TREATISE ON ZOOLOGY – ANATOMY, TAXONOMY, BIOLOGY

THE CRUSTACEA

COMPLEMENTARY TO THE VOLUMES TRANSLATED FROM THE FRENCH OF THE

TRAITÉ DE ZOOLOGIE

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VOLUME 9

PART C-II

DECAPODA: BRACHYURA (Part 2)

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BRILL
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2015

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This work has been published with the help of the French Ministère de la Culture – Centre National du Livre.

PARASITES AND DISEASES OF BRACHYURA[1])

BY

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Contents. – **Introduction. Pathogens, parasites, and symbionts of brachyuran crabs** – Microbial parasites – Protozoans – Metazoans. **Fouling communities of crabs. Significance of parasitism and diseases of brachyurans and directions for future research. Acknowledgments. Appendix. Bibliography.**

INTRODUCTION

Brachyura is a large and diverse group of crabs with myriad **symbionts**, including **pathogens**, **parasites**, and other types of **associates**. As with most marine hosts, brachyurans are infected by **viruses**, **bacteria**, **fungi**, **protists**, **helminths**, as well as **crustaceans**. There are even **insects** that live in symbiotic association with terrestrial crabs. Some parasites, such as rhizocephalan barnacles, often have a high degree of host specificity whereas others, such as some protists, are host generalists, infecting many crab species as well as other taxa. Some host-parasite relationships involving brachyurans represent highly specialized associations that include modification of host physiology and behaviour, in contrast to other associates that simply use the host's carapace as a **substrate**. Parasites, pathogens, and symbionts can also induce a number of unusual effects on their crab hosts, ranging from the mundane to the bizarre, particularly those leading to **castration** and **feminization**. Most parasites occur as relatively benign **infections** and produce **disease** only as high-intensity infections or under conditions that are physiologically stressful to the host. Several microbial pathogens, however, can cause considerable physiological alteration and occasionally fulminate into epizootics, or outbreaks, resulting in significant mortalities.

[1]) Manuscript concluded March 2015; latest additions June 2015.

Parasites have a negative effect on their hosts (usually while deriving energy from the host), whereas **pathogens** are typically microorganisms (viruses, bacteria, and fungi) that reproduce asexually within the host and cause disease (Lafferty & Kuris, 2002). There is some confusion in the use of the term "**symbiosis**" in the literature (see Chapter 71-10 in this volume). Symbiosis means "living together", and is inclusive of **pathogens**, **parasitism**, **commensalism**, **mutualism**, and **phoresy**, but not **predation**. A symbiont is therefore any organism that has some form of close or intimate association with its host (de Bary, 1879; Overstreet, 1978). A disease imparts an abnormal imbalance or dysfunction within the host, and parasites and pathogens can cause disease by disrupting physiological functions within the host. **Hyperparasitism** is the condition when one parasite infects another parasite, and there are a few examples of it with symbionts of brachyurans. A **facultative symbiont** is not physiologically dependent on a host but can establish an opportunistic relationship under certain conditions, whereas an **obligate symbiont** has a physiological dependency on its host. We use "**infection**" and "**infestation**" specifically as internal and external invasion of the host, respectively. Commensalism and the related **inquilinism** and **phoresy** are associations where the symbiont derives benefit from the association but the host is not affected by the association. Many examples of commensalism are difficult to accurately classify and can change, grading from commensalism to parasitism or mutualism, depending on abiotic and biotic factors (McDermott et al., 2010; Zapalski, 2011). **Epibionts** (see Chapter 71-11 in this volume) and **ectoparasites** are organisms that live externally on the surface of their hosts. Mutualism occurs when both the symbiont and the host benefit or derive metabolic dependency from the association (see Chapter 71-10 in this volume). We follow the terminology of Margolis et al. (1982) and Bush et al. (1997) for defining **prevalence**, **incidence**, **intensity**, and **abundance** of parasites in host populations. An **epizootic**, or **epidemic**, is an outbreak of a disease that is larger than the normal background levels of the pathogen. An epizootic is referred to as a **panzootic** or **pandemic** outbreak when occurring over a wide geographic area.

We present an overview of the parasites, including microbial pathogens, and other symbionts that use brachyurans as hosts, and we highlight key features of their host-parasite associations including data on their **biodiversity** and **biogeography**. This synthesis is meant to show the gaps in our understanding of the primary pathogens and parasites of brachyurans and provide a framework for future work. We have not attempted an exhaustive analysis of all of the symbionts and pathogens of brachyurans, but rather focus on recent findings that highlight new or unusual aspects of the host-symbiont associations. Several earlier reviews have covered crustacean diseases in general (Couch, 1983; Johnson, 1983; Overstreet, 1983; Brock & Lightner, 1990; Meyers, 1990), diseases of species such as the blue crab *Callinectes sapidus* (Portunidae; Trilles & Hipeau-Jacquotte, 2012) (Messick & Sinderman, 1992; Noga et al., 1998; Shields & Overstreet, 2007), the mud crab *Scylla serrata* (Portunidae) (Hudson & Lester, 1994), the Japanese shore crab *Hemigrapsus sanguineus* (Varunidae) (McDermott, 2007, 2011), the brown crab *Cancer pagurus* (Cancridae) (Stentiford, 2008), and a few other species. Several additional studies have focused on specific parasitic taxa such as ciliates (Bradbury, 1994; Morado & Small, 1995),

dinoflagellates (Shields, 1994; Stentiford & Shields, 2005), and rhizocephalans (Høeg & Lützen, 1985, 1995).

We use "crabs" throughout to refer to members of Brachyura unless otherwise noted. Host names have been updated to reflect current classification.

PATHOGENS, PARASITES, AND SYMBIONTS OF BRACHYURAN CRABS

Microbial parasites

VIRUSES

Of the known viruses of decapods, the best studied are those from penaeid shrimps, largely due to the emergence of serious viral pathogens in intensive commercial **aquaculture**. Nonetheless, at least 30 viruses have been reported from crabs (Bonami & Zhang, 2011), but only a few have been investigated in detail (table I). In contrast, only one virus has been reported in natural infections from a lobster (Shields & Behringer, 2004). Viral infections in the portunids *Carcinus maenas* and *Callinectes sapidus* are probably the best known in crabs, primarily from early biochemical studies (Bonami et al., 1971; Bonami, 1973) and descriptive ultrastructural studies (Johnson, 1976a, b, 1977a). Recent advances in molecular biology have increased the number of diagnostic tools available for working with viruses and this has opened the door to discoveries and in-depth analyses using genomic approaches, particularly for two cultured crabs, *Eriocheir sinensis* (Varunidae) and *Scylla serrata*, in China (Chen et al., 2011a; Deng et al., 2012; Guo et al., 2013). Metagenomic approaches should help considerably in identifying new viral agents.

A limiting factor in studying viruses is the lack of established continuous cell lines for crustaceans. Primary cell cultures can be used to quantify viral loads (Li & Shields, 2007), but they have limitations. Even though the lack of continuous cell lines is a serious impediment, many viral infections in crustaceans reach enormous levels in their host tissues, making it possible to purify viruses from host tissues for molecular characterization (Mari & Bonami, 1986; Deng et al., 2012). Early studies focused on histopathological, ultrastructural, and biophysical approaches, as well as initial infection trials to establish **infectivity**. Controls are missing in many cases, however, which could cause problems in interpretation of results. For example, tissue homogenates of a host can introduce foreign proteins that are known to elicit defensive responses in many organisms, and they can impose significant effects on naïve hosts. Mortality assessments must also include sham trials in uninfected controls, and replication should be done with individuals in separate tanks to rule out independence artifacts.

An important consideration in documenting new viruses is determining their **pathogenicity**. Many viruses cause damage to individual cells, but they are not pathogenic at the organismal level. For example, several benign viruses (**RhVB** and **Baculovirus-B**) occur in *Callinectes sapidus*. Infection studies, such as inoculation or exposure experiments, are thus crucial in determining pathogenicity or causality of disease. It is also important

TABLE I

Viruses of brachyurans organized by family, with size of the virion, presence of arrays or inclusions in host cells, tissue predilection, host, and key references (– = no data)

Virus family	Virus	Virion size (nm)	Inclusions	Tissue predilection	Host	Key references
REOVIRIDAE	P virus	58-65	Paracrystalline	Connective tissues, haemocytes	*Liocarcinus depurator*	Vago, 1966; Bonami, 1973; Bonami et al., 1976; Mari & Bonami, 1987
	W virus	–	–	–	*Carcinus maenas*	Hukura & Bonami, 1991; Bonami & Zhang, 2011
	W2	57-65	–	Connective tissues, haemocytes	*Carcinus aestuarii*	Mari & Bonami, 1986, 1988a, b; Montanié et al., 1993a
	RC84	70-75	Ordered arrangements	B-cells in hepatopancreas	*Carcinus aestuarii*	Mari & Bonami, 1987
	RLV, CsRV	55-60	Paracrystalline	Mesodermic, endodermic cells	*Callinectes sapidus*	Johnson & Bodammer, 1975; Johnson, 1977a, b, 1983
	EsRV905	55		Connective tissues	*Eriocheir sinensis*	Zhang, 2006
	EsRV816	60	–	Connective tissues	*Eriocheir sinensis*	Zhang et al., 2004; Zhang & Bonami, 2012
	MCRV	55	Paracrystalline	Connective tissues	*Scylla serrata*	Weng et al., 2007
	SsRV	70		Connective tissues	*Scylla serrata*	Chen et al., 2008
Dicistrovirus	MCDV	30			*Scylla paramamosain*	Guo et al., 2013
BIRNAVIRIDAE	IPN-like virus				*Liocarcinus depurator*	Clotilde, 1984

TABLE I
(Continued)

Virus family	Virus	Virion size (nm)	Inclusions	Tissue predilection	Host	Key references
BUNYAVIRIDAE	S virus	Pleomorphic 80-150 × 190-230 50-70 × 240-320		Endothelial cells of heart and hepatopancreas	*Liocarcinus depurator*	Bonami et al., 1975; Bonami, 1980
	CHV	55-80		Haemocytes	*Carcinus aestuarii*, *Carcinus maenas*	Bang, 1971, 1974; Hoover & Bang, 1978
	CpBV	60-70		Connective tissues, haemocytes	*Cancer pagurus*	Corbel et al., 2001, 2003
	EsBV			Connective tissues, haemocytes	*Eriocheir sinensis*	Zhang, 2006
PICORNAVIRIDAE	CBV	30	Paracrystalline	Ectodermal cells, haemocytes	*Callinectes sapidus*	Johnson, 1978
	HoPV?	25	Paracrystalline		*Hemigrapsus oregonensis*	Kuris et al., 1979
	EsPV?	28-30			*Eriocheir sinensis*	Lu et al., 1999
	F-N virus				*Liocarcinus depurator*	Bonami, 1980
RONIVIRIDAE	EsRNV	24-42 × 60-170	Paracrystalline	Connective tissues of gills	*Eriocheir sinensis*	Zhang & Bonami, 2007
RHABDOVIRIDAE	RhLV-A (EGV2)	110-170, 600 × 20-30		Mesodermal, endodermal tissues	*Callinectes sapidus*	Jahromi, 1977
	RhLV-B (EGV1)	100-170 × 50-70		Mandibular organ	*Callinectes sapidus*	Yudin & Clark, 1978, 1979
	EHV	Pleomorphic 105 × 194 105 × 300		Haemocytes, haematopoietic tissues	*Callinectes sapidus*	Johnson & Farley, 1980
	Y-organ virus	70-90 × 150-170		Y-organ	*Carcinus maenas*	Chassard-Bouchaud et al., 1976

TABLE I
(Continued)

Virus family	Virus	Virion size (nm)	Inclusions	Tissue predilection	Host	Key references
Enveloped bacilliform viruses	Baculovirus A	60-70 × 260-300	Paracrystalline	Hepatopancreatic epithelial cells	*Callinectes sapidus*	Johnson, 1976a, 1983, 1986a
	Baculovirus B	100 × 335	Ordered arrays	Haemocytes	*Callinectes sapidus*	Johnson, 1983, 1986a
	CpBV	60 × 211	None	F- and R-cells of the hepatopancreatic epithelia	*Cancer pagurus*	Bateman & Stentiford, 2008
	Tau	80-90 × 340-380		Hepatopancreatic epithelial cells	*Carcinus aestuarii*	Pappalardo & Bonami, 1979, 1986
	RV-CM, rod-shaped virus	75-80 × 230-280	None	Haemocytes, connective tissues	*Carcinus maenas*	Bazin et al., 1974; Johnson, 1988
	SsBV	42-46 × 230-307	Regular arrays	R-cells, hepatopancreatic epithelial cells	*Scylla serrata*	Anderson & Prior, 1992
	CoBV	144 × 338	Paracrystalline	Connective tissues, not in haemocytes	*Chionoecetes opilio*	Kon et al., 2011
	WSSV	70-150 × 275-380	Inclusions	Cuticular epithelium, haemocytes	Penaeid shrimps, many brachyuran crabs	See Escobedo-Bonilla et al., 2008

TABLE I
(Continued)

Virus family	Virus	Virion size (nm)	Inclusions	Tissue predilection	Host	Key references
HERPESVIRIDAE	Bifacies virus	174 × 191 197 × 233		Haemocytes, haematopoietic tissues, connective tissues	*Callinectes sapidus*	Johnson, 1976b, 1978, 1984
	RhHLV	75-80 100-110		Mesodermal cells of testes	*Rhithropanopeus harrisii*	Payen & Bonami, 1979
IRIDOVIRIDAE	MdIV	170-180		Connective tissues of hepatopancreas	*Liocarcinus depurator*	Montanié et al., 1993b
PARVOVIRIDAE	PC84	29-31		Connective tissues, myoepithelial cells	*Carcinus aestuarii*	Mari & Bonami, 1988a
	HPV		Inclusions	Hepatopancreatic tubules	*Scylla serrata*	Owens et al., 2010
Unclassified	V31				*Liocarcinus depurator*	Bonami, 1976
	V24				*Liocarcinus depurator*	Bonami, 1976
	Laem-Singh virus			Nerve tissue	*Scylla serrata*	Kumar et al., 2011
Unconfirmed	Large icosahedral virus	150		Muscle tissue	*Scylla serrata*	Song et al., 2003

to recognize that the presence of a virus in diagnostic tests such as **polymerase chain reaction** (PCR) assays or in metagenomic surveys may not necessarily indicate that the agents are pathogenic or that they are even in the appropriate host. Positive assays or genomic "hits" can simply reflect viral adherence to external surfaces or benign passage through the digestive tract (Burreson, 2008). Infection studies, histological assessment, and electron microscopy must be employed to substantiate viral **aetiology**, **pathology**, and information on host-virus relationships.

Reoviridae. – Eight **reoviruses** are known from crabs (table II), but only a handful of these are well characterized by molecular studies. The first viral infection to be identified from a brachyuran was found in *Liocarcinus depurator* (Portunidae) off Languedoc, France (Vago, 1966; Bonami & Vago, 1971). It was later named "**P virus**" and described as a reovirus based on its morphogenesis (Bonami, 1973; Bonami et al., 1976) and on the basis of its multi-segmented dsRNA genome (Mari & Bonami, 1987, 1988a). Crabs inoculated with tissue filtrates of the virus developed leg tremors around 6-9 days after exposure and eventually died. Mortality was 70-85% in inoculated crabs (Bonami et al., 1976). No prevalence studies have been undertaken for this virus, but a PCR diagnostic and gene probe using a dot-blot hybridization technique were developed for further study (Walton et al., 1999).

Two other reoviruses have been reported from *Carcinus* spp., **W2 virus** and **RC84 virus** from France. The W2 virus was described from *Carcinus aestuarii* from the Mediterranean coast of France (Mari & Bonami, 1986, 1988a). The W2 virus shares similarities with P virus, as they are serologically related and share similar patterns in gel electrophoresis (Montanié et al., 1993a). Both viruses show high host specificity and do not infect each other's host (Mari & Bonami, 1988a). Based on their biophysical and biochemical similarities, P virus and W2 were placed in the genus *Aquareovirus* of Reoviridae (Montanié et al., 1993a). The RC84 virus is a reo-like virus reported from *Carcinus aestuarii* from the Mediterranean coast of France (Mari & Bonami, 1987). It occurs in co-infections with other viruses; hence, the clinical diseases associated with the virus are not clear (Mari & Bonami, 1987). **PC84** virus is a parvo-like virus that should not be confused with RC84 (Mari & Bonami, 1988b; Montanié et al., 1993b).

