1959) n. comb. Syn.: *Carcinoecetes etisi* Ball, 1959 (12). In the crab *Etisus laevis* Randall. Bombay, India. *Carcinoecetes* Ball, 1938, is a junior synonym of *Nematopsis* (210). The description of the present species fits that of *Cephaloidophora* rather than that of *Nematopsis*.

Cephaloidophora foresti Théodoridès, 1967 (205). In the gut of the crab *Xantho poressa* (Olivier). Banyuls and Villefranche, France.

Cephaloidophora fossor (Léger & Duboscq, 1907) Trégouboff, 1912 (208). Syn.: *Aggregata coelomica* Léger, 1901 [partim] (110); *Frenzelina fossor* Léger & Duboscq, 1907 (116). In gut of the pea crab *Pinnotheres pisum* Penn, living in *Mytilus edulis* L. France (English Channel) (110).

Cephaloidophora guinotae Théodoridès, 1967 (205). In gastric ceca of the xanthid crabs *Xantho granulocarpus* Forest (205), *Pilumnus hirtellus spinifer* Milne-Edwards (205, 213) and *P. hirtellus* L. (205). The 1st 2 hosts at Banyuls and the 3rd at Villefranche, France (205); the 2nd also at Blanes, Spain (213).

Cephaloidophora knoeppfieri Théodoridès, 1962 (201). In gastric ceca of *Pinnotheres pinnotheres* (L.), a pea crab, commensal in the clam *Pinna nobilis* L. Banyuls, France (201); Blanes, Spain (213).

Cephaloidophora mithraxi (Ball, 1951) n. comb. Syn.: *Carcinoecetes mithraxi* Ball, 1951 (10). In the crab *Mithrax forceps* (Milne-Edwards). Bermuda. The generic name *Carcinoecetes* Ball, 1938 (7) is a junior synonym of *Nematopsis* (210). The present species does not resemble *Nematopsis* but its known characters are consistent with those of genus *Cephaloidophora* to which genus it is here transferred.

Cephaloidophora nephropis Tuzet & Ormières, 1961 (210). Syn.: *Porospora nephropis* Léger & Duboscq, 1915 [partim] (126). In the gut of the Norway lobster, *Nephrops norvegicus* (126, 127, 210, 212). Roscoff, France (126, 127, 210, 212).

Cephaloidophora nigrofusca (Watson, 1916) Kamm, 1922 (90). Syn.: *Frenzelina nigrofusca* Watson, 1916 (216). In gut of the fiddler crabs *Uca pugnax* and *U. pugilator*. Cold Spring Harbor, New York, USA.

Cephaloidophora ocellata (Léger & Duboscq, 1907) Kamm, 1922 (90). Syn.: *Aggregata vagans* Léger & Duboscq, 1903 [partim] (112, 116); *Frenzelina ocellata* Léger & Duboscq, 1907 (116). In gut lumen of the hermit crab *Eupagurus prideauxi* Leach. Banyuls, France (112, 201).

Cephaloidophora olivia (Watson, 1916) Kamm, 1922 (90). Syn.: *Frenzelina olivia* Watson, 1916 (216). In gut of 2 littoral crabs *Libinia dubia* Milne-Edwards (216) and *Ocyrops cursor* L. (46). Cold Spring Harbor, New York, USA, (216) and Kalade, Lebanon (46).

Cephaloidophora pinguis Ball, 1963 (13). In gut of the xanthid crab *Carpilodes rugatus*. Coconut Island, Hawaii, USA.

Cephaloidophora poissoni Théodoridès, 1967 (205). In the

alpheid shrimp *Alpheus ruber* Milne-Edwards and *A. dentipes* Guerin. Banyuls, France.

Cephaloidophora (?) *praemorsa* (Diesing, 1851) Kamm, 1922 (90). Syn.: *Gregarina praemorsa* Diesing, 1851 (90); *Aggregata praemorsa* (Diesing, 1851) Labbé, 1899 (107); *Frenzelina praemorsa* (Diesing, 1851) Léger & Duboscq, 1907 (116). In gut and vesicles adhering to the ovary of the crab *Cancer pagurus* L. As Kamm (90) pointed out, this nominal species is based on a mere reference by Redi, in 1684, to something which might have been a gregarine.

Cephaloidophora sp. Syn.: *Carcinoecetes* sp. Ball, 1948 (8). Mainly in the digestive gland but also in the gut lumen of the sand crab *Emerita analoga*. Southern California, USA. Since genus *Carcinoecetes* Ball, 1938 (7) is a junior synonym of *Nematopsis* Schneider, 1892 (210), this species needs to be reassigned. Most known gregarines of crabs belong either to genus *Cephaloidophora* or *Nematopsis*. The known characters of this species seems to be more like those of the former genus.

Genus *Cephalolobus* Kruse, 1959 (99).

Cephalolobus penaeus Kruse, 1959 (99). Attached to filter of stomach of shrimp *Penaeus aztecus* Ives and *P. duorarum* Burkenroad. Florida, USA. Type species. Kruse considered the systematic position of the genus in detail. He did not place it in a family but concluded, "If the life cycle of *C. penaeus* is proven to be similar to that of *Anisolobus*, both genera should be placed in a new family." Théodoridès (202), for reasons not very convincing assigned the genus to family Cephaloidophoridae, where it is here listed for convenience.

Cephalolobus petiti Théodoridès, 1964 (202). Active stages in stomach and cysts in hind-gut of the penaeid shrimp *Solenocera membranacea* (Risso). Banyuls, France.

Genus *Cardiohabitans* Ball, 1959 (12).

Cardiohabitans setnai Ball, 1959 (12). In the mid-gut of the shrimp *Penaeus semisulcatus* de Haan. Bombay, India. Type and only species. Ball did not assign the genus to a family but he compared it both with *Cephaloidophora* and genera in the Porosporidae; it is here provisionally listed with the Cephaloidophoridae. The validity of the genus is questionable.

Family URADIOPHORIDAE Grassé, 1953 (64).

Genus *Uradiophora* Mercier, 1912 (90).

Uradiophora athanasi Poisson, 1924 (154). In the gut of the alpheid shrimp *Athanas nitescens* Leach. Luc-sur-Mer (Calvados), France.

Uradiophora cuenoti (Mercier, 1911) Mercier, 1912 (90). Syn.: *Cephaloidophora cuenoti* Mercier, 1911 (90). In the gut of the shrimp *Atyaephyra desmaresti* Millet. Nancy, France.

Family POROSPORIDAE Labbé, 1899 (107).

Genus *Porospora* Schneider, 1875 (171).

Porospora gigantea (Beneden, 1869) Schneider, 1875 (171). Syn.: *Gregarina gigantea* Beneden, 1869 (17). In the lobster *Homarus gammarus* (L.) and the gastropod *Trochocochlea mutabilis* Philippi. Roscoff (171) and Banyuls (201), France. This is the type and the only species for which the essential generic character, naked sporozoites in a molluscan host, has been demonstrated. This demonstration was by a laboratory infection experiment performed by Hatt (72). The same author (71) obtained partial development also in *Mytilus minmus* Poli.

Porospora nephropis Léger & Duboscq, 1915, emend. Tuzet & Ormières, 1961 (210). Syn.: *Porospora nephropis* Léger & Duboscq, 1915 [partim] (126). In gut of the lobster *Nephrops norvegicus* L. Molluscan host unknown. Roscoff, France.