The **reo-like virus** (**RLV** or CsRV) from the blue crab *Callinectes sapidus* was initially described from juvenile crabs held under crowded conditions (Johnson & Bodammer, 1975) (fig. 71-12.1). Infected glial cells lead to necrosis of the nerve cells and infected crabs exhibit tremors, paralysis, and death (Johnson, 1977a, 1983). RLV has been implicated as a source of mortality in the production of soft shell *Callinectes sapidus*. Bowers et al. (2010) used antisense copies of the viral genome to develop a sensitive and specific PCR assay for the virus. Infection trials indicate that the virus is highly pathogenic. Based on molecular data, Tang et al. (2011) renamed the virus ***Callinectes sapidus* reovirus** (**CsRV**). Additional studies should resolve whether this virus is the same as that found in *Liocarcinus depurator* (see Hukuhara & Bonami, 1991). Several viruses occur as co-infections with RLV. **Rhabdovirus A** (RhVA) was noted in all RLV-infected crabs investigated by TEM (Johnson, 1978, 1983). Johnson (1983) speculated that damage

TABLE II
Bacterial pathogens reported from brachyurans, by agent, region, host, and tissue predilection

Agent	Region	Host	Tissue	Reference
Acholeplasma cf. *laidlawii*	Zhejiang, China	*Scylla serrata*	Gill epithelium	Chen et al., 2011b
Spiroplasma eriocheiris	Jiangsu, China	*Eriocheir sinensis*	Haemolymph and connective tissues	Wang et al., 2004, 2010
Rickettsia-like organism	Mediterranean France	*Carcinus aestuarii*	Connective tissues	Bonami & Pappalardo, 1980
	Wales, U.K.	*Carcinus maenas*	Connective tissues of hepatopancreas, fixed phagocytes, but not haemocytes	Eddy et al., 2007
	Chesapeake Bay, U.S.A.	*Callinectes sapidus*		Messick & Kennedy, 1990; Messick, 1998
Chlamydia-like organism	Washington state, U.S.A.	*Cancer magister*	Connective tissues	Sparks et al., 1985
	Laboratory	*Cancer irroratus*, *Cancer borealis*	Haemocytes and haematopoietic tissue	Leibovitz, 1988
Rhodobacteriales-like organism	Wales, U.K.	*Carcinus maenas*	Connective tissues and blood vessels	Eddy et al., 2007
Enterococcus faecalis	Mediterranean France	*Carcinus aestuarii*	Connective tissues of hepatopancreas	Pappalardo & Boemare, 1982
Clostridium botulinum type F	Chesapeake Bay?	*Callinectes sapidus*	Haemolymph	Williams-Walls, 1968
Vibrio parahaemolyticus	Chesapeake Bay, U.S.A.	*Callinectes sapidus*	Haemolymph	Krantz et al., 1969
	Chesapeake Bay, U.S.A.	*Callinectes sapidus*	Haemolymph	Colwell et al., 1975; Sizemore et al., 1975; Sizemore & Davis, 1985; Welsh & Sizemore, 1985
	Texas, U.S.A.	*Callinectes sapidus*		Davis & Sizemore, 1982
	U.K.	*Eriocheir sinensis*	Haemolymph	Wagley et al., 2009

TABLE II
(Continued)

Agent	Region	Host	Tissue	Reference
Vibrio pectinicida	Wales, U.K.	*Cancer pagurus*	Haemolymph	Smith et al., 2013a
Vibrio cholerae	Chesapeake Bay, U.S.A.		Gut	Huq et al., 1983
	Chesapeake Bay, U.S.A.		Hepatopancreas	Johnson, 1983
	South Carolina, U.S.A.		Gills	Babinchak et al., 1982
	Puerto Rico	*Callinectes bocourti*		Rivera et al., 1999
Vibrio spp.	Asia	Larvae of several crab species	Internal in larvae	Talpur et al., 2011; Wan et al., 2011; Peng et al., 2012; Xu et al., 2013; Zhang et al., 2014
Vibrio sp.	Connecticut, U.S.A.	*Cancer irroratus*		Newman & Feng, 1982
		Cancer irroratus, *Carcinus maenas*		Spindler-Barth, 1976
Vibrio spp., several clades	Canary Islands, Spain	*Maja brachydactyla*	Haemolymph	Gomez-Gil et al., 2010a
Photobacterium swingsii	Canary Islands, Spain	*Maja brachydactyla*	Haemolymph	Gomez-Gil et al., 2010a, b
Psychrobacter cibarius	Oregon, U.S.A.	*Cancer magister*	Haemolymph	Scholnick & Haynes, 2012

TABLE II
(Continued)

Agent	Region	Host	Tissue	Reference
Several species of chitinoclastic bacteria: *Vibrio*, *Aeromonas*, *Pseudomonas*, *Kingella*, *Serratia*	New York Bight, U.S.A.	*Callinectes sapidus*	Shell	Rosen, 1967, 1970; Cook & Lofton, 1973; Sandifer & Eldridge, 1974; Young & Pearce, 1975; Iversen & Beardsley, 1976; Noga et al., 1994
	Alaska, U.S.A.	*Cancer magister*	Shell	Morado et al., 1988
	Wales, U.K.	*Cancer pagurus*	Shell	Ayre & Edwards, 1982; Vogan et al., 1999, 2001; Vogan & Rowley, 2002; Powell & Rowley, 2005
	New York Bight, U.S.A.	*Cancer irroratus*	Shell	Young & Pearce, 1975
	Mid-Atlantic Bight, U.S.A.	*Chaceon quinquedens*	Shell	Haefner, 1977
	Southern Florida, U.S.A.	*Menippe mercenaria*	Shell	Iversen & Beardsley, 1976
	New York Bight, U.S.A.	*Chaceon quinquedens*	Shell	Bullis et al., 1988; Young, 1991
	South Atlantic Bight, U.S.A.	*Chaceon fenneri*	Shell	Wenner et al., 1987
	Gulf of St. Lawrence, Canada	*Chionoecetes opilio*	Shell	Benhalima et al., 1998b
	Alaska, U.S.A.	*Chionoecetes tanneri*	Shell	Baross et al., 1978

TABLE II
(Continued)

Agent	Region	Host	Tissue	Reference
Aeromonas trota	Brittany, France Hangzhou, China	*Cancer pagurus* *Eriocheir sinensis*	Haemolymph Haemolymph, hepatopancreas, muscle	Leglise & Raguenes, 1975 Xu & Xu, 2002
Filamentous bacterium	Chesapeake Bay, U.S.A.	*Callinectes sapidus*	Lumen of hepatopancreas	Johnson, 1976c, 1983; Messick, 1998
Leucothrix mucor	Chesapeake Bay, U.S.A., cosmopolitan	*Callinectes sapidus*, *Cancer* spp., many crustaceans	External on shell, eggs, setae, gills	Johnson et al., 1971; Bland & Amerson, 1974
Aerococcus viridans var. *homari*	Maine, U.S.A.	*Cancer borealis*, *Cancer irroratus*	Haemolymph	Gallagher et al., 1979

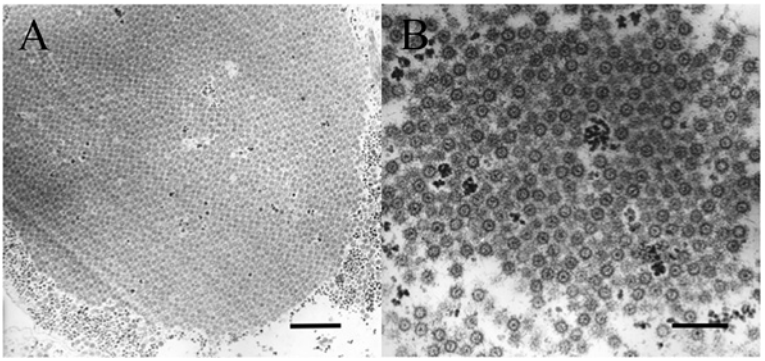

Fig. 71-12.1. Reo-like virus from *Callinectes sapidus*: A, infected haemocytes showing paracrystalline array of virus particles (bar = 500 nm); B, detail of reo-like virus (bar = 240 nm). [From the TEM archives of P. T. Johnson.]

to the nervous system was probably a synergistic effect between the two viruses. Enveloped helical virus and Baculovirus A and B have also been reported in co-infections (Johnson, 1983). Several of these viruses have only been seen in crabs held under crowded laboratory conditions. Their role in the pathology associated with RLV remains unknown.

Two **reoviruses** have been identified from the commercially important mitten crab *Eriocheir sinensis*. The crab is intensively cultured in China and Korea, and several diseases have been reported from cultures in China. **"Tremor disease"** or **"trembling disease"** has been associated with viral and spiroplasma infections (see *Spiroplasma*, below). **EsRV905** is a reovirus originally thought to be associated with tremor disease (Zhang et al., 2004). Crabs inoculated with partially purified suspensions of the virus experienced 30% mortality over one month, but crabs affected by the virus did not show the characteristic tremor associated with "tremor disease" (Zhang et al., 2004). Co-infections with a **bunya-like virus** were also observed. EsRV905 has a 12-segmented genome and was placed in the Cardoreoviruses (Zhang et al., 2004). **EsRV816** also infects *Eriocheir sinensis* (see Zhang & Bonami, 2012). It has a 10-segmented genome and is distinct from EsRV905 (Zhang & Bonami, 2012). Crabs inoculated with partially purified suspensions of EsRV816 experienced 30% mortality over 20 d at 28°C, but no mortality at 20°C. Affected crabs did not show signs of "tremor disease".

Mud crab reovirus (**MCRV**) was described from cultured *Scylla serrata* from southern China (Weng et al., 2007). The virus causes **"sleeping disease"** and mortalities are associated with high temperatures. Affected crabs are lethargic, show a loss of appetite, have an atrophied hepatopancreas, and can develop a grey coloration. A PCR diagnostic based on reverse-transcriptase indicates the virus occurs in several organ systems in early infections (Guo et al., 2008). MCRV was found to be infectious to crabs via bath exposure, inoculation of infected filtrates, cohabitation with infected crabs, and feeding of infected tissues. Mortalities occurred within 10 days in all exposure routes and varied from 80% in cohabitation to 100% in other treatments (Weng et al., 2007). Co-infection with a **dicistrovirus** was also observed (Guo et al., 2013). MCRV was placed in the genus

Crabreovirus by Deng et al. (2012). This was further supported by a three-dimensional analysis of the capsid coat (Huang et al., 2012). ***Scylla serrata*** **reovirus** (**SsRV**) infects mud crabs in southern China (Chen et al., 2008). SsRV and a mollucite, *Acholeplasma* sp., have been associated with outbreaks of **"waterclear disease"** or **"clearwater disease"** in Zhejiang Province (Chen et al., 2008; Chen et al., 2011a). Genetic comparisons indicate that SsRV belongs in its own genus (Chen et al., 2008).

Dicistroviridae. – Members of Dicistroviridae are small **ssRNA viruses** that belong in Picornavirales. Only two dicistroviruses are known from crustaceans. One of these is the highly pathogenic **Taura Syndrome Virus**, which has caused significant damage to shrimp aquaculture in the Americas (Hasson et al., 1995). The other is **Mud Crab DicistroVirus-1** (**MCDV-1**), which infects *Scylla paramamosain* from China (Guo et al., 2013). In a controlled experiment, crabs inoculated with purified suspensions of the virus began dying within 3-4 days and experienced 100% mortality after 7 days.

Bunyaviridae. – Another early record of a viral infection in a brachyuran was **Crab Haemocytopenic Virus** (CHV) from *Carcinus maenas* and *Carcinus aestuarii* (see Bang, 1971; Hoover & Bang, 1978). The virus had a low prevalence in naturally infected crabs (1 of 700, 0.14% prevalence) (Bang, 1971). Haemolymph from the affected crab showed abnormal clotting and haemocyte clumping. Crabs inoculated with haemolymph filtrates containing the virus became infected over 10 days. Haemocyte densities dropped in infected animals, but mortality during the infection experiments was not attributed to the virus (Bang, 1971, 1974). Recovery of clotting ability occurred in about 66% of these animals, with some hosts recovering this ability within 4-6 days. The virus remained present in the haemocytes, however, making exposed crabs difficult to assess for infection (Bang, 1974; Johnson, 1983).

The **S virus** is an unclassified virus in *Liocarcinus depurator* from the Mediterranean coast of France (Bonami et al., 1971, 1975); it shares features with Paramyxoviridae and Bunyaviridae. Mortality was 70-80% over 15-20 days in experimental infections (Bonami et al., 1971). S virus can be highly prevalent in crabs from the Mediterranean (Bonami et al., 1971).

Only two viruses are known from *Cancer pagurus*. A **bunya-like virus**, the first described from this host, was found in crabs from Brittany, France (Corbel et al., 2003) and a baculo-like virus, ***Cancer pagurus*** **bacilliform virus** (**CpBV**), in crabs from England (see below). The bunya-like virus was accidentally discovered as part of an investigation into the host range of **White Spot Virus** (**WSV** or **WSSV**, **White Spot Syndrome Virus**) in Europe (Corbel et al., 2001). The virus, named *Cancer pagurus* systemic bunya-like virus (**CpSBV**), was found in crabs dying in holding facilities (66% mortality) during transmission experiments with WSSV. Infected haemolymph had free viral particles and the virus could be detected in haemolymph using transmission electron microscopy. Crabs died 7-12 days after inoculation with partially purified virus in experimental infections. The virus was thought to be a potential issue in mortalities within holding tanks in Europe.

A bunya-like virus purportedly infects *Eriocheir sinensis* from China, but details are incomplete (Zhang, 2006).

Picornaviridae. – Four **picornaviruses** have been described from brachyurans. **Chesapeake Bay virus** (CBV) is a picorna-like virus reported from captive juvenile *Callinectes sapidus* (see Johnson, 1978, 1983). The virus is pathogenic, but has a slow course of infection that ultimately leads to death over the course of 1-2 months. Ommatidia of the eye can be damaged by the virus. The resulting blindness, in combination with pathological changes to gas exchange and osmotic control from infected gill epithelia, can lead to erratic swimming and resting behaviours. Several crabs infected with CBV had co-infections with RhVA or EHV (Johnson, 1983). A picornavirus infects both *Hemigrapsus oregonensis* (Varunidae) as well as *Portunion conformis*, an internal parasitic isopod in the crab (Kuris et al., 1979). The isopod was often found dead or dying within the **haemocoel** of the host (Kuris et al., 1979); however, virions were also found in healthy hosts and isopods. Two types of virions (25 nm and 58 nm in diameter) were isolated from infected tissues. The smaller particle was identified as a picornavirus; the larger was not identified. A picornavirus was found in *Eriocheir sinensis* from China during investigations into "trembling" disease (Lu et al., 1999). Histopathology on crabs inoculated with the virus showed oedematous changes to the tissues with cell necrosis in infected tissues. A **picorna-like virus**, tentatively named **F-N virus**, purportedly infects *Liocarcinus depurator* from France but the details of this finding are incomplete (Bonami, 1980).

Roniviridae. – Two roniviruses, **yellow-head virus** and **gill-associated virus**, are important pathogens of shrimps. Other than an infection experiment with yellow-head virus in *Callinectes sapidus* (see Ma et al., 2009) there is only one **ronivirus** known from a brachyuran. ***Eriocheir sinensis* ronivirus** was found in mitten crabs during an investigation of **black gill syndrome** or **"sighs" disease** (Zhang & Bonami, 2007). Crabs with black gill syndrome had dark grey or black areas at the tips of the gills, within the lamellae, and sometimes in the branchiae. Histopathology showed tissue necrosis, granulomatous areas within the gills, abnormal, apoptotic and pycnotic nuclei, sometimes with eosinophilic inclusions. Infection trials with tissue homogenates reproduced infections in naïve crabs, with 100% mortality over 17 days. The "sighs" disease was reproduced in 30% of experimentally infected animals, but not the black gill syndrome; it was thought to be coincident with other environmental factors (Zhang & Bonami, 2007). The virus could impose significant economic losses on cultures of mitten crabs (Bonami & Zhang, 2011).

Rhabdoviridae. – Four **rhabdoviruses** have been described from crabs. **Rhabdo-like virus A** (**RhV-A**) infects *Callinectes sapidus* (fig. 71-12.2) (Johnson, 1978). It was first observed by Jahromi (1977) while studying muscles of the foregut, but was described from the mandibular organ, incorrectly termed the ecdysial gland, and named **EGV2** (Yudin & Clark, 1978, 1979; see Johnson, 1983). The virus has been reported as infecting *Callinectes sapidus* from the Atlantic and Gulf of Mexico coasts of the U.S.A. (Johnson, 1983), but this requires confirmation. It has only been observed in crabs living in stressful conditions or in co-infections with other viruses (RLV, EHV, CBV, HLV and Baculovirus B; see Johnson, 1983). Single infections with RhV-A may not be pathogenic; however, crabs experimentally inoculated with both RLV and RhVA died within 3 days (Johnson, 1983). Little is known about the **Rhabdo-like virus B** (**RhV-B**) that also infects *Callinectes*

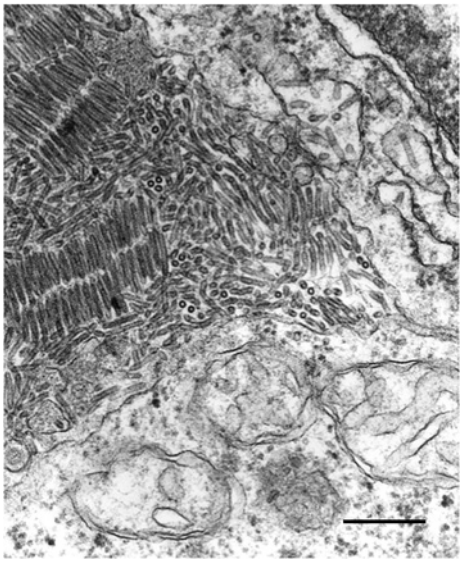

Fig. 71-12.2. Rhabdovirus A from *Callinectes sapidus*. The virus particles are ordered within the endoplasmic reticulum of an infected cell (bar = 250 nm). [From the TEM archives of P. T. Johnson.]

sapidus. It was reported in *Callinectes sapidus* from the Gulf of Mexico where it had a low prevalence (2 of 60, 3.3%) (Yudin & Clark, 1978, 1979). It was also identified from the mandibular organ, and inaptly named **ecdysial gland virus 1** (**EGV1**) (see Johnson, 1983). One crab with EGV1 also had a co-infection with RhV-A (Spann et al., 1997; Zhang & Bonami, 2007). **Enveloped helical virus** (**EHV**) is another rhabodvirus from *Callinectes sapidus* (see Johnson & Farley, 1980). It was tentatively associated with Paramyxoviridae or Orthomyxoviridae, but later placed in Rhabdoviridae (Johnson, 1986a). Little is known of its pathology. EHV was always found in co-infections with other viruses (Baculovirus B, RhV-A, and CBV). A virus similar to EHV and the S virus was described from the Y-organ of *Carcinus maenas* from Roscoff, France (Chassard-Bouchaud et al., 1976). Additional studies on EHV, the S virus and the Y-organ virus of *Carcinus maenas* are warranted as they exhibit similarities in morphogenesis (Johnson, 1983). EHV and RhVB could be the same virus, even though there are differences in size between their virions (Shields & Overstreet, 2007).

Baculoviridae/Enveloped bacilliform viruses. – These viruses are probably **nudiviruses**, close relatives of **baculoviruses**, based on their lack of occlusions, but they need to be better characterized (Jehle, 2010). Eight baculoviruses have been reported from five crab species, mostly as anecdotal observations. Baculoviruses can be significant pathogens in other crustaceans. The well-known shrimp scourge, White Spot Virus or White Spot Syndrome Virus (WSSV), is a baculovirus known to infect crabs, with many other crustaceans as reservoir hosts (see below).

Baculovirus-A and Baculovirus-B infect *Callinectes sapidus* (see Johnson, 1976a, 1986a). Baculovirus-A has a predilection for R-cells in the hepatopancreas and infections

are typically localized (focal) to a few adjacent cells; consequently, infected crabs do not appear to be affected by the virus, even in heavy infections (Johnson, 1976a, 1983). Infected *Callinectes sapidus* have been found from Long Island Sound and one tributary of Chesapeake Bay, U.S.A. (Johnson, 1983). Prevalence levels varied from 4-52% (Johnson, 1976a). Baculovirus-B has a predilection for haemocytes, but it does not infect mature granulocytes and haematopoietic cells (Johnson, 1983, 1986a).

Two baculoviruses have been reported from *Carcinus* spp.: the **rod-shaped virus** from *Carcinus maenas* (see Bazin et al., 1974) and the **tau virus** from *Carcinus aestuarii* (see Pappalardo & Bonami, 1979). The rod-shaped virus was detected during studies on host **autotomy** and **regeneration** (Bazin et al., 1974). It could also be the rod-shaped virus described as RV-CM in *Carcinus maenas* from Woods Hole, MA, U.S.A. (Johnson, 1988). Nucleocapsids are polarized, with a specialized apex, presumably a feature of their morphogenesis. The viral envelope has an unusual external tract that connects both ends of the virus together (Pappalardo et al., 1986). Infection experiments successfully transmitted the virus to naïve hosts, and infected hosts became lethargic, showed a loss of appetite, and eventually died (Pappalardo et al., 1986). Animals given partially purified virus died within 10-20 days, and the virus was detectable via TEM in 55% of the cases, whereas those exposed by feeding had a lower prevalence, with virus detectable in only 35% of the cases (Pappalardo et al., 1986).

A **bacilliform virus** (CpBV) occurs in juvenile *Cancer pagurus* from the English Channel (Bateman & Stentiford, 2008). Virus particles have a tail-like protuberance at one end. Infections are limited to F- and R-cells of the hepatopancreas. Prevalence in juvenile crabs was 5% and it was not found in adult crabs (Bateman & Stentiford, 2008).

A non-occluded bacilliform virus, ***Scylla serrata* baculovirus**, was identified in laboratory-held mud crabs from near Darwin, Australia (Anderson & Prior, 1992). Infections were typically found only in the R-cells of the hepatopancreas. Naturally infected crabs from near Townsville, Australia had a histological prevalence of 8.9% (reported as SsIBV) (Owens et al., 2010). Larval crabs from females held as broodstock had prevalence levels of 32 and 53%, indicating that the virus was likely present in maternal crabs.

A bacilliform virus, tentatively designated **CoBV**, was found during an investigation of **milky haemolymph syndrome** in *Chionoecetes opilio* (Oregoniidae) from the Sea of Japan (Kon et al., 2011). Milky or opaque haemolymph was the major sign of the disease, but discoloration of the ventral surface of the shell and poor calcification of the arthrodial membranes of the legs were also noted.

Whispoviridae — white spot syndrome virus. – **WSSV** is the best-studied virus from crustacean hosts. Pandemics of WSSV have killed large numbers of cultured shrimp since 1993. It is a non-occluded, rod-shaped virus with an apical envelope extension. Infected cells of shrimps can be diagnosed histologically by the presence of intranuclear inclusion bodies in the hypertrophied nuclei of cuticular epithelial and connective tissue cells, and the virus gets its name from the resulting necrosis of the cuticular epithelial cells that form white spots of dead cells in the cuticle of infected shrimp. WSSV has become established in the Americas and southern Europe through the introduction of infected broodstock and

infected bait products (Hasson et al., 2006). Mortality in affected shrimp can be very high. **Selection pressure** can operate on naïve host populations exposed to the virus as they show marked mortalities followed by ameloriation of viral pathogenicity over time (Flegel, 2007). Concerns about the importation of viruses in frozen, raw crustacean products have led to legislation and monitoring programmes in the European Union in order to improve biosecurity of imported crab, shrimp, and lobster products (Stentiford et al., 2009).

WSSV has a broad host range, is infectious to over 40 invertebrate species and has been found as natural infections in 14 species of brachyurans (see Escobedo-Bonilla et al., 2008). Bioassays and exposure studies were initially used to examine the suitability of crabs and other crustaceans as reservoirs, but as the virus escaped into natural systems, field studies focused on assessing natural infections in **native species**. WSSV infections were found in captive and cultured *Scylla serrata* from Taiwan (Lo et al., 1996) and Thailand (Flegel, 1997). It was later found in larval mud crabs captured off Thailand (Chen et al., 2000), where up to 60% of wild-caught larvae tested positive for the virus. Infection studies showed that the virus could impose additional mortality on the sensitive larval stages (Chen et al., 2000) and PCR-positive samples were obtained from moulted exuviae. A prevalence of 96.4% was reported in hatchery-reared and released *Portunus trituberculatus* (Portunidae), and a prevalence of 79.3% was found in natural populations of adults (Meng et al., 2009). These findings highlight that nearly every life history stage is susceptible and hatcheries for many species should be monitored, as they can serve as foci for the release of WSSV into natural systems.

Three types of WSSV infections occur in crabs (Hameed et al., 2003; Bateman et al., 2012): (1) acute infections with large numbers of infected cells that result in rapid mortality within 5 days post exposure, (2) subacute infections with moderate numbers of infected cells with high mortality over 10 days post exposure, and (3) infections with little to no pathology. The route of infection is also important in the presentation of the disease (Bateman et al., 2012). Studies indicate that host species showing few overt signs of infection can serve as carriers of the virus to new host populations. These types of disease classifications are very useful for initial studies, but additional studies should determine if potential hosts can serve as carriers for WSSV, because many crustaceans can fill this role.

Herpesviridae. – Two **herpes-like viruses** have been reported from crabs. The best known is **bi-facies virus** (BFV) in *Callinectes sapidus* (see Johnson, 1976b). BFV was initially described as a herpes-like virus, but with better fixation protocols, features of its morphology and morphogenesis became apparent (fig. 71-12.3); however, it is still considered related to Herpesviridae (Bonami & Lightner, 1991). The virus has two forms: a large ovoid particle, 197-233 nm in diameter, with two envelopes, and a smaller ovoid particle, 174-191 nm in diameter, with one envelope (Johnson, 1988). Infected crabs show few signs of disease until just before death when they become lethargic and stop feeding (Johnson, 1976b). The virus had a prevalence of 13% in juvenile crabs from Assawoman and Chincoteague bays, eastern U.S.A. (Johnson, 1983). Inoculation of infected haemolymph into healthy crabs resulted in death 30-40 days later (Johnson, 1978), and apparently naturally infected crabs survived for at least 60 days (Johnson,

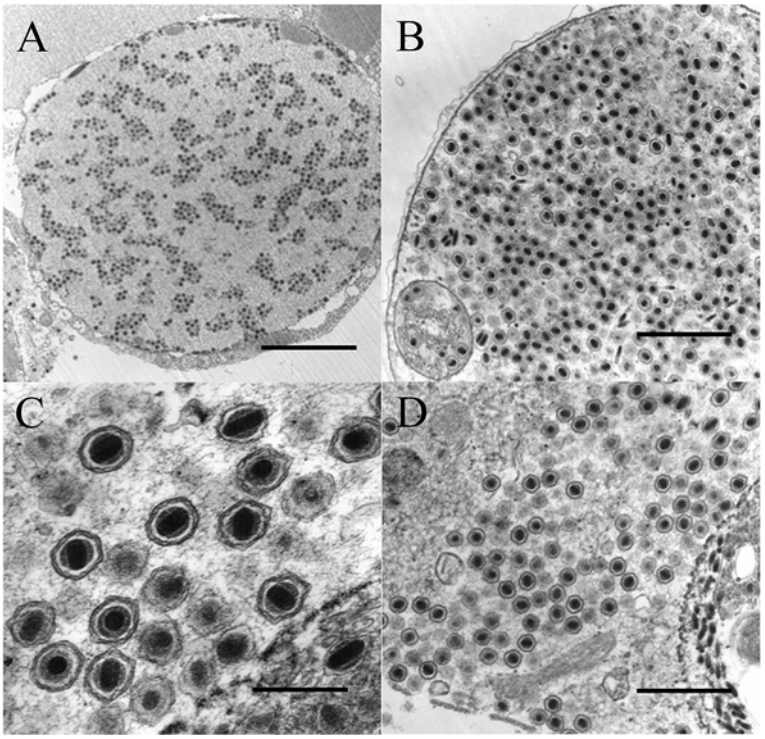

Fig. 71-12.3. Bi-facies virus from *Callinectes sapidus*: A, infected haemocyte with hypertrophied nucleus filling almost the entire protoplasm of the cell; clumps of viral particles within the stroma of the infected nucleus (bar = 3.0 μm); B, hypertrophied nucleus with many mature and immature viral particles (bar = 1.3 μm); C, detail of viral particle showing two membranes around an icosahedral particle with an electron-opaque nucleoid surrounded by an electron-dense toroid (bar = 300 nm); D, ordered arrangement of the bi-facies virus in the nucleus of an infected cell (bar = 1.0 μm). [From the TEM archives of P. T. Johnson.]

1983). Natural transmission can be through water-borne routes as healthy juvenile crabs developed disease after exposure to water from a source containing infected crabs. Additional studies on this virus are warranted because of its relatively high prevalence, water-borne transmission, and pathogenicity. The other Herpes-like virus was found during a study of spermatogenesis in *Rhithropanopeus harrisii* (Panopeidae). The virus was observed in the germinative layer of the testis, but no pathology was described (Payen & Bonami, 1979).

Iridoviridae. – **Iridoviruses** are relatively common in insects and isopods and often impart an **iridescent sheen** to their infected hosts (Anthony & Comps, 1991). Only one **irido-like virus** has been identified from a brachyuran. While working with viral infections in *Liocarcinus depurator* from the Mediterranean, Montanié et al. (1993b) discovered *Macropipus depurator* Irido-like Virus (**MdIV**, so named because at the time *Macropipus depurator* was the accepted name for the host) in a co-infection with P and S virus. Little is known of this virus.

Parvoviridae. – The **densonucleoviruses**, or **densoviruses**, are a subset of **parvoviruses**. They are small ssDNA viruses that infect insects (Tijssen & Arella, 1991). At least two densoviruses cause significant diseases in cultured shrimps: **infectious hypodermal and haematopoietic necrosis virus** (**IHHNV**) and **hepatopancreatic parvovirus** (**HPV**, or more aptly named ***Penaeus monodon*** **densonucleovirus**, **PmDNV**) (Flegel, 2012). Two **parvo-like viruses** have been identified from crabs. The first is **PC84**, a virus identified in *Carcinus aestuarii* (see Mari & Bonami, 1988a). It has two forms, L and H particles, based on buoyant densities. The L particles are complete virions, the H particles are empty or damaged virions. In transmission experiments, purified preparations of the virus were lethal, with crabs dying 10-25 days after inoculation. Infected animals developed weakness, lethargy, and a lack of appetite. Hepatopancreatic parvo-like virus (HPV) normally infects penaeid shrimps, but it was found in *Scylla serrata* from Australia (Owens et al., 2010). An assessment of disease in wild-caught crabs and larvae from an aquaculture facility indicated that HPV was naturally occurring in the mud crab. As indicated by Owens et al. (2010), these findings complicate the husbandry of both host species, the mud crab and the banana prawn, *Fenneropenaeus merguiensis*.

Unclassified viruses. – A few unclassified viruses have been reported from crabs. Two viral particles (**V31** and **V24**; names refer to the size of the naked, paraspherical viral particles) were found in *Liocarcinus depurator* (see Bonami, 1976). The details of these viruses are incomplete (see Bonami, 1980). Partially purified aliquots of **Laem-Singh Virus** (**LSNV**), a small positive-sense ssRNA virus related to Luteoviridae, inoculated into *Scylla serrata* did not cause overt disease but was detectable over 20 days with a very sensitive, nested PCR assay, not with an RT-PCR assay (Kumar et al., 2011). The virus was not found in natural infections in *Scylla serrata*. A large icosahedral virus reportedly caused muscle necrosis in cultured *Scylla serrata* from China (Song et al., 2003). The muscles apparently atrophied and turned white.

Viruses in crab aquaculture. – Viral pathogens represent significant impediments to the development and establishment of crustacean aquaculture, including crabs, shrimps, lobsters, and other taxa (Stentiford et al., 2012). Studies on the few crabs that have been exploited for aquaculture (*Eriocheir sinensis*, *Scylla serrata*, soft-shell *Callinectes sapidus*) show that several viruses can have devastating consequences on cultured crabs under conditions of host crowding and environmental stress. The high densities used in culturing crabs, particularly in production of juveniles and in the production of soft-shell crabs, provide ideal conditions for outbreaks of viral pathogens and the spread of viruses into nearby natural environments. This has already happened with WSSV. The virus moved from aquaculture facilities into native crustacean populations (Escobedo-Bonilla et al., 2008). There is also increasing potential for the spread of crab viruses through the transportation of crustaceans (as food and their use as live bait) to new regions. Live soft-shell *Callinectes sapidus* can be found in several national and international markets; the host range of the viral pathogens of this species, such as CsRV, are not well known. There is therefore a need to develop molecular diagnostics for these pathogens and to characterize infections and identify potential alternative hosts.

More work is needed to fully characterize the known viruses in crabs, to determine their host range and degree of host specificity, geographic range, prevalence of infection in native populations, pathogenicity, and means of transmission. A common theme is the appearance of viruses as co-infections with other viruses. In several portunid hosts (*Callinectes sapidus*, *Carcinus maenas*, *Liocarcinus depurator*, and *Scylla serrata*) co-infections are relatively common, and the pathogenic relationships among the different viruses need to be more fully assessed. Temperature stress and stressful culture conditions can contribute to outbreaks of disease (Johnson, 1978, 1984, 1986a; Messick & Kennedy, 1990). Once a virus has been identified and characterized, experimental studies should focus on delineating transmission and understanding how environmental conditions contribute to its infectivity, pathogenicity, and dispersal.

BACTERIA

Bacterial infections in crabs are quite common, but surprisingly few causative agents have been identified (table II). There are several well-documented studies on *Vibrio* infections in *Callinectes sapidus*, infection studies with different species of *Cancer*, and a model system is developing with *Eriocheir sinensis*. These have been reviewed by Johnson (1983), Shields & Overstreet (2007), and Wang (2011). **Bacteria** such as *Vibrio vulnificus*, *Listeria monocytogenes*, and *Clostridium botulinum* also represent human health hazards as they have been reported from raw crustacean products including crab meat, raising concerns regarding proper food handling and safety (Williams-Walls, 1968; Fishbein et al., 1970; Rawles et al., 1995; Peterson et al., 1997; Soares de Lima Grisi & Gorlach-Lira, 2010). For example, several **serovars** of the human pathogen *Salmonella enterica* have been isolated from a terrestrial crab, *Cardisoma guanhumi* (Gecarcinidae), which is frequently consumed in the Caribbean (Peterson et al., 2013), and human faecal contamination is a common source for this bacterium in many estuaries. A streptomycin-resistant isolate of *Plesiomonas shigelloides* was obtained from *Callinectes sapidus* purchased from retail markets in Louisiana, leading to speculation that resistance was due to the contamination of the estuarine waters with waste waters (Marshall et al., 1996). Here we highlight recent studies on bacteria in crabs and elaborate on important examples.