Porospora pisae Léger & Duboscq, 1911 (123). In the spider crabs *Pisa gibbsii* (123) and *P. armata* (213). Cette (123) and Villefranche-sur-Mer (209), France; northeast coast of Spain

(213). Trégouboff (209) observed peculiarities in this species which convinced Léger and Duboscq (127) that it is not a *Porospora*. These authors did not attempt a reclassification for lack of information on final development of the cysts. Vivarès and Rubió concluded that it is neither a *Porospora* nor a *Nematopsis* (213). It is kept here in *Porospora* provisionally because there is still no clue as to its proper generic classification.

Porospora sp. Théodoridès & Laird, 1970 (206). In gut of the lobster *Homarus americanus*. St. Andrews, New Brunswick, Canada.

Genus *Nematopsis* Schneider, 1892 (172).

Nematopsis calappae (Ball, 1951) n. comb. Syn.: *Carcinoecetes calappae* Ball, 1951 (10). In gut of the oxystomatous crab *Calappa flammea* (Herbst). Intermediate host unknown. Bermuda. *Carcinoecetes* Ball, 1938, is a junior synonym of *Nematopsis* (210). Excepting rare intracellular stages, which could belong to another species, the known characters of this species are consistent with those of *Nematopsis*, to which genus this species is here provisionally assigned. It is noteworthy that Ball's figures show a porosporid character which the author did not mention, the "muscular collar" of the protomerite.

Nematopsis dorippe Bogolepova, 1953 (18). In gut of the oxystomatous crab *Dorippe granulata* de Haan. Sea of Japan.

Nematopsis duorari Kruse, 1966 (100, 101). In gut of the shrimp *Penaeus duorarum* Burkenroad. Spores in the pelecypods *Aequipecten irradians*, *Cardita floridana*, *Chione cancellata*, *Macrocallista nimbosa*. Florida, USA.

Nematopsis goneplaxi Tuzet & Ormières, 1961 (210). Syn.: *Porospora petiti* Théodoridès, 1962 (201). In gut of the crabs *Goneplax angulata* (Penn.) (210, 201) and *G. rhomboides* (213). Intermediate host unknown. Cette (210) and Banyuls (201), France; northeast coast of Spain (213).

Nematopsis grassei (Théodoridès, 1962) Vivarès & Rubió, 1969 (213). Syn.: *Porospora grassei* Théodoridès, 1962 (201). In gut of the oxystomatous crab *Calappa granulata* L. (201). Intermediate host unknown. Banyuls, France (201); northeast coast of Spain (213).

Nematopsis hesperus (Ball, 1938) Tuzet & Ormières, 1961 (210). Syns.: *Carcinoecetes hesperus* Ball, 1938 [TYPE SPECIES] (7); *Porospora hesperus* (Ball, 1938) Théodoridès, 1961 (200); [?] *Nematopsis* sp. Ball, 1951 (11). In gut of the grapsid crab *Pachygrapsus crassipes* Randall. Intermediate host unknown. California, USA.

Nematopsis legeri (de Beauchamp, 1910) Hatt, 1931 (73). Syns.: *Nematopsis mediterranean* Léger, 1905 [nomen oblitum] (113); *Porospora legeri* de Beauchamp, 1910 (16); *P. galloprovincialis* Léger & Duboscq, 1925 (127, 73). In gut of the crabs *Eriphia spinifrons* (16) and *E. verrucosa* (214); spores in the mussel *Mytilus galloprovincialis* and possibly other molluscs (73). Southern coast of France (16) and coast of Tunisia (214). This is one of the best known species of *Nematopsis*, due largely to the work of Hatt (70, 71, 73), who studied its entire life cycle by means of experimental infections. Previously only parts of the life cycle of a porosporid gregarine had been made known experimentally (124, 179). Tuzet and Ormières (210) recently made a careful study of this species to confirm the generic characters.

Nematopsis maraisi (Léger & Duboscq, 1911) Sprague, 1954 (179). Syn.: *Porospora maraisi* Léger & Duboscq, 1911 (123). In gut of the crabs *Macropipus* (= *Portunus*) *depurator* L. (123), *M. vernalis*, *Portunus latipes* (214) and *Macropipus depurator* (213). Intermediate host unknown. Cette, France (123); coast of Tunisia (214); northeast coast of Spain (213).

Nematopsis matutae (Ball, 1959) Tuzet & Ormières, 1961 (210). Syn.: *Carcinoecetes matutae* Ball, 1959 (12). In gut of the crab *Matuta lunaris* (Forskål). Intermediate host unknown. Bombay, India.

Nematopsis mizoulei (Théodoridès, 1964) n. comb. Syn.: *Porospora mizoulei* Théodoridès, 1964 (202). In gut of the

penaeid shrimp *Solenocera membranacea* (Risso). Intermediate host unknown. Banyuls, France. This species is transferred to genus *Nematopsis* because its vegetative stages are similar to those of confirmed species of this genus in crabs and shrimp but strikingly different from those of the single confirmed species of *Porospora*, known only in the lobster.

Nematopsis ostrearum Prytherch, 1938, emend. Sprague, 1949 (176). Syns.: *Nematopsis ostrearum* Prytherch, 1938 [partim] (159), *N. ostrearum* Prytherch, 1940 [partim] (160), [non] *N. legeri* (de Beauchamp, 1910): Kudo (103, 104). In gut of the xanthid crabs *Panopeus herbstii* Milne-Edwards (159, 160), *Eurypanopeus depressus* (Smith) (159, 160), *Neopanope texana sayi* (Smith) (97), *Eurytium limosum* (Say) (176, 180). Spores in the oyster *Crassostrea virginica* (Gmelin). Gulf and Atlantic coasts of North America, as far north as New York (109).

Nematopsis panopei Ball, 1951 (10). In the gut of the xanthid crabs *Panopeus occidentalis* Saussure and *P. herbstii* Milne-Edwards. Intermediate host unknown. Bermuda.

Nematopsis parapeneopsisi (Setna & Bhatia, 1934) n. comb. Syns.: *Hirmocystis* (?) *parapeneopsisi* Setna & Bhatia, 1934 (173); *Protomagalhensia* (?) *attenuata* Setna & Bhatia, 1934 (173). In gut of the shrimp *Parapeneopsis sculptilis* (Heller). Possible intermediate host unknown. Bombay, India. Grassé (64) concluded that these 2 species described by Setna and Bhatia were erroneously assigned as to genera. Although mature cysts were not seen, the known characters (especially disappearance of septa in the satellites) of both species seem to be consistent with those of the Porosporidae. Furthermore, the difference between the 2 (slight difference in shape) seems to be insignificant. Thus, they are treated here as the same species. The specific name of that one appearing first in the paper is retained. Assignment is here made to genus *Nematopsis* because the known stages are much more like corresponding stages of this genus than those of *Porospora* and because the former (100) but not the latter is known to occur in shrimp. Théodoridès (202) suggested that these gregarines may belong to genus *Uradiophora* or maybe *Cephaloidophora*, but this suggestion is untenable because the septa of satellites do not disappear in these genera.

Nematopsis penaeus Sprague, 1954 (179). Syn.: *Porospora penaeus* (Sprague, 1954) Théodoridès, 1965 (203). In the gut of the shrimp *Penaeus aztecus* Ives. Intermediate host unknown. Barataria Bay, Louisiana, USA. Sprague (179) evidently mistook something else for intracellular stages of this parasite, for presence of these has not been confirmed. Kruse (99) reported this species in *P. aztecus*, *P. duorarum* and *P. setiferus*. Hutton et al. (79) found it in these and also *Sicyonia*. Later, Hutton (80) reported it in *P. aztecus*, *P. setiferus* (L.), *P. duorarum* Burkenroad, *P. brasiliensis* Latreil, *Sicyonia typica* Boeck, *Trachypenaeus similis* (Smith), *T. constricta* (Stimson), *Xiphopenaeus kroeyeri* (Heller) and *Solenocera atlantidis* Burkenroad. Considering that gregarines in these hosts have not been studied in detail, that Kruse found 2 species in 1 host, and that ecologic factors related to the different shrimp are diverse, it is probable that several species of *Nematopsis* in these shrimp have been mistaken for one. The work of Kruse (100, 101) supports Sprague's original generic determination.

Nematopsis portunidarum (Frenzel, 1885) Hatt, 1931 (73). Syns.: *Aggregata portunidarum* Frenzel, 1885 [partim] (61, 116, 127); *Nematopsis schneideri* Léger, 1903 (111, 127, 73); *Frenzelina portunidarum* (Frenzel, 1885) Léger & Duboscq, 1907 (116); *Porospora portunidarum* (Frenzel, 1885) Léger & Duboscq, 1911 (122). In gut of crabs *Carcinus maenas* (61, 122) and *C. mediterraneus* (214). Originally reported also in *Macropipus* (= *Portunus*) *arcuatus* (61) but Léger and Duboscq (122) reserved the specific name *portunidarum* for the gregarine in *Carcinus*. Develops experimentally in *Macropipus* (124, 125, 127). Spores in the molluscs *Cardium edule*, *Scrobularia plana* and perhaps others (127). Naples, Italy (61); Etang Pérols, near Montpellier, France (122); coast of Tunisia (214). Théodoridès (201, 203), apparently overlooking experimental proof

by Léger & Duboscq (124, 125) that this is a *Nematopsis*, has continued to call it *Porospora*. *N. schneideri*, represented by spores in *Solen vagina*, is nominal type species by monotypy but, since this is regarded as a junior synonym of *N. portunidarum* (127, 73), the latter is now generally accepted as the type.

Nematopsis prytherchi Sprague, 1949 (176). Syn.: *Nematopsis ostrearum* Prytherch, 1938 [partim] (159); *N. ostrearum* Prytherch, 1940 [partim] (160). In the stone crab *Menippe mercenaria* (Say). Spores in the oyster *Crassostrea virginica* (Gmelin). Louisiana, Florida and the south Atlantic states of USA.

Nematopsis raouadi Vivarès, 1970 (214). In gut of the crab *Portunus latipes*. Coast of Tunisia. It is curious that Vivarès, when comparing *N. raouadi* with *N. maraisi* in the same host, found gymnosporos of the former to be the same size (3.8-4.5 μ) as that given by Léger and Duboscq (122) for the latter (4 μ), while finding the latter to be 7-8 μ .

Nematopsis soyeri (Théodoridès, 1965) n. comb. Syn.: *Porospora soyeri* Théodoridès, 1965 (203). In gut of the penaeid shrimp *Aristeus antennatus* (Risso). Intermediate host unknown. Banyuls, France. Desportes and Théodoridès (45) studied the ultrastructure of the gymnosporos. This species is transferred to genus *Nematopsis* because its vegetative stages are similar to those of confirmed species of this genus in crabs and shrimp but strikingly different from those of the single confirmed species of *Porospora* known only in the lobster.

Nematopsis sp. Kruse, 1966 (100). In the gut of the shrimp, *Penaeus duorarum* Burkenroad. Intermediate host unknown. This is the "small gymnosporos species of *Nematopsis*" which was found in shrimp with *N. duorarum* (the "large gymnosporos species") but which was not produced by spores from the pelecypods. Florida, USA.

Nematopsis sp. Sprague, 1954 (179). In 1932, Pearse (142) reported the presence of "gregarine cysts" on the walls of the rectum of the calico crab *Eriphia gonagra* (Fabricius) collected at Dry Tortugas off the coast of Florida, USA. Sprague (179) expressed the opinion that this is a *Nematopsis*, not only because the limited description is characteristic of the porosporid gregarines but also because the best known species *N. legeri*, also occurs in a species of *Eriphia*, *E. spinifrons*.

Nematopsis sp. Vivarès & Rubió, 1969 (213). In gut of the crab *Ethusa mascarone*. Northeast coast of Spain (Blanes).

Nematopsis sp. Vivarès & Rubió, 1969 (213). In gut of the crab *Parthenope angulifrons*. Northeast coast of Spain (Blanes).

[*Nematopsis* sp. ?] "Gregarines" Cuckler & Fichter, 1939 (42). In the gut of the crab *Cancer productus*. Argyle Bay, San Juan Island, Washington, USA. Since this gregarine was found in a crab host and since as many as 3 nuclei were seen in 1 compartment (suggesting fusion of satellites), there is reason to suspect that it is a species of *Nematopsis*.

Genus *Pachyporospora* Théodoridès, 1961 (200).

Pachyporospora lamellaris (Bogolepova, 1953) Ormières, 1968 (141). Syn.: *Nematopsis lamellaris* Bogolepova, 1953 (18); *Tricystis plicata* Poljanskij & Chejsin, 1965 (52). In gut of a crab. Sea of Japan. Poljanskij and Chejsin (52), in their revision (1965) of Dogiel's (1951) book on protozoa, reproduced Bogolepova's (1953) sketch of this species and said it was from Dogiel (1951). They did not say where they got the name *Tricystis plicata* and we have been unable to find it elsewhere in the literature.

Pachyporospora laubieri Théodoridès, 1961 (200). In the gut of the crabs *Ateleocyclus septemdentatus* Montagu (200) and *A. rotundatus* (213). Banyuls, France (200); northeast coast of Spain (213). TYPE SPECIES.

Pachyporospora retorta Ormières, 1968 (141). In gut of the crabs *Macropipus holsatus* (F.) (141, 214) and *M. vernalis* (213). Sète, France (141); coast of Tunisia (214); northeast coast of Spain (213).

Family and genus uncertain

Gregarina portuni Frenzel, 1885 (61). In gut of the crab *Macropipus* (= *Portunus*) *arcuatus*. Naples, Italy. Monocystid gregarine, certainly not genus *Gregarina* and unlike other known gregarines in decapods.

Gregarines, identity not specified. Heckmann (74) found intestinal gregarines in a number of decapods in Hawaii. Heldt (75) described, without naming, gregarines from the shrimp *Penaeus kerathurus* (Forskål) in the Gulf of Tunis. Théodoridès (202) judged that these last ones belonged to 2 species, a *Uradiophora* and a *Porospora*.

Poljanskij and Chejsin (52) mentioned "certain species of *Merogregarina* from the alimentary tract of crabs" but we have been unable to find mention of them elsewhere.

Subclass COCCIDIA Lcuckart, 1879 (78).

Order EUCCOCIDA Léger & Duboscq, 1910 (78).