Aetiological investigations into bacterial diseases must be done carefully. In the 1970s there was debate in the literature regarding whether the haemolymph of crabs was sterile like that of vertebrates and many invertebrates (Bang, 1970). High prevalence levels of bacteria, including several species of *Vibrio* were found in the haemolymph of apparently healthy *Callinectes sapidus* (see Colwell et al., 1975; Tubiash et al., 1975). Debate ensued as to whether crabs were naturally infected with vibrios or whether they obtained them from handling on their way to markets or impoundments (Johnson, 1976c). Later studies showed that bacterial infections were present at low to moderate levels in the haemolymph and various other tissues of freshly caught, unstressed crabs, and mean densities of bacteria ranged from low to moderate levels (10^3 to 10^5 bacteria per ml) (Davis & Sizemore, 1982; Messick & Kennedy, 1990). Stress, which results from capture, handling, crowding, transport, increased temperature, wounding, and poor water quality, especially in poorly

managed recirculating systems (Johnson, 1976c), is a major effector in the aetiology and development of bacterial infections in crustaceans (Brock & Lightner, 1990). It is thus important to understand the role of stressors in compromising homeostasis in the host when attempting to identify bacterial agents in the aetiology of disease.

Careful studies are required to establish an agent as a pathogen. Koch's postulates (see, e.g., Evans, 1976) must be addressed when working with suspect bacterial pathogens. Simple inoculation studies can elicit disease at high inoculation or exposure levels (10^7 bacteria per ml) but not at lower levels (10^5 bacteria per ml), yet they may not indicate the real agent of disease, rather that the bacteria are simply overwhelming defensive responses in hosts subjected to handling stress. Similarly, exposure studies using bath systems or water-borne routes must have controls consisting of non-infectious species, because high biological oxygen demand (BOD) from bacterial loading alone can impose significant hypoxic stress in poorly maintained laboratory systems. High BOD is associated with poor water quality; hence water quality parameters must be stringently maintained in exposure studies and these parameters should be reported. In both inoculation and bath exposure studies, the inclusion of appropriate controls using a non-infectious bacterial species is critical to the final conclusions regarding causality. These types of controls are often missing from challenge studies.

Bacteria are ubiquitious on and in crabs. Several surveys of *Callinectes sapidus* show that the bacterial flora is richly diverse. Using culture-dependent techniques, several genera of bacteria were identified from the haemolymph of purchased as well as freshly caught "hardshell" crabs (Colwell et al., 1975; Sizemore et al., 1975). These include *Aeromonas* spp., *Pseudomonas* spp., *Vibrio* spp., *Bacillus* spp., *Acinetobacter* spp., *Flavobacterium* spp., and coliform bacteria similar to *Escherichia coli*, as well as several isolates that could not be identified. Forty-nine different bacterial isolates were obtained from *Callinectes sapidus*, with 41 of these isolated from the haemolymph (Overstreet & Rebarchik data in Shields & Overstreet, 2007). Sterile haemolymph was noted in only 24.3% of the 111 crabs examined. In six specimens of *Callinectes bocourti* (Portunidae), 23 different bacterial isolates were obtained from haemolymph samples, including several human pathogens: *Aeromonas hydrophila*, *Pasteurella multocida*, *Burkholderia mallei*, *Burkholderia cepacia*, *Shewanella putrefaciens*, *Salmonella* sp., *Shigella flexneri*, *Vibrio cholerae*, and *Yersinia pseudotuberculosis*, but not *Vibrio parahaemolyticus* (see Rivera et al., 1999).

Surveys of bacterial flora show similarities in the culturable species, with *Vibrio* spp. as dominant members. Several pathogenic bacteria were isolated from the gut of adult *Portunus pelagicus* (Portunidae), including *Vibrio harveyi*, *Vibrio parahaemolyticus*, *Pseudoalteromonas piscicida*, and *Staphylococcus epidermidis* (see Talpur et al., 2011). Pathogenicity studies showed that several of these bacteria caused disease in larval crabs exposed in bath cultures. Probiotic applications of *Lactobacillus* spp. showed small increases in relative survival over time (Talpur et al., 2012a, b). Bio-flocculent applications using probiotic bacteria have been tested against *Vibrio harveyi* and they can help reduce mortality in culture situations (Candelaria et al., 2010). In another study, 117 bacterial isolates were obtained from the tissues of *Ocypode platytarsis* (Ocypodidae), a crab eaten

by humans, with *Micrococcus* being the dominant genus (Sankar et al., 2013). Several bacterial isolates exhibited antibiotic resistance and were therefore considered potential human pathogens. Similar findings have been reported for cultured *Scylla serrata* (see Lalitha & Thampuran, 2012). The presence of human and aquaculture pathogens and their antibiotic resistance highlight that these systems have contamination issues with human waste.

Bacteria require a **portal of entry** into a crab in order to cause infection. The portal of entry is typically through wounding, limb autotomy, or rough handling (Tubiash et al., 1975; Johnson, 1976c). Circumstantial evidence suggests that invasion likely occurs through the gut (Davis & Sizemore, 1982). The infection can also be introduced through the carapace, and can result from injury or moulting (Sizemore & Davis, 1985). Although variable, injured crabs typically have higher prevalence levels and heavier infections than uninjured ones, which also implicates the external surfaces as the sites of invasion (Tubiash et al., 1975; Davis & Sizemore, 1982; Welsh & Sizemore, 1985). Similarly, crabs with shell disease often have **septicaemia** arising from the portal of entry caused by the disease (Vogan et al., 2001). Using high throughput sequencing techniques, this was further substantiated for *Callinectes sapidus* in a comparison of microflora from carapace, gut, and haemolymph; the bacterial community in the haemolymph more closely resembled that on the carapace (Givens et al., 2013). Crabs typically show few signs of internal bacterial infections until septicaemia is rampant. Heavily infected crabs are weak, lethargic, or moribund (Krantz et al., 1969; Welsh & Sizemore, 1985). Pathology of bacterial infections has been well described in *Callinectes sapidus* by Johnson (1976c).

New tools are available to more fully characterize the microflora on the shells and within the bodies of crustaceans. Previous work relied on culture-dependent methods or on microscopical detection, both of which have limitations. Bacterial communities in tissues, gut, or on shell can now be more readily characterized and quantified with **genomic profiling** using density gradient gel electrophoresis, length heterogeneity PCR, and high-throughput sequencing (Chistoserdov et al., 2012; Meres et al., 2012). Work with brachyurans is just starting in this arena (Li et al., 2012; Givens et al., 2013). Application of new techniques to investigate crustacean **immunology** in relation to bacterial pathogens is rapidly expanding, with important comparisons among crustacean taxa (Fang et al., 2013; Li et al., 2013a). Research in this arena tends to group all decapods as having similar immune systems, yet there will be major differences in expression systems and biological properties among taxa.

Mollicutes: Spiroplasma and Mycoplasma. – **Mollicutes**, a class in the phylum **Firmicutes**, are small (0.3-0.8 μm), pleomorphic, **Gram-negative bacteria** characterized by the lack of a cell wall (Razin, 2006). They are intracellular parasites of many plants and animals, including insects and other arthropods, and are well known contaminants in vertebrate cell cultures. **Mycoplasmas** and **spiroplasmas** are members of Mollicutes. Few mollicutes are known from crustaceans, with only one mycoplasma and one spiroplasma documented from crabs. While studying the mud crab reovirus in *Scylla serrata*, Chen et al. (2011b) isolated and purified a species of *Acholeplasma*, closely related to *Acholeplasma laidlawii*, from the gill epithelia of dead and moribund crabs. The mycoplasma

did not cause substantial disease in exposure trials, nor did signs of disease mimic those caused by the virus.

Although only one spiroplasma species, *Spiroplasma eriocheiris*, is known from a crab, it has been well studied. It is the causative agent of **tremor disease** in *Eriocheir sinensis*, a host that supports a multi-billion dollar industry in China (Wang & Gu, 2002; Wang et al., 2004, 2010). Epizootics of tremor disease caused significant losses to the mitten crab industry in the 1990s (Wang, 2011). Several studies attempted to identify the causal agent of disease (see viruses above), and the agent was initially thought to be a virus or **rickettsia** causing tremor disease by invading muscle and nervous tissues, but it also infects haemocytes and connective tissues (Wang et al., 2004, 2010). Infection trials using pure cultures indicate a 7-14 day course of infection in crabs. The time course and severity of infections show a strong correlation with temperature (Wang et al., 2004). It has been detected in environmental samples from aquaculture ponds stocked with *Eriocheir sinensis* (see Ding et al., 2007). Infected crabs can be treated with **oxytetracycline** (Liang et al., 2009; Feng et al., 2011). Several diagnostic tests have been developed to study *Spiroplasma eriocheiris*. Sequence data, PCR primers, and probes were developed to characterize the bacterium (Bi et al., 2008), and a simple extraction method and PCR assay were developed for assessing hosts and environmental samples (Ding et al., 2007, 2013). An ELISA test was developed for rapid diagnostics (Wang et al., 2009). A spiralin-like protein, SLP31, and an adhesion-like protein from the bacterium may also be useful for characterizing infections (Meng et al., 2010a, b, c).

Wolbachia. – *Wolbachia* is a genus of endosymbiotic bacteria in the **alpha-Proteobacteria**. They infect a wide range of insects and nematodes and are often transmitted sexually or through **vertical transmission** (i.e., ovarian transmission) (Werren et al., 2008). The symbiotic bacteria often induce unusual cytoplasmic incompatibilities between host gametes, thus affecting reproduction. Although decapods are not known to harbour *Wolbachia*, they have been reported from isopods (Cordaux et al., 2012). These bacterial symbionts are cryptic in nature, but they are likely to be discovered in more crustaceans, including crabs, particularly during anatomical studies of gonadal development, in broodstock analysis for aquaculture, or in studies of mating systems.

Rickettsia-like organisms. – The order **Rickettsiales** is comprised of small, Gram-negative bacteria that lack a cell wall and are intracellular parasites. Several species cause significant disease in humans and are vectored by arthropods, notably ticks. Those reported from crustaceans have not been well characterized, and may not fit within the order Rickettsiales, hence they are termed **rickettsia-like organisms** (**RLOs**).

Few RLOs have been reported from crabs. The first was reported from *Carcinus aestuarii* from the Mediterranean coast of France in crabs serving as controls for infection trials with viruses (Pappalardo & Bonami, 1980). The organism has three distinct forms: a multiplicative form (1.5-2.0 μm long by 0.7 μm in diameter), a giant cell type (up to 3.5 μm long by 1.6 μm diameter), and a smaller, electron-dense form found in the haemolymph. Crabs inoculated with a preparation of infected hepatopancreas became infected with the RLO and died over 30-35 days. Another RLO was observed in a single

specimen of *Callinectes sapidus* by Messick (1998). The RLO was present as a focal infection in the hepatopancreatic epithelial cells; however, because epithelial cells are sloughed naturally, the infection was not considered lethal. A low prevalence of an RLO was noted in holding systems as well, but no details of the infections were given (Messick & Kennedy, 1990). A disease called **milky haemolymph syndrome** in *Carcinus maenas* was caused by an RLO (Eddy et al., 2007). The pathogen was classified as a member of the alpha-Proteobacteria, but with no close affinities to known members within that taxon. Prevalence was highest in late summer and early fall (about 25%) but was otherwise very low (less than 1%). Infection trials were unsuccessful at transmitting the disease to naïve hosts. A rickettsial agent reported from *Eriocheir sinensis* was later identified as *Spiroplasma eriocheiris* (see Wang et al., 2004; see also above).

Chlamydiales. – *Chlamydia* were once thought to be related to Rickettsiales, but they are now in **Chlamydiales** (Everett, 2000). They are small Gram-negative bacteria that are obligate intracellular parasites, but unlike Rickettsiales, they have a cell wall that does not possess **peptidoglycans**. *Chlamydia* have a biphasic life cycle with a compact, infectious elementary body and a larger replicative stage called the **reticulate body**. A few are known from crustaceans, including two from crabs, but they are all poorly characterized.

The first chlamydial infection from a crab was identified in the Dungeness crab, *Metacarcinus magister* (Cancridae), from Washington state, U.S.A. (Sparks et al., 1985). Infections were systemic, but the organism had a predilection for connective tissues. Heavily infected organs were necrotic. Infected crabs were lethargic or moribund and had small spherical bodies within their haemolymph. Infections were only found in winter months, December through March, and prevalence ranged from 6-13% in one year. The organism could have caused a mortality of the crab along the Washington coastline (Stevens & Armstrong, 1984), as the discovery of both the agent and dead crabs somewhat coincided, but moribund crabs were not assessed for pathogens at the time of the event. A chlamydial infection was reported from *Cancer borealis* and *Cancer irroratus* (Cancridae) from Massachusetts, U.S.A. (Leibovitz, 1988). The infection was easily passed from crab to crab in the laboratory, but little is known of this organism.

Vibrio infections. – Vibrios are aerobic, motile, **Gram-negative rods** that are ubiquitious in the marine environment. The study of *Vibrio* infections in crabs and other crustaceans make good model systems because of their ubiquity, ease of culture, and common occurrence in and on crustaceans (Holman et al., 2004; Burnett et al., 2006; Thibodeaux et al., 2009; Schock et al., 2010; Johnson et al., 2011). The Gram-negative cell wall, composed of **lipopolysaccharides**, can induce several pathways involved in host defencses in crustaceans, making it possible to compare defensive responses to nonpathogenic and pathogenic species. Most species of *Vibrio*, including *Vibrio cholerae*, show a predilection for chitin in the hindgut or shell of crustaceans (Huq et al., 1983; Parenrengi et al., 1993; Pruzzo et al., 1996). Because these bacteria attach to chitin, they can be potentially transmitted to humans by contaminated copepods (e.g., Huq et al., 1983; Montanari et al., 1999), or through poor food handling practices (Blake et al., 1980). Although *Vibrio cholerae* has been reported from many crustaceans, including crabs (Vezzulli et al.,

2010), only specific serovars cause disease in humans; therefore, rapid identification of the pathogenic serovars is important for diagnosis. A case of necrotizing fasciolitis caused by *Vibrio vulnificus* has been reported from handling crabs (Kushawaha et al., 2010).

Several species of *Vibrio* have been isolated from the carapace, haemolymph, and digestive tract of many crab species (table II). In *Callinectes sapidus*, prevalence levels ranged from 2 to 23% and varied by *Vibrio* species and tissue predilection (Davis & Sizemore, 1982). A species of *Vibrio* was isolated from the haemolymph of *Cancer irroratus* from Long Island Sound, U.S.A., and prevalence levels varied seasonally from 10-60% (Newman & Feng, 1982). *Vibrio pectinicida* and other bacteria were isolated from the haemolymph of *Cancer pagurus* from Wales (Smith et al., 2013a). In an introduced population of *Eriocheir sinensis* in the U.K., all of the crabs tested positive for *Vibrio parahaemolyticus*, and pathogenicity markers for two haemolysin genes, indicative of potential to cause illness in humans, were present in one isolate (Wagley et al., 2009); levels of the bacterium were highest in summer. Several clades of different *Vibrio* spp. were found naturally occurring in the haemolymph of *Maja brachydactyla* (Majidae) from Spain (Gomez-Gil et al., 2010b). Vibrios were represented by 37 operational taxonomic units (OTUs), with an average of 15-17 OTUs (species) per host individual. In colder waters off Galicia, the vibrios in the *Splendidus* clade showed more diversity than other clades and in the warmer waters of the Canary Islands, the vibrios in the *Harveyi* clade were more diverse. *Photobacterium swingsii*, isolated from the haemolymph of *Maja brachydactyla*, was characterized as part of these studies (Gomez-Gil et al., 2010a). There can also be associations between vibrios and crab microhabitats, as in *Vibrio parahaemolyticus*, which had a much higher density within the burrows of fiddler crabs (*Uca pugilator* and *Uca pugnax* [Ocypodidae]) from South Carolina, U.S.A., than in adjacent creek and interstitial waters (Gamble & Lovell, 2011).

Some species of *Vibrio* can cause disease in crabs, particularly in hosts in overcrowded conditions or poor-quality water. Mortalities in production hatcheries for *Portunus trituberculatus* in China were attributed to *Vibrio harveyi* (see Zhang et al., 2014) and those in grow-out ponds to *Vibrio metschnikovii* (see Wan et al., 2011). In both cases, exposure studies with megalopae showed a strong dose response with bacterial density. A mass mortality of larvae of *Portunus pelagicus* was attributed to *Vibrio harveyi* in a hatchery in Malaysia (Talpur et al., 2011); the LD_{50} was estimated at 10^3 CFU/ml. Bath and oral challenge studies with *Vibrio parahaemolyticus* and *Vibrio alginolyticus* indicated that they can cause mortality of the first stage zoeae of *Scylla paramamosain* (see Peng et al., 2012). Zoeae 4 were somewhat more resistant than zoeae 1. Challenge studies with *Vibrio alginolyticus* in *Charybdis japonica* (Portunidae) also indicated some pathogenicity (Xu et al., 2013).