Family SELENOCOCCIDIIDAE Poche, 1913 (153).

Genus *Selenococcidium* Léger & Duboscq, 1909 (120).

Selenococcidium intermedium Léger & Duboscq, 1909 (120). In gut of European lobster *Homarus*. France. This is the type of the genus and the only species in the family. The authors described it only briefly in 1909 and more fully in 1910 (121).

Family AGGREGATIDAE Labbé, 1899 (107).

Genus *Aggregata* Frenzel, 1885 (61), emend. Léger & Duboscq, 1906 (114).

Aggregata coelomica Léger, 1901, emend. Léger and Duboscq, 1906 (114). Syn.: *Aggregata coelomica* Léger, 1901 [partim] (110, 114). In gut wall of the crab *Pinnotheres pisum* Penn., which lives in *Mytilus edulis* L. The original "species" eventually became in part the gregarine, *Cephaloidophora fossor*. France (English Channel) (110). Found recently by Vivarès and Rubió (213), in the same host, on the northeast coast of Spain.

Aggregata eberthi (Labbé, 1895) Léger & Duboscq, 1906 (115). Syn.: *Aggregata portunidarum* Frenzel, 1885 [partim] (61); *Benedenia eberthi* Labbé, 1895 (105) [cited by Labbé, 1899 (107), altho we can find no mention of this name in the 1895 paper]. Schizogonic stages in the portunid crabs *Macropipus* (= *Portunus*) *arcuatus* (61), *M. depurator* (115, 213), *M. tuberculata* (213), *M. bolivari* (213), *M. corrogatus* (214) and probably, *M. vernalis* (214). Sporogony in the cuttlefish *Sepia officinalis*. Common and widespread. Naples, Italy (61); Sète, France (115); Tunisia (214); northeast coast of Spain (213). Since the synonymy is quite complicated, only the most significant synonyms are given here. [See Labbé, 1899 (107) and Léger and Duboscq, 1908 (117) for more details.] Why the junior synonym *eberthi* was conserved instead of the original name *portunidarum* we have been unable to determine, altho the former is now fixed by the provisions of Art. 23(b) of the International Code of Zoological Nomenclature (82). We believe that this species, as Calkins (22) said, is the type; altho Pellérdy (143) said *A. octopiana* (Schneider, 1875) is the type. Our reasoning is that the former, being the only original species in genus *Aggregata*, must be type by monotypy as provided by Art. 68(c) (82). It may be pertinent, however, to note that the name *A. portunidarum* was originally applied inadvertently to 2 species, 1 a gregarine which later became *Nematopsis portunidarum*. This species has been the object of important life cycle studies by Léger and Duboscq (114, 115, 117), Pixell-Goodrich (150) and Dobell (49), and electron microscope studies by Porchet-Henneré and Richard (156, 157, 158).

Aggregata inachi Smith, 1905 (174), emend. Léger & Duboscq, 1906 (114). Schizogony stages in the gut wall of the crabs *Inachus dorsettensis* (174, 214) and *I. communissimus* (213); indistinguishable forms in *I. scorpio* (174). Stages in molluscan host unknown. Naples, Italy (174); coast of Tunisia (214); northeast coast of Spain (213). Smith, like earlier workers, presumed that

the cysts in the gut wall belonged to a gregarine with free stages in the lumen, altho he saw only cysts of this species. Léger and Duboscq (114, 117) pointed out the incorrectness of this view.

Aggregata leandri Pixell-Goodrich, 1950 (152). Schizogony stages in gut wall of the shrimp *Leander squilla* L. Molluscan host unknown. Naples, Italy. Found also in the shrimp *Solenocera membranacea* (Risso) and *Acanthephyra eximia* Smith by Théodoridès (204) at Banyuls, France.

Aggregata vagans Léger & Duboscq, 1903, emend. Léger & Duboscq, 1906 (114). Syn.: *Aggregata vagans* Léger & Duboscq, 1903 [partim] (112). In gut wall of the crab *Eupagurus prideauxi* Leach. Banyuls, France. The original species eventually became in part the gregarine *Cephaloidophora ocellata*.

Aggregata sp. Léger & Duboscq, 1908 (117). In coelom of the crab *Pachygrapsus marmoratus* F. France (117). Found recently in the same host by Vivarès and Rubió on the northeast coast of Spain (213).

Aggregata sp. Setna & Bhatia, 1934 (173). Schizogony stages in gut wall of the shrimp *Parapeneopsis sculptilis* (Heller). Molluscan host unknown. Bombay, India.

Aggregata sp. Vivarès & Rubió, 1969 (213). Unidentified species of *Aggregata* were found in the crabs *Corystes cassivelaunus*, *Ateocyclus rotundus*, *Xantho porressa*, *Goneplax rhomboides*, *Parathenope angulifrons*, and *Macropodia rostrata*. North-east coast of Spain.

Aggregata sp. Vivarès, 1970 (214). Unidentified species of *Aggregata* were found in the crabs *Carcinus mediterraneus*, *Dromia personata*, *Portunus latipes*, *Xaiva biguttata*, *Macropipus vernalis*, *Pilumnus spinifer* and *Pilumnus hirtellus*. Coast of Tunisia.

Subphylum MICROSPORA Sprague, 1969 (188).

Class MICROSPOREA Corliss & Levine, 1963 (38).

Order MICROSPORIDA Balbiani, 1882 (6).

Family NOSEMATIDAE Labbé, 1899 (107).

Genus *Nosema* Nägeli, 1857 (135), emend. Pérez, 1905 (146).

Nosema frenzelinae Léger & Duboscq, 1909 (118, 119). Hyperparasite of the gregarine *Cephaloidophora conformis* (Diesing) in the crab *Pachygrapsus marmoratus* (Fabricius). France.

Nosema michaelis Sprague, 1970 (191). Syn.: *Nosema sapidi* DeTurk, 1940 [partim] (47); *N.* sp. Sprague, 1965 (182). In muscles of the crab *Callinectes sapidus* Rathbun. Atlantic and Gulf states of North America. A significant factor in crab mortality. DeTurk mistook spores of this species for sporoblasts of *N. sapidi*. Sprague et al. (187) made an electron microscope study of *N. michaelis*.

Nosema nelsoni Sprague, 1950 (177). Syn.: [non] *Nosema pulvis*: Jones (86). In muscles of penaeid shrimp. Widely distributed. First reported in *Penaeus aztecus* Ives in Louisiana, USA. Later found by Woodburn et al. (217), Hutton (80) and Hutton et al. (79) also in *P. duorarum* Burkenroad in Florida, USA. Recently found by Sprague and Vernick (189), who studied its fine structure, in *P. setiferus* from Georgia, USA. H. F. P. Champion (pers. com.) found a similar or identical species in the muscles of *Metapenaeus monocercus* in the Republic of South Africa. Kruse (pers. com.) reported *Nosema* sp., which may be identical with *N. nelsoni*, in the shrimp *Solenocera vioscai* and *Xiphopeneus kroyeri*, in Louisiana, USA.

Nosema pulvis Pérez, 1905 (145). In muscles of the crab *Carcinus maenas*. France. First described very briefly, this parasite was described more fully in the same year (146).