Bacterial intensities in *Vibrio* infections can be quite high. Mean densities of 10^5-10^6 colony forming units (CFU) ml^{-1} in haemolymph have been reported from *Callinectes sapidus* by Colwell et al. (1975), and densities of 2.9×10^7 CFU ml^{-1}, with direct counts up to 4.64×10^{11} bacteria ml^{-1} have been reported from *Callinectes bocourti* by Rivera

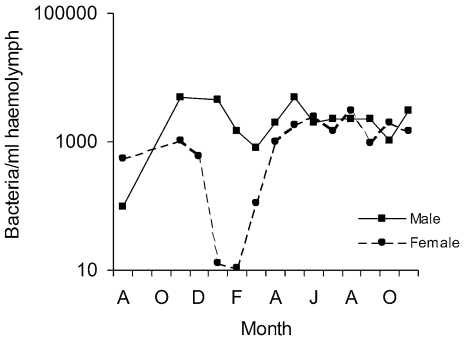

Fig. 71-12.4. Seasonal intensity (log scale) of bacterial infections in haemolymph of male and female *Callinectes sapidus*. Note the nadir in winter months in females. The combined prevalence of infections was 69.6% in winter, 80.6% in summer. [Redrawn from Tubiash et al., 1975.]

et al. (1999). Numbers over 10^4 CFU ml^{-1} are rare, possibly because of disease-induced mortality at higher intensities (Welsh & Sizemore, 1985).

Vibrio infections typically show distinct seasonality in occurrence (fig. 71-12.4). Mortalities of *Callinectes sapidus* due to *Vibrio* infections sometimes occur during rapid changes in water temperature in the spring and summer (Johnson, 1976c). The prevalence and intensity of *Vibrio* infections in Chesapeake Bay was highest in summer and lowest in winter (Tubiash et al., 1975). In Galveston Bay, Texas, the prevalence of *Vibrio* infections was higher in summer than in winter, but there was no significant association between intensity of infection and season (Davis & Sizemore, 1982). Intensity of infection near Wilmington, North Carolina, U.S.A., showed strong positive correlations with water temperature (Welsh & Sizemore, 1985). Moreover, mean intensity and prevalence of *Vibrio* infections was higher in crabs subject to higher levels of handling stress than those subjected to less stress.

Other bacterial pathogens. – The well-known lobster pathogen, *Aerococcus viridans* var. *homari*, causative agent of **gaffkemia**, was isolated from the haemolymph of naturally infected *Cancer irroratus* and *Cancer borealis* from Maine, U.S.A. (Gallagher et al., 1979). Prevalence ranged from 1.1-4.4%, which is similar to that reported for naturally infected lobsters, *Homarus americanus* (see Stewart et al., 1966; Lavallée et al., 2001). The bacterium is known to be highly pathogenic to lobsters, and its pathogenicity is directly related to temperatures higher than 10°C (Stewart et al., 1969a). It is markedly less pathogenic in experimentally infected crab hosts such as *Cancer irroratus*, *Cancer borealis*, *Chaceon quinquedens* (Geryonidae), *Chionoecetes opilio*, and *Libinia emarginata* (Epialtidae) (Cornick & Stewart, 1968, 1975; Rabin & Hughes, 1968). The bacterium requires a portal of entry through the cuticle of lobsters for transmission. It cannot penetrate intact cuticle nor can it be transmitted through feeding (Stewart et al., 1969b), so natural infections in *Cancer* spp. are unlikely to be transmited to lobsters through predation. The susceptibility of different decapods highlights the fact that crustacean immune defences differ markedly between taxa. This pathogen would make an excellent model for

exploring the nature of susceptibility among hosts; work with lobsters has shown that anti-lipopolysaccharide genes are differentially expressed in challenge experiments (Clark et al., 2013).

The human bacterium *Enterococcus* (= *Streptococcus*) *faecalis* was identified from *Carcinus aestuarii* found near a **sewage** treatment plant during summer months along the Mediterranean coast of France (Pappalardo & Boemare, 1982). Characteristic encapsulated, **Gram-positive cocci** and **diplococci** were observed in the spongy connective tissues (interstitial cells) surrounding the hepatopancreatic tubules, in some cases forming large plaques. Infection studies reproduced the disease via feeding infected tissues to naïve hosts as well as inoculating uninfected crabs with different densities of bacteria from pure culture. Low densities of inocula killed crabs over 30-40 days.

Psychrobacter cibarius, a **Gram-negative bacillococcus**, was isolated from the haemolymph of *Metacarcinus magister* from Oregon, U.S.A. (Scholnick & Haynes, 2012). Natural infections of the bacterium increased in intensity in relation to hypoxic conditions. It was not associated with mortality in the host, but did provide a useful model for studying the effect of **hypoxia** on natural and experimental infections.

An unusual strand-like or filamentous Gram-negative bacterium was identified from the lumen of the midgut and hepatopancreas from *Callinectes sapidus* (see Johnson, 1983; Messick, 1998). Foci of the bacterium were attached to the epithelial cells of the hepatopancreas (fig. 71-12.5). The bacterium had a low prevalence level of 2% in crabs from the Atlantic and Gulf coasts of the U.S.A. (Johnson, 1983). The prevalence ranged from 12% in flow-through culture systems to 31% in a recirculating system (Messick & Kennedy, 1990). The bacterium had a higher prevalence in the summer compared to other months and was more common in juvenile crabs than in adults (Messick, 1998). Because this bacterium was focal in nature and attached to the epithelial cells, it was not considered a pathogen (Johnson, 1983; Messick, 1998).

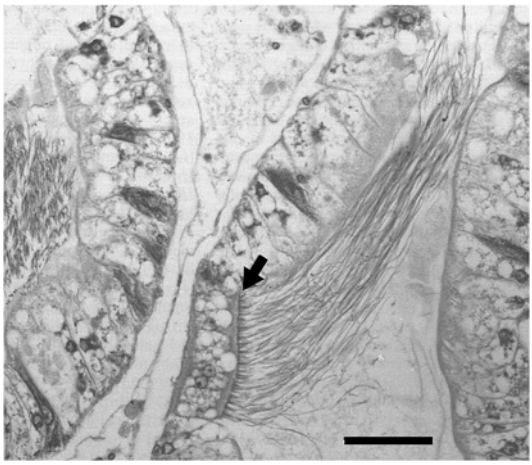

Fig. 71-12.5. Strand-like bacterium in a hepatopancreatic tubule of *Callinectes sapidus*. The bacteria are attached (arrow) to the luminal surface of an epithelial cell and project into the lumen (bar = 50 μm). [After Messick, 1998.]

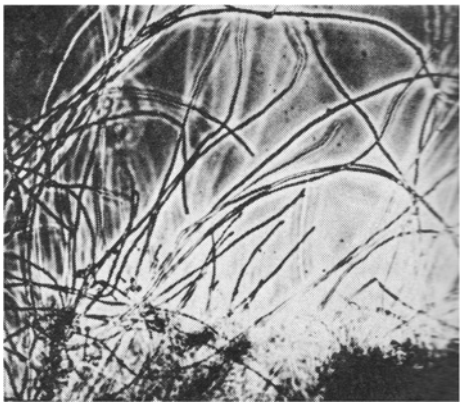

Fig. 71-12.6. Heavy infestation of the filamentous bacterium *Leucothrix mucor* on a pleopod of *Carcinus maenas*. [After Johnson et al., 1971.]

Leucothrix mucor is a filamentous Gram-negative bacterium found on external surfaces, such as gills, eggs, algae, and other surfaces in marine environments (Johnson et al., 1971; Bland & Brock, 1973). It is common in the egg masses and occasionally on the gills of many crustaceans (fig. 71-12.6) (Bland & Amerson, 1974; Bodammer & Sawyer, 1981). The bacterium was thought to cause egg mortalities in *Cancer* spp. (Fisher, 1976), but in an experimental system its contribution to mortalities was negligible (Shields & Kuris, 1988). The presence of the bacterium is typically an indicator of excess nutrients, such as contamination with **pollutants** or nutrient loading (Sawyer et al., 1984; Schuwerack et al., 2001). Antibacterial treatments have been tested on brine shrimp to reduce bacterial mats with formulations of oxytetracycline being most effective (Solangi et al., 1979).

Red sternum disease is an emerging disease in the culture of *Scylla serrata* from Thailand (Salaenoi et al., 2006). Signs of the disease include a red colour to the sternum, abnormal hardening of the cuticle, abnormal clotting ability, flaccid muscle, lethargy, and a loss of appetite. The pathophysiology of the disease indicates significant changes to levels of **oxyhaemocyanin** and **trace metals**, particularly copper, iron, magnesium, and zinc (Salaenoi et al., 2006). The aetiology of this disease remains to be fully determined, but it could be a bacterial dysbiosis (microbial imbalance) as Areekijseree et al. (2010) identified several bacteria associated with different stages of infection. No obvious patterns were apparent.

Shell disease. – Shell disease is typically a non-fatal external bacterial infection of the "shell" or cuticle of crustaceans. The disease, which is sometimes termed a syndrome, has several underlying aetiologies; typically it arises when lacerations create a portal of entry through the epicuticle and exocuticle into the chitin-rich endocuticle (Cook & Lofton, 1973; Getchell, 1989). **Chitinoclastic bacteria** are a normal constituent of the bacterial flora found on crustaceans, but they do not normally penetrate through the phenolic barrier of the epicuticle, but bacterial **enzymes** such as chitinase, lipase, and proteases can facilitate infections (Dennel, 1960; Moret & Moreau, 2012). Shell disease

is typically associated with environmental stressors such as high **stocking densities**, long-term confinement, poor diet, moulting, and environmental pollutants (Rosen, 1967; Iversen & Beardsley, 1976; Johnson, 1983; Smolowitz et al., 1992). Although bacteria are clearly involved in the aetiology of the disease, **pollutants** (sewage sludge, dredge spoils, heavy metals, and organic debris) and other symbionts can play a significant role in the syndrome (Young & Pearce, 1975; Couch, 1983; Morado et al., 1988; Weinstein et al., 1992; Ziskowski et al., 1996; Andersen et al., 2000). Fungal infections can also cause shell disease in crustaceans (see below).

Shields (2013) distinguished the proximate and ultimate causalities of bacterial shell disease, with proximate causality being the aetiology of the observed disease condition and the ultimate causality being the underlying stressors that weakened the host, making it susceptible to bacterial invasion. Shell disease is in many cases associated with significant problems in **water quality**, which may weaken the cuticle (Gemperline et al., 1992; Weinstein et al., 1992; Vogan et al., 2008; Jacobs et al., 2012), ultimately rendering the carapace more susceptible to bacterial invasion (Laufer et al., 2012).

Although noted by Herrick (1909) and others, bacterial shell disease was first described in detail by Hess (1937). The best-known studies in crabs are from *Callinectes sapidus* (fig. 71-12.7). The shell disease **lesions** are essentially micro-communities of bacterial colonizers that include chitinoclastic and non-chitinoclastic forms (Rosen, 1970). Bacterial shell disease is typically caused by Gram-negative bacteria, such as *Vibrio* and *Pseudomonas* (Rosen, 1967; Cook & Lofton, 1973), but several genera (*Vibrio*, *Aeromonas*, *Pseudomonas*, *Kingella*, and *Serratia*) are capable of producing chitinase (Overstreet and Rebarchik data in Shields & Overstreet, 2007). Several vibrios and vibrio-like species (*Photobacterium* sp.) were isolated from shell disease lesions on *Chionoecetes tanneri* (Oregoniidae) from Oregon, U.S.A. (Baross et al., 1978) and *Cancer pagurus* from the U.K. (Vogan et al., 2001, 2002). Chitinoclastic bacteria are mostly isolated by streaking pieces of infected shell onto marine agar enriched with precipitated chitin (Skerman medium) (Cook & Lofton, 1973); thus, the culturable species are examined, but non-culturable forms could also be implicated in shell disease (Chistoserdov et al., 2012; Meres et al., 2012).

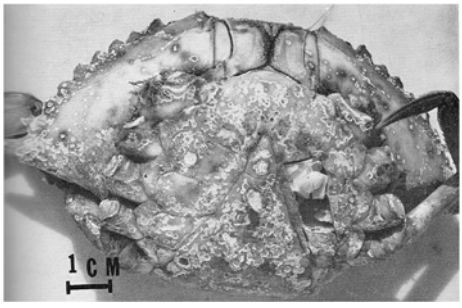

Fig. 71-12.7. Extensive shell disease on an immature *Callinectes sapidus* taken from a shedding float. This individual, 11 cm in carapace width, was alive when sampled. [After Rosen, 1967.]

Early lesions appear as small, punctate, or crater-like marks on the carapace, sternum or legs (Rosen, 1967; Johnson, 1983). Lesions initially tend to spread horizontally. As the lesions coalesce, they form broad, irregular necrotic areas that are friable, easily punctured, and turn black, brown, or dark orange from **melanin** deposition (Rosen, 1967; Overstreet, 1978; Johnson, 1983). Large, advanced lesions can penetrate through the membranous layer, and cause the limbs and spines to become necrotic and break off (Rosen, 1967). Any external cuticularized area can be attacked, even the gills (Johnson, 1983). In most cases, individuals can moult out of the disease (Rosen, 1967), but animals with **terminal anecdysis** can develop heavy infections that are likely fatal (Sandifer & Eldridge, 1974; Baross et al., 1978). Lesions can adhere to the new instar during moulting in advanced cases, resulting in death due to an inability to moult properly (Sandifer & Eldridge, 1974; Fisher, 1976; Overstreet, 1978; Johnson, 1983). Heavily infected animals can also die, presumably from secondary infections.

Histologically, the cuticle within shell disease lesions is often friable, with melanin deposition in the endocuticle. In severe cases, a pseudomembrane can form beneath the affected membranous layer with marked infiltration of haemocytes into the affected area (Noga et al., 2000; Vogan et al., 2001). Haemocytic aggregations, nodules, or granulomas often occur in systemic bacterial infections in crustaceans and they are frequently observed in animals with shell disease. Septicaemia is a common feature of shell disease infections (Vogan et al., 2002; Smith et al., 2013a). Several histopathological changes have been attributed to shell disease (Vogan et al., 2001; Costas-Ramos & Rowley, 2004; Ryazanova, 2005), presumably from bacterial invasion. The hepatopancreas of some affected individuals of *Cancer pagurus* appeared degraded, with a noticeable decline in free haemocytes (Vogan et al., 2001). *Cancer pagurus* inoculated with chitinoclastic bacteria isolated from diseased crabs exhibited few changes in haemolymph chemistry, but haemocyte densities were altered (Vogan & Rowley, 2002), and injections of extracellular products, particularly lipopolysaccharides from one isolate of *Pseudoalteromonas atlantica*, resulted in rapid death (Costa-Ramos & Rowley, 2004).

Bacterial shell disease has been correlated with declines in **immune functions**. The defensive peptide **callinectin** was lower in *Callinectes sapidus* with shell disease than in those without the disease (Noga et al., 1994, 1996; Khoo et al., 1996). Individuals from contaminated sites had less antibacterial activity than crabs from less contaminated sites (Noga et al., 1994). A similar pattern was observed in haemocyanin levels (Engel et al., 1993). Metal ions could play a role in augmenting chitinolytic activity (Vogan et al., 2008). Few studies have examined the effect of shell disease on immune function (Homerding et al., 2012), but this area could present rich opportunities for additional research.

Aetiological investigations with shell disease can take advantage of pair-wise treatments of the host carapace. The host carapace can be sterilized, gently rasped, sanded, or scraped to expose the exo- or endocuticle, and then the affected and unaffected areas can be inoculated with potential aetiological agents (Cook & Lofton, 1973; McKenna et al., 1990; Quinn et al., 2012). Shell necrosis typically occurs in the rasped area and not in the undamaged areas. A sentinel study using this method on *Callinectes sapidus* showed that areas with high contaminant loads developed shell disease more quickly than areas

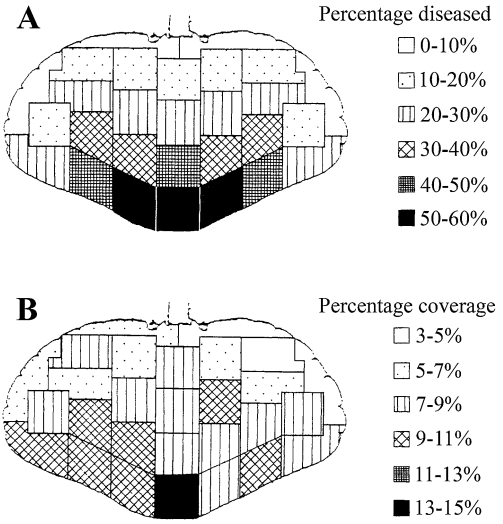

Fig. 71-12.8. Distribution of shell disease lesions on *Cancer pagurus*: A, percentage of crabs showing disease in different regions of the carapace ($n = 245$ crabs); B, percentage of region covered by shell disease lesions (infected crabs only). [After Vogan et al., 1999.]

with low contaminant load (McKenna et al., 1990). A higher prevalence of shell disease lesions in *Cancer pagurus* occurred on the posterior carapace and ventral surfaces of the limbs as a result of sand abrasion and subsequent infection from burying in the sediments (fig. 71-12.8) (Vogan et al., 1999). The prevalence of shell disease was higher in a site with a finer grain sediment and organic **pollution** load than in a site with coarse sediments and less organic load (Vogan & Rowley, 2002).