Nosema sapidi DeTurk, 1950, emend. Sprague, 1970 (191). Syn.: *Nosema sapidi* DeTurk, 1940 [partim] (47). In muscles of the crab *Callinectes sapidus* Rathbun. Beaufort, North Carolina, USA. This is distinguished from the other 3 species of *Nosema* described in muscles of decapods by having relatively large spores which (when stained) have light areas at the 2 ends and a dark band in the middle. DeTurk included in his

description also *N. michaelis* Sprague, 1970 (191), the spores of which he mistook for sporoblasts of *N. sapidi*.

Nosema spilotremae Guyénot & Ponce, 1925 (66). Hyperparasitic in encysted metacercariae of the digenetic trematode *Microphallus* (= *Spilotrema*) *carcini* (198), which is parasitic in the crab *Carcinus maenas*. Stanier et al. recently (193) did an electron microscope study of this species.

Nosema sp. In 1963, one of us (V.S.) found a species similar to *N. spilotremae* in encysted microphallid metacercariae in a crab *Callinectes sapidus* collected in Pry Cove on the eastern shore of Chesapeake Bay, Maryland, USA. M. W. Newman (pers. com.) found a *Nosema*, possibly the same species also, in North Carolina, South Carolina and Georgia, USA, in 1969.

Genus *Gurleya* Doflein, 1898 (51).

Gurleya miyairii (Kudo, 1924) Sprague, 1970 (191). Syn.: *Thelohania* sp. Miyairi, 1909 (102); *Cocconema miyairii* Kudo, 1924 (102). In the muscles of 2 species of *Atyephira*. Japan.

Genus *Thelohania* Henneguy, 1892 (77).

Thelohania cambari Sprague, 1950 (178). In muscles of the crayfish *Cambarus bartoni*. Georgia, USA.

Thelohania contejeani Henneguy, 1892 (77). In muscles of the crayfish *Astacus fluviatilis* (77); *A. palipes* (53, 168) and *A. astacus* (53, 199). France (77); Germany (168); Russia (170) and Finland (199).

Thelohania duorara Iverson & Manning, 1959 (83). Syn.: *Thelohania hunterae* Jones, 1958 [nomen nudum] (86); *Thelohania* sp. Kruse, 1959 (99). In muscles of the shrimp *Penaeus duorarum* (83, 80, 84), *P. brasiliensis* (84) and *P. aztecus* (80). Florida, USA.

Thelohania giardi Henneguy, 1892 (77). In muscles of the shrimp *Crangon vulgaris*. France. TYPE SPECIES by subsequent designation, Gurley, 1893 (65).

Thelohania macrocystis Gurley, 1893 (65). In muscles of the shrimp *Palaemonetes varians*. Italy. Kudo (102) questioned the validity of this species.

Thelohania maenadis Pérez, 1904 (144). In muscles (usually) of the crab *Carcinus maenas*. Pérez (147) reported 1 case in which an ovary was parasitized, resulting in parasitic castration. This parasite, first reported briefly, was described more fully in 1905 (146). France (Arcachon).

Thelohania octospora Henneguy, 1892 (77). In muscles of the shrimp *Palaemon rectirostris*, *P. serratus* and *P. elegans*. France, England and the Black Sea (76, 77, 151).

Thelohania paguri Pérez, 1927 (148). In body cavity of the hermit crab *Eupagurus bernhardus*. France.

Thelohania penaei Sprague, 1950 (177). In gonad of the shrimp *Penaeus setiferus*. Louisiana, USA. H. F. B. Champion (pers. com.) found a similar or identical parasite in the ovary of *Penaeus indicus* in the Republic of South Africa.

Thelohania petrolisthis Sprague, 1970 (191). Syn.: *Thelohania* sp. Sprague, 1950 (177). In muscles of the crab *Petrolisthes armatus*. Louisiana, USA.

Thelohania sp. Sogandares-Bernal, 1962 (175). In muscles of the crayfish *Cambarellus schufeldti*. Louisiana, USA.

Thelohania sp. Thomas. (M. M. Thomas. Pers. com.) In gonad and muscles of the shrimp, *Penaeus semisulcatus* de Haan. South India.

Genus *Pleistophora* Gurley, 1893 (65).

Pleistophora cargo (Sprague, 1966) Sprague, 1970 (191). Syn.: *Plistophora cargo* Sprague, 1966 (183). In muscles of the crab *Callinectes sapidus* Rathbun. Maryland, USA.

Pleistophora miyairii (Kudo, 1924) Sprague, 1970 (191). Syn.: *Nosema anomalum* (?) Miyairi, 1909 (102); *Plistophora miyairii* Kudo, 1924 (102). In digestive tract of *Atyephira* sp. Japan.

Pleistophora sogandaresi (Sprague, 1966) n. comb. Syn.: *Plistophora* sp. Sogandares-Bernal (175); *Plistophora sogandaresi*

Sprague, 1966 (183). In muscles of the crayfish *Cambarellus puer* Hobbs, Louisiana, USA. Since *Pleistophora* Labbé, 1899, is a junior synonym of *Pleistophora* Gurley, 1893 (186, 192), this species is transferred to the latter genus.

Pleistophora sp. Baxter, Rigdon & Hanna, 1970 (15). In the muscles of the shrimp *Penaeus setiferus* and *P. aztecus*. Galveston Bay, Texas, USA. Probably identical with *Pleistophora* sp. Kruse, 1970 (191) found in the same host.

Pleistophora sp. Sprague, 1970 (191). In muscles of the shrimp *Palaemonetes pugio* Holthius. Georgia, USA.

Class HAPLOSPOREA Caullery, 1953 (27).

Order HAPLOSPORIDA Caullery & Mesnil, 1899 (24).

Family HAPLOSPORIDIIDAE Caullery & Mesnil, 1905 (25).

Genus *Minchinia* Labbé, 1896 (106).

Minchinia louisiana Sprague, 1963 (181). Syn.: *Haplosporidium* sp. Sprague, 1954 (179). In the gut wall of the mud crab, *Panopeus herbstii*. Louisiana, USA.

Minchinia sp. Rosenfield, Buchanan, Chapman, 1969 (162). In gill, muscles and gut tissue of the crab *Eurypanopeus depressus*. Virginia, USA.

Genus *Urosporidium* Caullery & Mesnil, 1905 (26).

Urosporidium crescens DeTurk, 1940 (48). Hyperparasitic in encysted metacercariae of a distome identified by DeTurk as *Spelotrema nicolli*, now in genus *Microphallus* (198). North Carolina (48); Maryland and Virginia (191), USA. Sprague (191) recently made observations on the structure of this species, Couch (41) studied its effect on its trematode host and Perkins (149) studied its ultrastructure.

Urosporidium sp. Sprague, 1970 (191). Hyperparasite in encysted metacercariae of *Microphallus* sp. in the shrimp, *Palaemonetes pugio*. Georgia, USA.

Subphylum CILIOPHORA Doflein, 1901 (78).

Class CILIATEA Perty, 1852 (78).

Subclass HOLOTRICHIA Stein, 1859 (78).

Order ASTOMATIDA Schewiakoff, 1896 (78).

Family ANOPLOPHRYIDAE Cépède, 1910 (28).

Genus *Anoplophrya* Stein, 1860 (136).

Anoplophrya minima Léger & Duboscq, 1909 (120). This very rare species of astome ciliate was reported from the posterior intestine and rectum of the lobster, *Homarus gammarus*. France.

Order HYMENOSTOMATIDA Dèlage & Hérouard, 1896 (78).

Suborder TETRAHYMENINA Fauré-Fremiet, 1936 (78).

Family COHNILEMBIDAE Kahl, 1933 (78).

Genus *Anophrys* Cohn, 1866 (34).

Anophrys maggii Cattaneo, 1888 (23). Syn.: *Anophrys sarcophaga* Cohn, 1866 (34). Occurring naturally, but rarely, in hemolymph of *Carcinus maenas*. Western coast of France (155). Poisson (155) stated that the parasitic *A. maggii* of Cattaneo is identical with the free-living *A. sarcophaga* of Cohn, and thus the name *A. maggii* should be a junior synonym of *A. sarcophaga*. However, Tucker (14) argued that until more is known about these forms both names should be retained. Bang (14) was able to induce fatal experimental infections of *A. maggii* in *Carcinus maenas*, *Maia squinado* and *Macropipus depurator*. The ciliates within the hemolymph of these crabs were found to be eating host leukocytes. Bang (14) reported that the events leading to death in these *Anophrys*-infected crabs were anemia and asphyxiation followed by severe bacteremias.

Order APOSTOMATIDA Chatton & Lwoff, 1928 (78).

Family FOETTINGERIIDAE Chatton, 1911 (29, 32).

Genus *Synophrya* Chatton & Lwoff, 1926 (29, 32).

Synophrya hypertrophica Chatton & Lwoff, 1926 (32). Found

in gills of the following marine crabs along the west coast of France: *Macropipus* (= *Portunus*) *depurator* at Banyuls and Roscoff, *M. puber* at Roscoff and Wimereux, *M. holstatus* at Roscoff, *M. pusillus* at Roscoff and Banyuls, *M. tuberculatus* at Banyuls, and *Carcinus maenas* at Roscoff. Recently found by Vivarès and Rubió (213) in *Macropipus tuberculatus*, *M. bolivari*, *M. depurator* and *M. vernalis* on the northeast coast of Spain. Vivarès (214) found the following decapods infected with *S. hypertrophica* in the Gulf of Tunis: *Dorippe lanata*, *Carcinus mediterraneus*, *Portunus latipes*, *Macropipus arcuatus*, *M. corrugatus*, *M. vernalis*, *Pilumnus spinifer* and *P. hirtellus*. This apostome causes considerable pathogenesis in gills of hosts (32). Life cycle fully described and figured by Chatton and Lwoff (32).

Genus *Gymnodinioides* Minkiewicz, 1912 (130).

Gymnodinioides calkinsi Chatton & Lwoff, 1935 (32). Phoronts on the gills and trophonts on the cuticle of *Palaemonetes* sp. Woods Hole, Massachusetts, USA.

Gymnodinioides caridinae (Miyashita, 1933) Chatton & Lwoff, 1935 (32). Syn.: *Hyalospira caridinae* Miyashita, 1933 (132). Found on the "hairs" at base of antennules and on the gill filaments of *Xiphocaridina compressa* (freshwater shrimp of Japan), *Leander paucidens* and *Macrobranchium nipponense* by Miyashita in Japan. Reported as *Hyalospira caridinae* from *Palaemon varians* by Debaisieux (44) in Europe. Debaisieux gave a fairly detailed account of the life cycle of this species on the brackish water *Palaemon varians*.

Gymnodinioides inkystans Minkiewicz, 1913 (130). Phoronts on the gills and trophonts on the cuticles of *Eupagurus bernhardus*, *E. prideauxii* (130) and *Carcinus maenas* (32). Roscoff, France (32, 130). Also possibly observed by Minkiewicz, according to Chatton and Lwoff (32), on the following decapod genera: *Maia*, *Xantho*, *Porcellana* and *Galathea*. Trager (207) reported this species from the gills of *Pagurus longicarpus* at Woods Hole, Massachusetts, USA. According to Trager, the excystment of the phoronts of this species is synchronized with the molt of the host, and the conditions necessary to bring about excystment can be simulated in the laboratory.

Gymnodinioides sp. Chatton & Lwoff, 1935 (32). In the gastrovascular cavity of the anemone *Sagartia parasitica* found attached to *Eupagurus prideauxii*.

Gymnodinioides sp. Trager, 1957 (207). Phoronts on gills of *Uca pugnax*. Woods Hole, Massachusetts, USA. About 80% of the crabs examined were infested. Trager reported differences in this species and *G. inkystans* to be 10 or 11 ciliary bands rather than 9 as found on the latter. Also, this undescribed species had a more pointed and twisted posterior end than *G. inkystans*.

Genus *Phorophrya* Chatton, Lwoff & Lwoff, 1930 (30).

Phorophrya fallax Chatton, Lwoff & Lwoff, 1930 (30). A hyperparasite on the phoronts of *Gymnodinioides inkystans* on *Carcinus maenas*. Roscoff, France.

Phorophrya insidiosa Chatton, Lwoff & Lwoff, 1930 (30). Usually found as a hyperparasite on the phoronts of *Gymnodinioides corophii* on amphipods, but in at least 1 instance (32) reported as a hyperparasite of *Gymnodinioides* sp. from *Carcinus*. Members of this genus are characteristically hyperparasitic or phoretic on the phoronts of other apostomes (32).

Genus *Polyspira* Minkiewicz, 1912 (130).

Polyspira delagei Minkiewicz, 1912 (130). On the gills of the following hosts: *Eupagurus bernhardus*, *Galathea squamifera*, and *Macropodia rostrata*. Roscoff, France. Found only in decapod crustaceans (32). Chatton and Lwoff were unable to transmit it easily to *Macropipus* sp. in the laboratory (32). These authors reported that this species is often found in company with *Gymnodinioides inkystans*.

Genus *Phoretophrya* Chatton, Lwoff & Lwoff, 1930 (31).

Phoretophrya nebaliae Chatton, Lwoff & Lwoff, 1930 (31). Altho usually found on the non-decapod *Nebalia geffroyi*, this species has also been reported from *Carcinus maenas* and *Macropipus holsatus*. Roscoff, France.

Genus *Terebrospira* Debaisieux, 1960 (44).

Terebrospira lenticularis (Debaisieux, 1957) Debaisieux, 1960 (44). Syn.: *Chattonia lenticularis* Debaisieux, 1957 (43). On the cuticle of *Palaemon varians* collected from the mouth of Schelde River (brackish water) in Western Europe (Netherlands). Debaisieux (44) gave the life cycle and host-ciliate relationship of this species in some detail. This species penetrates the cuticle of its host shrimp and thus can cause some damage.

Genus *Hyalophysa* Bradbury, 1966 (21).

Hyalophysa chattoni Bradbury, 1966 (21). Phoronts found on the gills and trophonts on the molts of several different species of decapods from the coasts of Washington and California, USA: *Pagurus hirsutiusculus*, *P. samuelis*, *P. granosimanus*, *P. alaskensis*, *Cancer oregonensis*, and *Lophopanopeus belli*. According to Bradbury, the genus *Hyalophysa* belongs to that group of apostomes phoretic on Branchyura, Anomura, Isopoda and Cirripedia which develop in the exuvial fluid of their hosts. Other ecologically related genera are *Gymnodinioides*, *Polyspira* and *Phoretophrya*. *H. chattoni* requires only 1 host for its entire life cycle.