Bacterial shell disease is not usually a significant pathogen in most crustaceans. High prevalence levels indicate problems associated with environmental stressors. In crab populations, severe infections are typically equated with poor water quality and have remained somewhat localized in nature. Prevalence levels in *Callinectes sapidus* have been reported from 3% (Rosen, 1967) to a locally abundant 53.1% (Sandifer & Eldridge, 1974). Prevalence can vary with the season or with host sex (fig. 71-12.4) and it is typically highest in mature females that stop moulting (McKenna et al., 1990). In *Callinectes rathbunae* (Portunidae) from the Gulf of Mexico, however, there was no correlation between shell disease and infection with the rhizocephalan *Loxothylacus texanus*, which induces **anecdysis** (Vazquez-Lopez et al., 2012). Prevalence in *Cancer pagurus* near a site contaminated with sewage outfall ranged from 40-88%, but the intensity was low, with a mean of less than 1% of the body area covered with the disease (Vogan et al., 1999). There was little change in shell disease after the sewage outfall was closed, although there was a reduction in shell disease in smaller-sized crabs (Powell & Rowley, 2005). Prevalence in *Carcinus aestuarii* reached 100% in individuals from the highly impacted Volturno River, Italy, with several species of *Vibrio*, *Listonella anguillarum*, and *Aeromonas hydrophila* isolated from the lesions (Mancuso et al., 2013). Prevalence in *Chionoecetes tanneri* off Oregon was highest in adult crabs that were in the terminal moult, with 78% of the females

and 29% of the males exhibiting some form of shell disease lesion (Baross et al., 1978). Prevalence in *Chionoecetes opilio* from the Gulf of St. Lawrence, Canada, was much lower at 2.1% on male crabs (Benhalima et al., 1998b). Prevalence of shell disease and carapace deformities in *Neohelice granulata* (Varunidae) from a mangrove forest in Brazil was 1.8% (Gregati & Negreiros-Fransozo, 2009).

Enzootic, or classical, shell disease can be contagious, especially in combination with environmental stressors (Rosen, 1970; Sandifer & Eldridge, 1974). Because of the strong association with stressors, the underlying aetiology must be carefully determined (Brock & Lightner, 1990; Shields, 2013). For short- and intermediate-term settings, wound avoidance, proper attention to water quality and hygiene, and proper husbandry help control shell disease (Stewart, 1980). Malachite green, **antibiotic** baths (penicillin-streptomycin, furanace, erythromycin, oxolinic acid), and formalin have been used with modest success in some crustaceans (Fisher et al., 1978; Brock, 1983; El-Gamal et al., 1986). Because the disease can be contagious, heavily affected animals in aquaculture settings should be destroyed to prevent further spread.

FUNGI AND FUNGUS-LIKE PROTISTS

The kingdom Fungi has undergone rather significant revision, with most of the "lower fungi" now placed in Chromalveolata and the "higher fungi", including deuteromycetes, retained as true Fungi (Cavalier-Smith, 1993, 2000; Keeling et al., 2005). Members of oomycetes and phycomycetes, traditionally known as **water moulds**, are now considered in Stramenopiles, which is the sister taxon to Alveolata (Adl et al., 2005; Keeling et al., 2005; Parfrey et al., 2010). Both Stramenopiles and true Fungi include examples that are pathogens of crabs. Most mould and fungal infections in crustaceans are known as pathogens of embryos within the egg clutch of the maternal host, but several cause significant pathology in juvenile and adult hosts, and a few have occurred in epizootics outbreaks. One of the most notorious and damaging water moulds is *Aphanomyces astaci*, the aetiological agent of *Krebspest*, or **crayfish plague**. Mycotic diseases of crustaceans have been reviewed by several authors (Unestam, 1973; Alderman, 1976; Lightner, 1981; Johnson, 1983; Hatai, 2012).

Fungus-like protists: oomycetes. – The water moulds, oomycetes or **Oomycota**, produce hyphae and zoospores as do many of the fungus-like protists. They are common in the organically enriched environment of the crustacean egg clutch. Water moulds are primarily saphrophytic but several taxa, particularly species of *Lagenidium*, *Haliphthoros*, and *Atkinsiella*, as well as the fungus *Fusarium solani*, are known to infect crustacean embryos (fig. 71-12.9) and inflict significant damage to nascent aquaculture attempts (Lightner, 1981). The best-studied oomycete in crabs, *Lagenidium callinectes*, is often reported as a pathogen in culture systems. It was first isolated from the embryos of *Callinectes sapidus* by Couch (1942), but it is now known to occur on the embryos and larvae of many decapods as well as on algae. Its sporogenesis, sporulation, and infection of crab embryos have been well described (Bland & Amerson, 1973; Gotelli, 1974a, b), as has its physiology in culture (Gotelli, 1974a, b; Bahnweg & Bland, 1980; Bahnweg &

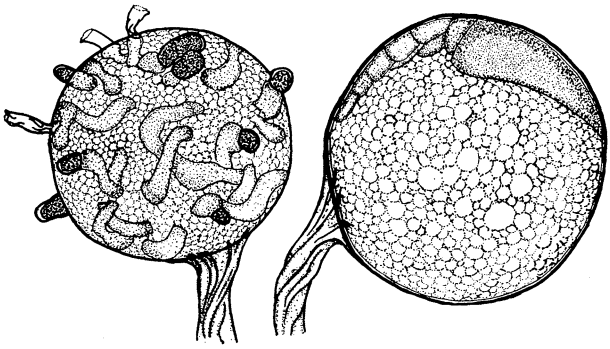

Fig. 71-12.9. Embryos of *Callinectes sapidus*: left, embryo infected with *Lagenidium callinectes*; right, embryo of an uninfected crab. [After Rogers-Talbert, 1948.]

Gotelli, 1980; Crisp et al., 1989; Bertke & Aronson, 1992). The nutrient requirements for the water mould are more representative of a saprophyte than a pathogen (Bahnweg & Bland, 1980). Zoospores enable rapid transmission to new hosts and extramatrical hyphae enable transmission between embryos (Bland & Amerson, 1973; Gotelli, 1974a, b).

Lagenidium callinectes has been reported from several hosts including *Callinectes sapidus* (see Sandoz et al., 1944; Rogers-Talbert, 1948), *Portunus pelagicus* by Nakamura & Hatai (1995), *Scylla serrata* (see Hamasaki & Hatai, 1993a; Roza & Hatai, 1999a; Hatai et al., 2000), and *Metacarcinus magister* by Armstrong et al. (1976). The embryos of several crab species are also known to be susceptible to the water mould based on infection studies. The embryos of several species of shrimps were susceptible to infection, but not those of *Libinia emarginata*, *Menippe mercenaria* (Menippidae), or *Armases cinereum* (Sesarmidae) (Rogers-Talbert, 1948; Bland & Amerson, 1974). Natural infections have also been reported from other taxa.

Two other species of *Lagenidium* have been reported as parasites of crab embryos and larvae: *Lagenidium scyllae* by Bian et al. (1979) and *Salilagenidium thermophilum* by Nakamura et al. (1995) both from *Scylla serrata*. Several closely related oomycetes are also known to attack and kill crab embryos and larvae, including *Haliphthoros milfordensis* and *Halocrusticida* sp. from larval *Scylla serrata* (see Roza & Hatai, 1999b; Hatai et al., 2000; Leano, 2002), *Atkinsiella hamanaensis* from *Scylla serrata* by Bian & Egusa (1980), *Haliphthoros milfordensis* and *Atkinsiella okinawaensis* from *Portunus pelagicus* by Nakamura & Hatai (1995), and *Atkinsiella dubia* in larvae of *Eriocheir sinensis* (see Atkins, 1954a; Roza & Hatai, 1999b). Two oomycetes have been reported from embryos of the pea crab *Pinnotheres pisum* (Pinnotheridae): *Pythium thalassium* by Atkins (1955) and *Leptolegnia marina* by Atkins (1954b). *Leptolegnia marina* also occurred internally in *Pinnotheres pisum* and infections were found in *Nepinnotheres pinnotheres* (Pinnotheridae) and *Callinectes sapidus* (see Atkins, 1954b; Johnson & Pinschmidt, 1963).

Embryos and larvae infected with water moulds exhibit 100% mortality (Nakamura et al., 1995; Hatai et al., 2000). Infected eggs appear as brown or grey patches in the clutch and are usually found along the periphery of the egg clutch (Couch, 1942; Rogers-Talbert,

1948). Heavily infected clutches can occur in natural and aquaculture settings (Rogers-Talbert, 1948; Hatai et al., 2000). Crab larvae can rapidly acquire infections, typically within two to three days of exposure to infected females or to water contaminated with zoospores (Armstrong et al., 1976). Larvae are apparently infected after moulting, as the germ tube of the water mould cannot penetrate the intermoult cuticle (Armstrong et al., 1976). Infected zoeae of *Metacarcinus magister* exhibited 40% mortality over seven days.

Oomycetes (*Lagenidium callinectes*, *Haliphthoros milfordensis*, and others) represent a significant threat to the culturing of crabs. Malachite green (Bland et al., 1976), trifluralin, captan (Armstrong et al., 1976), and furanace (Lio-Po et al., 1985) have been used to reduce fungal infections in shrimp culture. Formalin (Hamasaki & Hatai, 1993b; de Pedro et al., 2007) and high pH (Yasunobu et al., 1997) have been used to treat crab embryos and larvae in cultures. Malachite green, formalin, and furanace have been used to treat infections in lobster cultures (Abrahams & Brown, 1977; Fisher et al., 1978; Diggles, 2001). None of these compounds is currently available for use in aquaculture in the U.S.A. As with bacterial infections, disease due to water moulds is often related to poor hygiene of the culture system and poor water quality.

Other stramenopiles. – The **thraustochytrids** are members of Labyrinthulomycetes, phylum Stramenopiles. Most thraustochytrids are saprophytes and are rarely pathogenic, but a few cause significant disease, such as **QPX** in clams (Bivalvia) (Whyte et al., 1994) and abalones (Gastropoda) (Bower, 1987), and wasting disease in sea grasses (Alismatales, Zosteraceae) (Short et al., 1987). They are infrequently reported as parasitic on the egg masses or at least as saprobes on dead eggs within egg masses of brachyurans (Shields, 1990). An unidentified thraustochytrid was observed in the egg masses of *Callinectes sapidus* by Rogers-Talbert (1948). Another unidentified thraustochytrid caused significant egg mortality in two ovigerous *Scylla serrata* from a hatchery in Australia (Kvingedal et al., 2006). The parasite was identified using molecular sequencing and was shown to be a thraustochytrid, but had no clear affinity to any known species. Sori, or clusters of sporangia, of the pathogen were present externally on the chorion of the embryos, with **rhizoids**, or rootlets, penetrating into the interior of the embryo. In the milieu of the egg mass, several protists, including thraustochytrids, oomycetes, and true fungi, are attracted to dead eggs, which make an excellent medium for benthic saprobes. A few studies have examined whether these are parasitic or saprophytic (Shields, 1990).

For many years, members of Eccrinales were considered true fungi in Zygomycota. Recent molecular studies have shown that the taxon belongs in the protistan class Mesomycetozoa, sometimes refered to as Icthyosporea, within the order Ichthyophonida (Cafaro, 2005). Eccrinales are obligate symbionts on and in arthropods; they are osmotrophic, and their symbiosis ranges from commensalism to parasitism, but little work has been done on their host-symbiont associations. A few species are known from crustaceans, including crabs (see Lichtwardt, 1986; Glockling et al., 2013). Two species, *Enteromyces callianassae* and *Taeniella carcini* live in the hindgut of their axiidean and brachyuran hosts (Lichtwardt, 1986). Six brachyurans, *Uca rapax*, *Uca pugilator*, *Uca longisignalis* (Ocypodidae), *Armases cinereum*, *Sesarma reticulatum* (Sesarmidae), and *Aratus pisonii* (Sesarmidae), in Florida are infected with *Enteromyces* sp. and *Taeniella* sp. (Mattson,

1988). Prevalence levels were highest (70%) in *Uca rapax*. Only grapsids and ocypodids were infested, not portunid, xanthid, or majid crabs. The association with grapsids and ocypodids was thought to be due to their deposit feeding. A similar species of *Enteromyces* was identified in *Uca rapax* and *Uca burgersi* (Ocypodidae) from Puerto Rico (Roa et al., 2009). The varunids *Hemigrapsus nudus* and *Hemigrapsus oregonensis* are infected by *Taeniella carcini* and *Hemigrapsus penicillatus* by *Enteromyces callianassae* (see Lichtwardt, 1986; McDermott, 2011).

True fungi: yeasts and Ascomycota. – Few true fungi are pathogenic in crustaceans with only one yeast-like organism, *Ophiocordyceps* sp., reported from the crabs, *Cancer pagurus* and *Liocarcinus depurator*, as co-infections with *Hematodinium* sp. (Stentiford et al., 2003; Smith et al., 2013b). A saprophytic chytrid was identified from the embryos of *Metacarcinus anthonyi* (Cancridae) and other cancrids from California (Shields, 1990). The chytrid, *Rhizophydium littoreum*, was capable of rapidly attacking and killing living embryos under certain conditions, but it preferentially attacked dead embryos. Two ascomycete fungi have been identified as primary pathogens in brachyurans: *Trichomaris invadens* and *Exophiala cancerae*.

Trichomaris invadens causes **black mat syndrome** on the shell of *Chionoecetes opilio* from Alaska (Sparks & Hibbits, 1979). The **ascocarp**, or **perithecium**, of the fungus is globose and black in colour, and that latter feature, along with darkly pigmented encrusting hyphae, gives rise to the name of the syndrome (fig. 71-12.10). Both the ascocarp and the hyphae grow in the cuticle of the crab. The ascospores bear a long, hair-like appendage at both ends (Hibbits et al., 1981; Porter, 1982) that may function as entanglement holdfasts (Porter, 1982). Hyphae initially grow into the cuticle and spread laterally, but they are capable of penetrating through the endocuticle and membranous layer into the epidermal tissues (Sparks & Hibbits, 1979). Hyphae can invade virtually any organ in severe infections. In early infections the eyes and eyestalks become infected (Sparks, 1982) and the gills can show significant necrosis. There was a relative increase in granulocytes in relation to severity of infection, but total haemocyte densities were not established (Mix & Sparks, 1980).

The prevalence of black mat syndrome can be high in populations of the snow crab (*Chionoecetes opilio*). Over disparate temporal periods, prevalence averaged 50% in crabs from locations around Kodiak Island (Hicks, 1982; Dick et al., 1998). Prevalence was lowest in animals that had moulted during the year, but was much higher in crabs that had skipped moulting over one to two years (Dick et al., 1998). The fungus likely inhibits moulting and can negatively affect the fishery for snow crabs in areas with high prevalence levels (Sparks, 1982). The mean prevalence at four processing plants was 12.7% ($n = 1500$ crabs) in Anchorage, Alaska (Hoskin, 1983). Black mat syndrome does not occur in the fishery off eastern Canada (Benhalima et al., 1998b).