Order CHONOTRICHIDA Wallengren, 1895 (78).

Family CHILODOCHONIDAE Foche, 1913 (153) emend.
Mohr, 1948 (133).

Genus *Chilodochona* Wallengren, 1895 (215).

Chilodochona microchilus Wallengren, 1895 (215). On mouth parts of *Macropipus depurator*. Southern Sweden.

Chilodochona quennerstedti Wallengren, 1895 (215). On *Ebalia turnebecki* and *Macropipus depurator*. Southern Sweden (87). Mohr (133) divided the Order Chonotrichida into 3 families and pointed out that most chonotrichs found on decapod crustaceans are in the family Chilodochonidae.

Genus *Kentrochona* Rompel, 1894 (161).

Kentrochona nebaliae Rompel, 1894 (161). On the decapods *Ebalia turnebecki* and *Portunus depurator*. Southern Sweden. Also reported by Doflein (50) from Trieste and Rovigno, in the northern Adriatic.

Subclass PERITRICHIA Calkins, 1933 (78).

Order PERITRICHIDA Stein, 1859 (78).

Suborder SESSILINA Kahl, 1933 (78).

Family VORTICELLIDAE Ehrenberg, 1838 (140).

Genus *Vorticella* L., 1767 (136), emend. Ehrenberg, 1838 (140).
Vorticella verrucosa Dons, 1915 (55). Found on *Laomedea* sp. from Norway. Of many described species of *Vorticella* (87, 137, 140), this form is the only named vorticellid habitually found on decapods. Many species have been reported from non-decapod crustaceans.

Genus *Zoothamnium* Bory, 1826 (19).

Zoothamnium carcini Kent, 1881 (98). On *Carcinus maenas* from the south coast of England.

Zoothamnium procerius Kahl, 1933 (87). On legs of the crayfish *Astacus fluviatilis* from vicinity of Erlangen, Germany. Nenninger (137) reported a variety of this species, which she named *Z. procerius* var. *varius* from both gammarids and crayfish, but until subspecies names are more generally accepted for ciliates, this form is recognized as *Z. procerius*.

Zoothamnium sp. Ryder, 1883 (163). On "back and legs" of the oyster commensal decapod *Pinnotheres ostreum* Say, Maryland, USA. Ryder suggested that because the *Zoothamnium* supported on its "stalks" bacteria and "vibriones," it might be of benefit as a source of food to the oyster in which its crab host lives.

Family EPISTYLIDIDAE Kahl, 1933 (87).

Genus *Epistylis* Ehrenberg, 1832 (58).

Epistylis astaci Nenninger, 1948 (137). On the gills of *Astacus fluviatilis*, Germany.

Epistylis bimarginata Nenninger, 1948 (137). On legs of *Astacus fluviatilis*, Germany. Nenninger described this peritrich from the crayfish as a variety, *E. bimarginata* var. *urnula*, but again, until subspecific names are more generally accepted for ciliates this form is recognized only as a member of the species *E. bimarginata*.

Epistylis cambari Kellicott, 1885 (94). On gills of a species of *Cambarus*. Northeastern United States.

Epistylis niagarae Kellicott, 1883 (92). On body surface of crayfish (?) in freshwater. Northern United States.

Epistylis sp. Hutton, 1964 (80). On the commercial shrimp *Penaeus duorarum*. Numerous localities in Florida, USA.

Epistylis sp. Hutton, 1964 (80). On the deep-water shrimp *Hymenopenaeus robustus*, from 170 fathoms off Daytona Beach, Florida.

Epistylis sp. Pearse, 1932 (142). On gills of *Coenobita clypeastus*, at Garden and Long Keys, Florida, USA. On *Geograpsus lividus* and *Pachygrapsus transversus* in the Florida keys, USA.

Genus *Carchesium* Ehrenberg, 1832 (58).

Carchesium granulatum Kellicott, 1887 (95). On surface of freshwater crayfish of genus *Cambarus*. USA.

Family VAGINICOLIDAE de Fromentel, 1874 (62).

Genus *Vaginicola* Lamarck, 1816 (108).

Vaginicola paguri (André, 1910) Kahl, 1933 (87). Syn.: *Cothurnia paguri* André, 1910 (2). From cuticle of *Eupagurus bernhardus*. Roscoff, France.

Genus *Cothurnia*, Ehrenberg, 1832 (58).

Cothurnia astaci Stein, 1854 (195). On the branchial appendages of *Astacus fluviatilis*. Europe. Thought to be associated with mass mortalities of freshwater crayfish in Italy as reported by Ninni (139) and by Kent (98). Kent (p. 721) said, "During a fatal epidemic among the freshwater crayfish of Lombardy and Venetia in the year 1863, it is reported by Ninni that the dying crustacea were completely infested with an Infusorium, referable to the genus *Vaginicola*, probably identical with the present species [*C. astaci*], its abnormal development on the branchial appendages apparently producing the death of the crustacean through asphyxia."

Cothurnia curca Stein, 1854 (195). From freshwater crayfish. Europe.

Cothurnia sieboldi Stein, 1854 (195). On the branchial appendages of the freshwater crayfish *Astacus fluviatilis*. Europe.

Cothurnia variabilis Kellicott, 1884 (93). Occurs by thousands on gills of crayfish *Cambarus affinis* (93) and *Astacus fluviatilis* (137).

Family LAGENOPHRYIDAE Kahl, 1935 (89).

Genus *Lagenophrys* Stein, 1852 (194).

This large genus of loricate peritrichs (52 species at present) is remarkable in that it has 22 species that are found only on decapod crustaceans and have strong host specificity.

Lagenophrys aegleae Mouchet-Bennati, 1932 (134). On the gills of the freshwater crayfish *Aeglea laevis*. Uruguay.

Lagenophrys articularis Nie & Ho, 1943 (138). On the antennae, legs, and swimmerets of *Palaemon nipponensis*. China.

Lagenophrys awerinzewi Abonyi, 1928 (1). On gills of the freshwater river crab *Telphusa fluviatilis*. Africa. Abonyi gave this lagenophryiid its specific name based upon the description of Awerinzew (5).

Lagenophrys bispinosa Kane, 1965 (91). On swimmerets of *Cherax rotundus setosus*. Stream near Newcastle, New South Wales, Australia.

Lagenophrys branchiarum Nie & Ho, 1943 (138). On the gills (only) of *Palaemon nipponensis*. China.

Lagenophrys callinectes Couch, 1967 (40). On both surfaces of the gill lamellae of the commercial, marine and brackish water crab *Callinectes sapidus*. From Chesapeake Bay, Maryland and Virginia; south to Gulf of Mexico estuarine waters wherever blue crab is found. During summer months infestations are so heavy that the gill surfaces of the crab may be completely covered.

Lagenophrys communis Kane, 1965 (91). On the telsons, swimmerets, and cuticles of the crayfish *Cherax destructor*, *C. albidus*, *Euastacus serratus*, *E. nobilis*, and *Engaeus* sp. Australia.

Lagenophrys darwini Kane, 1965 (91). On the gill filaments of *Cherax quadricarinatus*. Freshwater, near Darwin, northern Australia.

Lagenophrys deserti Kane, 1965 (91). In the branchial chambers and on gill filaments of *Cherax tenuimanus* and *C. quinquecarinatus*. Rivers in southeastern Australia.