An unusual fungal disease emerged in the mangrove crab *Ucides cordatus* (Ucididae) from Brazil in the late 1990s. The syndrome, known as **lethargic crab disease**, was initially thought to have several anthropogenic causes but results from histological investigations (Boeger et al., 2005, 2007), molecular studies (Pie et al., 2011), and infection trials

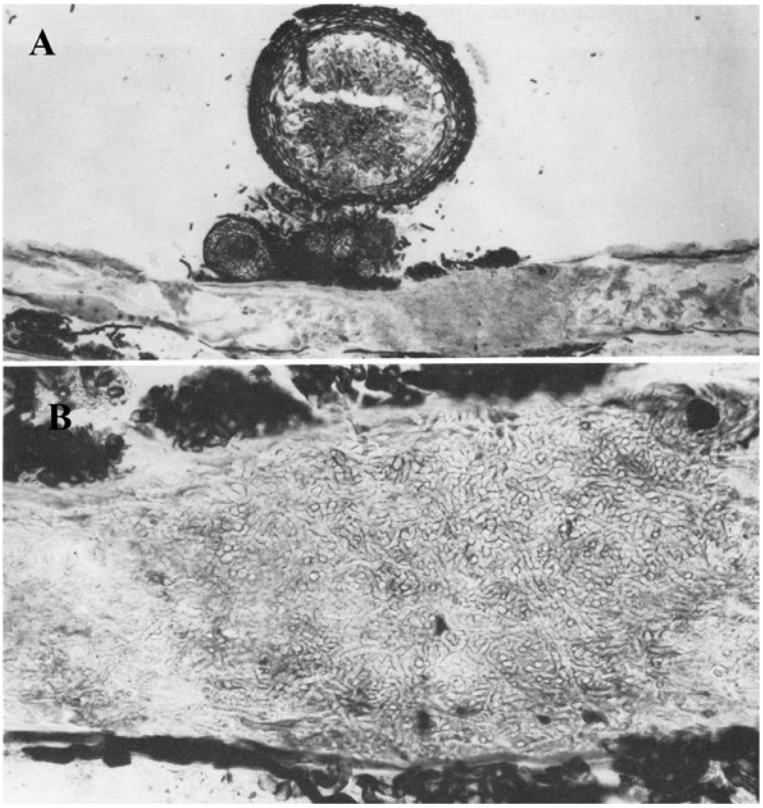

Fig. 71-12.10. *Trichomaris invadens* on the gill lamellae of *Chionoecetes opilio*: A, pigmented external hyphae and perithecia of the fungus externally on the gill, ×100; B, detail showing proliferation of hyphae within the lamella and ineffectual host melanization response (upper right), ×380. [After Sparks, 1982.]

to demonstrate Koch's postulates (Orélis-Ribeiro et al., 2011) have conclusively demonstrated that a black yeast, *Exophiala cancerae*, causes the disease. Another black yeast, *Fonsecaea brasiliensis*, occurs in co-infections with *Exophiala cancerae* (see Vicente et al., 2012). Black yeasts are true ascomycete fungi; they are typically free-living saprobes that can cause disease in warm- and cold-blooded vertebrates (De Hoog & Guarro, 1995).

Crabs infected with *Exophiala cancerae* become lethargic, develop tetany, and show ataxia before dying, hence the common name for the disease (Boeger et al., 2005). Signs of disease and concurrent mortalities occur within 2-3 weeks of inoculation with fungal elements (Orélis-Ribeiro et al., 2011). Infections are systemic, but few yeast cells are apparent in the tissues. Hyphae, conidia, and yeast cells can be present in the tissues of most organ systems, but other tissues are also invaded (Boeger et al., 2007). The host response includes intense haemocytic infiltration, encapsulation, and phagocytosis as is seen with many fungal infections. Several molecular diagnostics have been developed to assess the presence of the yeast in tissue and environmental samples (Pie et al., 2011;

Vicente et al., 2012). Sampling techniques did not find the agents in environmental samples, but other black yeasts were identified from mangroves (Guerra et al., 2013). Pathogenic black yeasts can show host specificity (De Hoog & Guarro, 1995) and, thus, may not be normal constituents in environmental samples (Vicente et al., 2012).

Ucides cordatus supports artisanal fisheries in Brazil. Outbreaks of lethargic crab disease in this species have reduced fishing yields by 84 to 98% in some localities (Alves & Nishida, 2003; Nóbrega & Nishida, 2003). The impact of the disease may be severe because the crab is considered a keystone species in mangrove communities (Orélis-Ribeiro et al., 2011). Epidemiological models have been developed to examine how the disease spreads rapidly from its initial emergence. A basic model of **susceptible-infected-recovered** (SIR) individuals showed that changes in disease-induced mortality rates can promote disease endemicity. Further development of the SIR model to reflect spatial and temporal changes allowed analysis of the geographic diffusion of the disease spatially as a model for a travelling wave epidemic (Ávila et al., 2012). The range of studies on *Exophiala cancerae* exemplifies the multidisciplinary approach required to better understand emerging disease phenomena. Additional questions remain as to how the pathogen is transmitted, whether it is a host specialist, and whether crabs can survive infections and develop resistance to it.

Phylum Microsporidia. – **Microsporidians** are considered highly derived fungi, with affinities to **Zygomycetes** (Lee et al., 2008). The phylum has five major clades, with host specialization appearing in clades infecting vertebrates and invertebrates (Smith, 2009). All members of the phylum are obligate intracellular parasites that produce small (usually less than 6 μm) unicellular spores with a highly resistant, chitin-rich spore wall (fig. 71-12.11). The life cycle has two stages: a proliferative stage, or intracellular meront, and a spore stage for transmission to new hosts (fig. 71-12.12). The spore stage possesses a sporoplasm and an elaborate structure with an extrusible polar tube used for invading host cells. Many genera, including *Plistophora* and *Thelohania*, have spores that develop inside a **sporophorous vesicle** (SPV), whereas in other genera, including *Ameson*, the spores develop freely within the cytoplasm of the host cell. Microsporidians typically have direct life cycles but a few have indirect life cycles. The life cycles of those that use crabs are thought to be direct, but they are mostly unknown and require further study. Recent advances in molecular techniques have facilitated descriptions of new taxa (Stentiford et al., 2010), as well as highlighted new **phylogenetic associations** (Lee et al., 2008).

Approximately 187 genera of microsporidians are known, with eight genera infecting crabs (Stentiford et al., 2013a). Although microsporidians can be the most frequently observed parasites in crustaceans (Sprague & Couch, 1971; Couch, 1983; Stentiford et al., 2013a), only 12 recognized species use brachyurans, and they are not well described or studied from these hosts (table III). Their diversity is likely higher as, for example, at least six species of microsporidians are known to infect *Callinectes sapidus*, but only one, *Ameson michaelis*, has been described adequately using TEM, and the taxonomic placement of another, *Plistophora cargoi*, is uncertain because its description is based

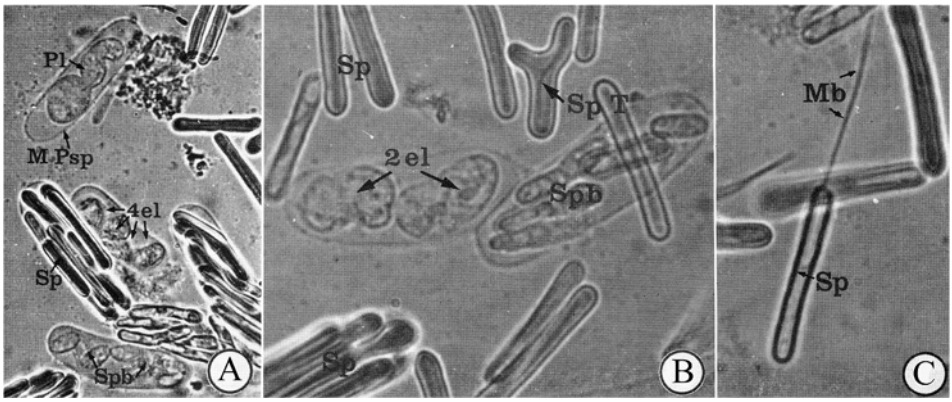

Fig. 71-12.11. Life history stages of *Ormieresia carcini* from the muscle of *Carcinus aestuarii*: A, development of the parasite within the pansporoblast (M Psp) showing the plasmodia (Pl), four nuclei (4el), sporoblasts (Spb) or 8 spore (Sp) stages within the pansporoblast, ×1000; B, pansporoblasts with two binuclear cells (2el), a sporoblast (Spb), and spores (Sp), and an unusual teratogenic spore (Sp T), ×1600; C, spore (Sp) with an extroverted manubrium (Mb), ×1600. [After Vivarès et al., 1977.]

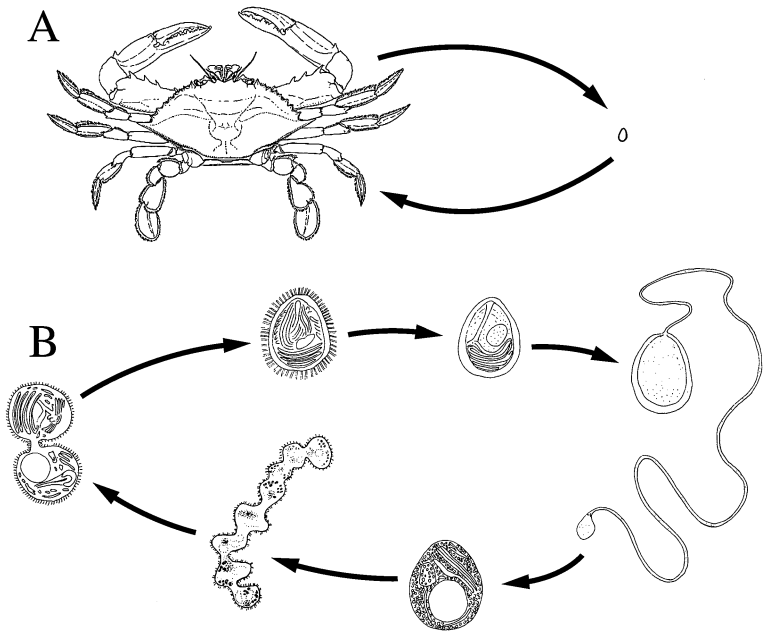

Fig. 71-12.12. Life cycle of *Ameson michaelis* in *Callinectes sapidus*: A, the microsporidian has a direct life cycle in the crab, consisting of intracellular stages in the musculature; B, the spores (far right) infect cells by injecting the infectious protoplasm via the polar filament; the meront divides asexually via merogony and eventually becomes a sporont that produces spores. [After Overstreeet, 1978.]

TABLE III
Microsporidia reported from brachyurans, by species, host, and tissue predilection

Microsporan species	Host	Tissue specificity	Key reference
Abelspora portucalensis	*Carcinus maenas*	Hepatopancreas	Azevedo, 1987
Ameson metacarcini	*Cancer magister*	Muscles	Small et al., 2014
Ameson michaelis	*Callinectes sapidus*	Muscles, haemocytes	Sprague, 1965
Ameson pulvis	*Carcinus maenas*, *Carcinus aestuarii*	Muscles	Pérez, 1905; Vivarès et al., 1976
Ameson sp.	*Libinia dubia*	Epithelium lining the vas deferens	Walker & Hinsch, 1972, 1975
Enterospora canceri	*Cancer pagurus*	Hepatopancreatic epithelia	Stentiford et al., 2007
Enterospora sp.	*Cancer pagurus*	Hepatopancreatic epithelia	Stentiford et al., 2011
Hepatospora eriocheir	*Eriocheir sinensis*	Hepatopancreatic epithelia	Wang & Chen, 2007; Stentiford et al., 2011
Nadelspora canceri	*Cancer magister*	Muscles	Olson et al., 1994
Nosema sapidi	*Callinectes sapidus*	Muscles	DeTurk, 1940; Sprague, 1970
Ormieresia carcini	*Carcinus aestuarii*	Muscles	Vivarès et al., 1977
Plistophora cargoi	*Callinectes sapidus*	Muscles	Sprague, 1966
Plistophora sp.	*Callinectes sapidus*	Muscles	Sprague, 1966
Thelohania grapsi	*Chiromantes haematocheir*	Muscles	Prowazek, 1910
Thelohania maenadis	*Carcinus maenas*, *Carcinus mediterraneus*	Muscles, ovary (one case)	Pérez, 1904, 1906; Vivarès, 1975
Thelohania sp.	*Liocarcinus depurator*	Muscles	Vivarès, 1972
Thelohania sp.	*Callinectes sapidus*	Muscles	Weidner et al., 1990

on light microscopy. Another species of *Plistophora* has been reported but not described (Johnson, 1972), and a hyperparasite identified as a species of *Nosema* was found in an unidentified microphallid metacercaria infecting a blue crab host (Sprague & Couch, 1971). A species of *Thelohania* is known from the skeletal muscles of *Callinectes sapidus* (see Weidner et al., 1990) and infections can turn the muscle blue or purple (J. D. Shields, unpublished), but infections in *Callinectes sapidus* are extremely rare. *Nosema sapidi* was originally described in an unpublished thesis based on three crab hosts (DeTurk, 1940), with light micrographs presented in a later publication (Sprague, 1970).

The taxonomy of microsporidians from crabs was based on morphological studies with emphasis on spore formation and morphology. *Ameson pulvis* from *Carcinus maenas*, however, was found to have two different spore morphologies in the muscles of the crab host (Stentiford et al., 2013b). One spore, an elongated *Nadelspora*-like form, occurred primarily in the cardiac muscle, whereas the other, an ovoid *Ameson*-like form, occurred later in infections in skeletal muscles (fig. 71-12.13). The *Nadelspora*-like form was not observed in previous TEM studies of the parasite (Vivarès & Sprague, 1979). Molecular analysis of the SSU rRNA gene indicated that *Ameson pulvis* shared a 100% similarity with *Nadelspora canceri*. Although Stentiford et al. (2013b) suggested that these spore types represent different lineages, there could be other possibilities worth considering. Some microsporidians can change their spore characteristics, developing from free spores

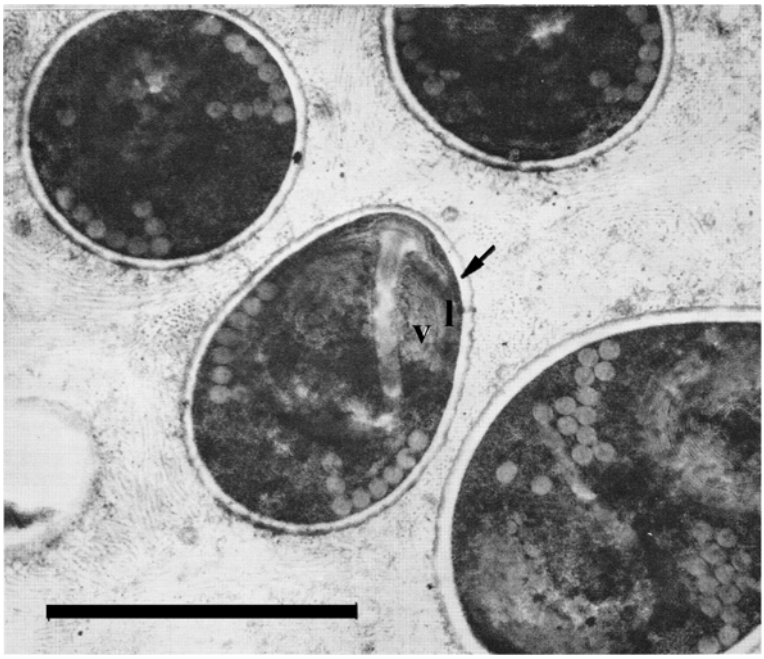

Fig. 71-12.13. Mature spores of *Ameson pulvis* from the muscles of *Carcinus aestuarii*: note the fusiform shape of the spore, the electron lucent endospore (arrow), and the coils of the polar filament, which appear as small circles on the interior margin of the spore (bar = 0.5 μm). Abbreviations: v, vesicular polarplast; l, laminar polarplast. [After Vivarès & Sprague, 1979.]

to octospores with increasing temperatures (Maddox & Sprenkel, 1978; Jouvenaz & Lofgren, 1984). Vivarès & Sprague (1979) examined crabs from the warmer Bay of Biscay, whereas Stentiford et al. (2013b) examined crab from the cooler English Channel. Perhaps subtle temperature changes could account for this variation in microsporidian morphology. Furthermore, because infections presumably started in cardiac muscles then moved into skeletal muscles, and the oval *Ameson*-like spores occurred in heavily infected muscles undergoing liquefaction (Stentiford et al., 2013b), it is possible that turgor pressure from cardiac compressions impose a morphological constraint on developing spores. The findings by Stentiford et al. (2013b) highlight the need for additional studies to better understand these parasites.

Microsporidians that infect crabs are most often found in skeletal muscle (table III). These include species in genera such as *Ameson*, *Abelspora*, *Nadelspora*, and *Ormieresia*, which produce free spores from sporogonal plasmodia, as well as *Plistophora* and *Thelohania*, which produce spores within **sporophorous vesicles** (SPVs). Those that form in SPVs are commonly observed with the light microscope as packets of spores with either eight or 32 or more spores per packet, respectively. Some of these taxa can infect other tissues as well, including cardiac muscle, ovary, and epithelial cells. Species in at least three genera, *Enterospora*, *Hepatospora*, and possibly *Abelspora*, infect the nuclei of epithelial cells of the hepatopancreas. Unlike the muscle-dwelling parasites, those in the hepatopancreas tend to cause focal infections that may not lead to obvious signs of disease, albeit they can cause focal destruction of the affected hepatopancreatic tubules (Stentiford et al., 2007). One parasite, an undescribed species of *Ameson*, infects the epithelial lining of the vas deferens (Walker & Hinsch, 1972) and another, *Thelohania maenadis*, reportedly infects the ovary (Pérez, 1906). Given that transovarial transmission occurs in microsporidians that infect amphipod hosts (Dunn et al., 2001), the finding of two species within the reproductive system suggests that vertical transmission is a possibility within brachyuran hosts.