Lagenophrys dungogi Kane, 1965 (91). On the gill filaments of a single specimen of *Euastacus* sp. Stream in Dungog, Australia.

Lagenophrys engaei Kane, 1965 (91). On brachiolegite membranes and gill filaments of crayfish *Engaeus victoriensis*, and on gill filament and gill bases of crayfish *Austroactaeus hemi-cirratalis*. Near Melbourne, Australia.

Lagenophrys eupagurus Kellicott, 1894 (96). On gills of hermit crab *Eupagurus* sp. Woods Hole, Massachusetts, USA.

Lagenophrys latispinosa Kane, 1965 (91). On the flat surfaces of gills, gill bases and brachiolegite membranes. On *Cherax destructor* near Melbourne, Australia. On *C. destructor* and *C. albidus* from Victoria, Australia. On *C. rotundus* from New South Wales, Australia. Kane remarked that the loricae of many generations of this species are superimposed on one another on the cuticle of older hosts.

Lagenophrys lawrii Kane, 1965 (91). On flat surfaces of the gills of *Cherax quadricarinatus*. Near Darwin, Australia.

Lagenophrys lingulata Kane, 1965 (91). Found mostly on gill filaments, occasionally on the brachiolegite membranes. On *Cherax destructor* and *C. albidus* from Victoria, Australia, and on *C. rotundus* in central New South Wales, Australia. Type host and locality are *Cherax destructor* from around Melbourne, Australia.

Lagenophrys lunatus Imamura, 1940 (81). On body cuticle of shrimp *Leander paucidens* (83) and *Palaemon varians* (44). Japan (81); Belgium (44). One of us (J.C.) has found this species on *Palaemonetes vulgaris* from Chincoteague Bay, Maryland. Debaisieux (44) has done an excellent job of working out the life-cycle of this species.

Lagenophrys metopauliadis Corliss & Brough, 1965 (39). On the gill lamellae of a freshwater crab *Metopaulias depressus*. Jamaica. This was the 1st species of *Lagenophrys* to be reported from a brachyuran crab.

Lagenophrys occlusa Kane, 1965 (91). Restricted to the anterior portion of the branchial chambers of *Cherax destructor*, *C. albidus*, and *C. rotundus*. Victoria and New South Wales, Australia.

Lagenophrys rugosa Kane, 1965 (91). On the gill filaments of freshwater crayfish *Geocherax falcata*. Western Victoria, Australia.

Lagenophrys seticola Kane, 1965 (91). Original description

based on specimens found on a land crayfish *Engaeus fultoni* from a burrow in a river bank near Melbourne, Australia. Found attached to setae, tail fan, swimmerets, gill base and edge of brachiolegites. Specimens referable to this species have also been found on *Cherax rotundus setosus*, *C. albidus*, *C. destructor* and *Euastacus nobilis* from Australia.

Lagenophrys spinosa Kane, 1965 (91). On the cuticle, swimmerets, telson and carapace of the crayfish *Cherax destructor*. Victoria, Australia.

Lagenophrys willisi Kane, 1965 (91). On gill filaments of freshwater crayfish *Cherax destructor*, *C. albidus* and *C. rotundus*. Australia.

Subclass SPIROTRICHIA Bütschli, 1889 (78).

Order HETEROTRICHIDA Stein, 1859 (78).

Suborder HETEROTRICHINIA Stein, 1859 (78).

Family FOLLICULINIDAE Dons, 1914 (54).

Members of this family belong to several different genera, all species of which are loricate. Species reported here as epibionts of decapods also may be, and usually are, found on substrates other than decapods and generally lack host specificity. Fauré-Fremiet (60) and Hadži (68) reviewed the species in this family and their various substrates.

Genus *Pebrilla* Giard, 1888 (63).

Pebrilla paguri Giard, 1888 (63). Found on the cuticle of *Pagurus bernhardus* by Giard, in 1888, at Pouliguen and at Roscoff, France. Later (1936), reported from cuticle of *Clibanarius misanthropus* from France by Fauré-Fremiet (60), who believed that, tho this species has features characteristic of members of genus *Folliculinopsis* Fauré-Fremiet, 1936, its generic name *Pebrilla* should be retained.

Genus *Platyfolliculina* Hadži, 1938 (67).

Platyfolliculina paguri Andrews & Reinhard, 1943 (3). On the abdomen of hermit crab *Pagurus pubescens*. State of Washington, USA.

Genus *Metafolliculina* Dons, 1925 (56).

Metafolliculina andrewsi Hadži, 1938 (67). On *Pagurus floridanus* as reported by Andrews (4). Texas Gulf Coast, USA. Andrews stated that the tests of *M. andrewsi* were found on the abdominal filaments, and "large holding appendages." This species was also found on oyster shells in same region by Andrews.

Genus *Folliculinopsis* Fauré-Fremiet, 1936 (60).

Folliculinopsis gunneri (Dons, 1928) Fauré-Fremiet, 1936 (60). Syn.: *Folliculina gunneri* Dons, 1928 (57). Found by Fauré-Fremiet on the cuticle of sacculinid parasite of *Carcinus maenas* and *Porcellana platycheles*. France.

Genus *Folliculina* Lamarck, 1816 (108).

Folliculina viridis (Wright, 1858) Fauré-Fremiet, 1936 (60). Syn.: *Lagotia viridis* Wright, 1858 (218). Found on tegument of sacculinid parasite of *Carcinus maenas* and *Porcellana platycheles* along with *Folliculinopsis gunneri* (60). France.

Subclass SUCTORIA Haeckel, 1866 (69).

Order SUCTORIDA Claparède & Lachmann, 1858 (78).

Family PODOPHRYIDAE Haeckel, 1866 (69).

Genus *Podophrya* Ehrenberg, 1835 (59).

Podophrya astaci Claparède & Lachmann, 1861 (33). From the freshwater crayfish *Astacus fluviatilis*. Europe.

Genus *Paracineta* Collin, 1912 (37).

Paracineta homari (Sand, 1899) Kahl, 1934 (88). Syn.: *Acineta homari* Sand, 1899 (164). Found on an unidentified

species of lobster, *Homarus*, and also on other decapods including *Pagurus* sp. Roscoff, France.

Family ACINETIDAE Stein, 1859 (196).

Genus *Acineta* Ehrenberg, 1833 (59), emend. Collin, 1912 (37).

Acineta constricta Collin, 1909 (36). On the legs of *Eupagurus cuanensis*. Cette (Sète), France.

Acineta sp. Couch, this paper. On the flat surfaces of gill lamellae of blue crabs, *Callinectes sapidus*. Chesapeake Bay, Maryland, USA, and Chincoteague Bay, Virginia, USA. This undescribed species is not common and occurs as solitary individuals attached near periphery of gill lamellae.

Family OPHRYODENDRIDAE Stein, 1867 (197).

Genus *Dendrosomides* Collin, 1906 (35).

Dendrosomides paguri Collin, 1906 (35). On the "long hairs" (setae) of the thoracic appendages of *Eupagurus excavatus* and *E. cuanensis*. Cette (Sète), France.

Genus *Ophryodendron* Claparède & Lachmann, 1861 (33).

Ophryodendron porcellanum Kent, 1881 (98). On the setae of the anomuran *Porcellana platycheles*. Jersey (English Channel Island) (98) and Roscoff, France (88).

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