Another microsporidian, *Abelspora portucalensis*, occurs in *Carcinus maenas* from Portugal and Spain (Azevedo, 1987; Kuris et al., 2005). The parasite forms **xenomas**, large tumor-like aggregates of spores within individual host cells, in the hepatopancreas. Formation of xenomas is specific to a host-parasite association and can result from a change in host cell expression, which in some respects resembles viral control of cell function (Lom et al., 2005). The schizont, or meront, of *Abelspora portucalensis* develops into two sporonts that further develop into two sporoblasts, giving four spores within the SPV, which is surrounded by a parasitophorus vesicle (Azevedo, 1987; Rocha & Monteiro, 1992).

The best-known crab microsporidian is *Ameson michaelis* in *Callinectes sapidus* from Chesapeake Bay (Sprague, 1965, 1970). The parasite has a direct life cycle that does not require another host (Weidner, 1970). The microspore is ovoid and relatively small, 2.2 μm long, with a polar tube about 40 μm long, but there is some variation in the size of the spore in relation to location in the host body (Weidner, 1970; Sprague, 1977; Overstreet, 1988). The parasite grows along muscle fibers and lyses muscle and adjacent tissues (Weidner, 1970). Heavily infected crabs sometimes have whitish coloration around their arthrodial

membranes, with grey or white sterna, and the musculature is friable, with whitish streaks or milky white coloration.

Blue crabs are highly cannibalistic, and when tissues infected with *Ameson michaelis* are eaten by another suitable host, the spore rapidly everts the polar filament, which penetrates and injects its sporoplasm into an epithelial cell lining the gut (fig. 71-12.12). The spores also infect haemocytes and skeletal muscle (Weidner, 1970). Dead or moribund crabs serve as the reservoir for new infections to cannibalistic conspecifics. Experimentally infected crabs become lethargic and moribund with some dying from infection (Weidner, 1970; Overstreet & Whatley, 1976). Fishermen refer to the condition as "cotton crab" due to the poor texture of the flesh. Prevalence levels were generally less than 1% in Louisiana, U.S.A. (Overstreet & Whatley, 1976).

Pathophysiological changes have been reported for *Ameson michaelis* in *Callinectes sapidus* (see Vernick & Sprague, 1970; Findley et al., 1981) and *Thelohania maenadis* in *Carcinus maenas* (see Vivarès & Cuq, 1981). Infected individuals had increased lactate and free amino acids and decreased glucose in their haemolymph, with additional changes to these constituents in muscle and hepatopancreas (Findley et al., 1981). Infected *Carcinus maenas* exhibited increased activity and decreased agonistic reaction time, strength, and locomotive speed (Vivarès, 1975).

An unusual nucleus-infecting microsporidian, *Enterospora canceri*, was described in *Cancer pagurus* from the U.K. (Stentiford et al., 2007). The parasite infected the epithelial cells of the hepatopancreatic tubules, with heavily infected cells having the appearance of large inclusions within the host nuclei, reminiscent of viral inclusions. In heavy infections the epithelial cells were degenerating or necrotic and contained a multitude of spores. Crabs exhibited no obvious external signs of infection and prevalence was 3.5%. A similar type of intranuclear microsporidian, *Hepatospora eriocheir*, occurs in *Eriocheir sinensis* from China (Wang & Chen, 2007) and the U.K. (Stentiford et al., 2011). The parasite infects the epithelial cells of the hepatopancreatic tubules and produces four or eight spores within the SPV (Wang & Chen, 2007). In a survey of *Eriocheir sinensis* from the Thames River, prevalence levels were as high as 70%, and some infections showed extensive infection with degeneration of the hepatopancreatic tubules (Stentiford et al., 2011). Molecular data indicate that *Hepatospora eriocheir* can also infect *Cancer pagurus*, but the molecular comparison was based on only one gene region (Stentiford et al., 2011).

Nadelspora canceri, with its needle-like spores, occurs in *Metacarcinus magister* from the west coast of the U.S.A. (Olson et al., 1994). Infected crabs were first noticed by fishermen who complained of poor flavour in some crabs. The generic name is derived from the appearance of the elongated spores: one end is needle-like, the other blunt and rounded. This species is distinct from other microsporidians both morphologically and developmentally (Olson et al., 1994). In a study of over 12 600 crabs, *Nadelspora canceri* was shown to range from central California to southern Washington (Childers et al., 1996). It was more prevalent in estuaries than in the open ocean. Male crabs had a higher prevalence of infection than females (10.7% and 3.3%, respectively), and prevalence was positively correlated with host size. Twelve individuals were also infected by a *Microsporidium*-like parasite (Childers et al., 1996). The rock crab *Cancer productus*

(Cancridae) may also serve as a host for *Nadelspora canceri* (see Amogan et al., 2007). A microsporidian, *Ameson metacarcini*, was recently described in *Metacarcinus magister* from British Columbia (Small et al., 2014), but it had a much lower prevalence than *Nadelspora canceri*. It could be the *Microsporidium*-like parasite previously observed from this host.

Another microsporidian with elongated spores, *Ormieresia carcini*, occurs in *Carcinus aestuarii* from the Mediterranean coast of France (Vivarès et al., 1977). The parasite was described from the skeletal muscles of a single male crab. Sporogony occurred within a pansporoblastic membrane, giving rise to eight spores (fig. 71-12.11). Given that *Ameson pulvis* and *Thelohania maenadis* have been reported from this host (Vivarès et al., 1977), that spore morphology may not be as useful a character as once thought (Stentiford et al., 2013b), and that temperature variations can cause aberrations in spore morphology (Maddox & Sprenkel, 1978), it is possible that *Ormieresia carcini*, *Ameson pulvis*, and *Thelohania maenadis* could represent different morphological manifestations of the same species.

Several microsporidians that develop within sporophorous vesicles have been identified from crabs, but their taxonomic placement is uncertain. *Plistophora cargoi* possesses 32 to more than 100 spores developing within a sporophorous vesicle (Sprague, 1966, 1977), but members of the genus are currently restricted to fish hosts. The genus *Thelohania* requires major taxonomic revision with better definition of species (Hazard & Oldacre, 1975). The genus is characterized by eight spores within the sporophorous vesicle, which are sometimes referred to as spore packets. At least three species are known from crabs. *Thelohania maenadis* in *Carcinus maenas* from France has received the most work (TEM and biochemical studies; Vivarès, 1975; Vivarès et al., 1976; Vivarès & Cuq, 1981).

As with viruses, microsporidians are underrepresented in crabs and we know very little of their diversity in common species. Several microsporideans are known from commercially or ecologically important hosts and a few have been discovered accidentally during other studies. A pea crab, *Pinnotheres pisum*, has at least two undescribed microsporidians, one in the hepatopancreatic epithelium and another in the musculature (Longshaw et al., 2012). An unidentified microsporidian was also found in up to 30% of *Hemigrapsus sanguineus* (Varunidae) in one locality from Japan, but none have been found in the introduced range of this host (Blakeslee et al., 2009). While many crabs are known to harbour these parasites, there is no doubt that their diversity in crabs is much higher than known at present. Microsporidians remain an enigmatic group, poorly characterized in crab hosts, yet presenting rich opportunities for scientific investigation.

Protozoans

PROTISTS

In large part due to the advent of rapid molecular sequencing techniques, the higher level **systematics** of **Protista** have been in a state of flux for several years, as in the case of Cercozoa, a phylum of protozoans that encompasses a number of disparate taxa that were previously split among Sarcodina, Ascetospora, and others (Cavalier-Smith & Chao,

2003). Rather than follow the latest systematic organization of the different taxa, which has been changing rapidly with new molecular data (see Keeling et al., 2005; Parfrey et al., 2010), we focus on specific parasites and give only a cursory view of their affiliations. There are a number of parasitic protozoans that infect crabs, but there is even higher diversity in ectosymbiotic protozoans of crabs, particularly the peritrich and apostome ciliates, as well as fouling organisms that are not reviewed here. In the egg masses of ovigerous hosts alone there is a highly diverse symbiont fauna, in some cases causing egg mortality or other negative effects (Kuris, 1991). The parasitic protozoans of crustaceans have been reviewed by Sprague & Couch (1971), Couch (1983), and Meyers (1990), with reviews of specific host species given by Shields & Overstreet (2007), Stentiford (2008), Morado (2011), and Morado et al. (2012).

Cercozoa: Ascetosporea: Paramyxida. – The order Paramyxida consists of five genera of protists that have an unusual cell-within-a-cell morphology. Infectious spores, known as **tertiary cells**, develop within a secondary cell formed by endogeny from within a primary cell. Paramyxida, such as *Marteilia* spp., are important pathogens of bivalves but a few are known from other hosts, including polychaetes and crustaceans. *Paramarteilia canceri* infects *Cancer pagurus* causing systemic infections (Feist et al., 2009). The parasite was found mostly as an extracellular form in the haemocoel and interstitial spaces of the crab host; however, intracellular infections were noted in the haemocytes, fixed phagocytes, connective tissues, and gametocytes. Primary and tertiary cells contained **haplosporosomes**, an organelle found only in Paramyxida and Haplosporidia. Secondary cells did not contain haplosporosomes and function as pansporoblasts for sporogenesis of the tertiary cells. Eight of 686 individuals of *Cancer pagurus* were infected by the parasite, with highest prevalence levels, 3%, occurring in winter (Fiest et al., 2009).

Cercozoa: Ascetosporea: Haplosporidia. – Haplosporidia was once considered a phylum or class within phylum Ascetospora but it is now tentatively placed as an order within Cercozoa (Cavalier-Smith & Chao, 2003), although this is disputed (Burreson & Ford, 2004). Haplosporidia are obligate parasites consisting of approximately 40 known species that form ornamented, operculated spores from a multinucleated plasmodial stage. Most species use molluscs as hosts, but a few infect crustaceans and other invertebrates (Burreson & Ford, 2004). No life cycles have been established for any species of Haplosporidia, despite several attempts to do so, and deciphering their complete life cycle remains an important goal. Recently a basal species, *Paramikrocytos canceri* was described from *Cancer pagurus*; it is closely allied with *Mikrocytos mackini*, an oyster pathogen (Hartikainen et al., 2014). *Paramikrocytos canceri* is an intracellular parasite that infects the epithelial cells of the antennal glands. It had a relatively high prevalence in crabs from the English Channel (Bateman et al., 2011) and Wales, ranging from 15-70%, with an apparent peak in winter (Thrupp et al., 2013).

Only two **haplosporidians** have been reported from crabs, and a third, *Urosporidium crescens*, is a **hyperparasite** found in trematode metacercariae within crabs. None of the described species are well known from crabs, but they can occur at relatively high prevalence levels in hosts from intertidal and nearshore zones. The paucity of described

species from crabs is no doubt due to a lack of attention because they have been observed in several disparate hosts and at relatively high prevalence levels. An undescribed species was reported from moribund *Callinectes sapidus* from the east coast of the U.S.A. (Newman et al., 1976) and another undescribed species was reported at a prevalence of 20% in *Necora puber* (Portunidae) during surveys for *Hematodinium perezi* (see Wilhelm & Miahle, 1996).

Urosporidium crescens infects the metacercariae of microphallid trematodes, particularly *Microphallus basodactylophallus*, which use *Callinectes sapidus* as a second **intermediate host**. The haplosporidian does not infect crab tissue, albeit free spores can be occasionally observed in the haemolymph, but it hyperparasitizes the trematode encysted within the crab (fig. 71-12.14). Infected cysts become inflated by the brown-black spores of the parasite, making the worms enlarge, becoming readily visible as black spots in the connective tissues of the crab. The infected worms thus appear as black spots colloquially known as "pepper crab", "pepper-spot", or "buck-shot" in the connective tissues of the skeletal muscles, visceral organs, and gills. Perkins (1971) described the ultrastructure and development of *Urosporidium crescens* and Couch (1974) detailed the histological changes in the trematode host. Consumers that eat infected crabs are often worried about "pepper-spots", as the disease can produce an unappetizing appearance that can negatively affect the crab fishery (Perkins, 1971; Couch & Martin, 1982; Overstreet, 1983). *Urosporidium crescens* will not infect humans, rather it kills the encysted metacercaria. The uninfected metacercariae of *Microphallus basodactylophallus*, which are normally not visible to the naked eye, nevertheless, can be infective and pathogenic to humans who eat raw or poorly cooked crab hosts (Heard & Overstreet, 1983).

Haplosporidium louisiana infects the connective tissues of a number of xanthoids such as *Panopeus herbstii* and *Rhithropanopeus harrisii* from the east and Gulf coasts of the U.S.A. (Sprague, 1963; Perkins, 1975). Sporogony occurs within large plasmodia and the resulting spores are brown and black. The spores can be dense enough to give the tissues of the host a black coloration (Sprague, 1963). *Haplosporidium cadomensis* from *Rhithropanopeus harrisii* from the English Channel (Marchand & Sprague, 1979) is morphologically similar to *Haplosporidium louisiana* and could be the same species (Perkins & Van Banning, 1981). *Haplosporidium littoralis* was described from *Carcinus maenas* from Europe (Stentiford et al., 2013c). Plasmodia of the parasite infected mesodermally-derived tissues and spore stages were observed in the haemolymph in late stages of infection. The parasite had a prevalence of 7.6% and was considered pathogenic in this host.

Kinetoplastida. – Kinetoplastid **flagellates** are important parasites of vertebrates, including humans and fishes, and several taxa use insects as hosts. None were known from crustaceans until recently. During the development of a diagnostic assay for *Hematodinium perezi* infections in *Callinectes sapidus*, a **kinetoplastid** flagellate was identified from the haemolymph of 34% of the crabs tested (Troedsson et al., 2008). No morphological data were obtained and infections were not examined histologically. Sequence data indicated that the protist was closely related to the free-living kinetoplastid *Procryptobia sorokini*. It was not related to *Perkinsiella amoebae*, the symbiotic kinetoplastid found as an organelle, the **parasome**, in species of *Neoparamoeba* in fishes (Dyková et al., 2003). Flagellates are

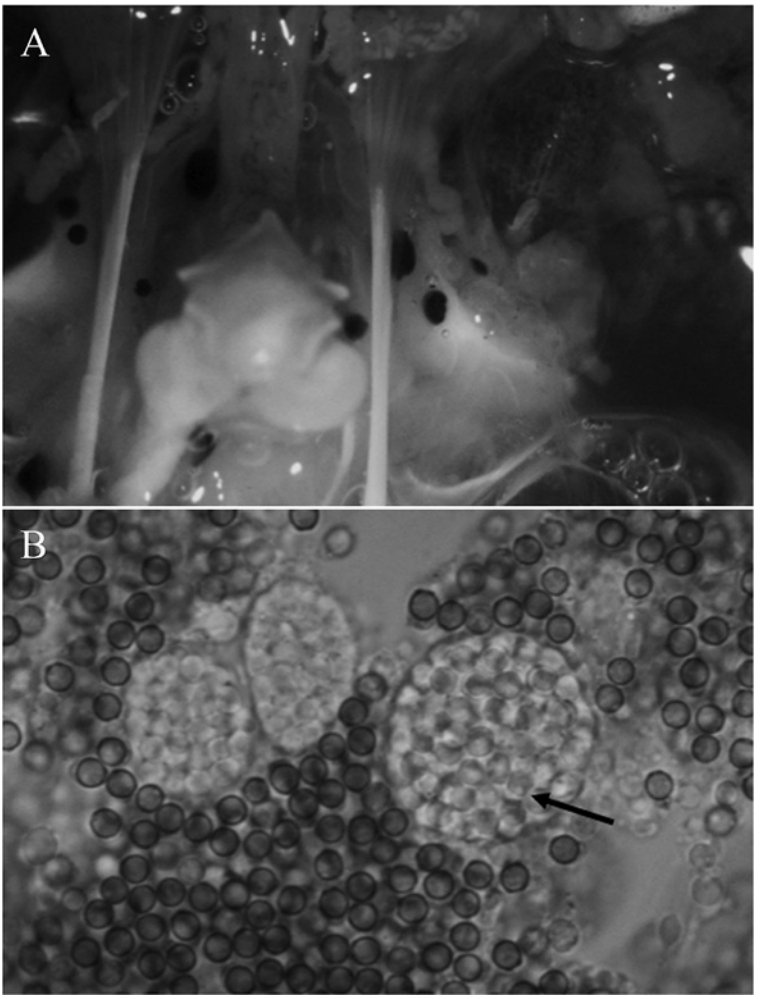

Fig. 71-12.14. A, Trematode metacercariae infected with *Urosporidium crescens* within the connective tissues of the foregut of *Callinectes sapidus*; B, mature spores of the hyperparasite are darkly pigmented, thus revealing the presence of the infected worm; sporogony occurs with the pansporoblast (arrow). [Photos by J. D. Shields.]

poorly known from crustaceans, and include an unsequenced hypersymbiont that could be related to *Perkinsiella amoebae* in *Paramoeba perniciosa* from *Callinectes sapidus* (see below).

Rhizopoda: Lobosea: Gymnamoebae. – Given the proximity of crustaceans to benthic habitats and their propensity for suspension feeding, one might expect that they have a diverse fauna of facultatively parasitic amoebae; however, this is not the case. Only one parasitic **amoeba**, *Paramoeba perniciosa*, is known to infect crabs (Sprague & Beckett, 1966; Sprague et al., 1969). *Paramoeba perniciosa* possesses a distinct symbiont as a

secondary nucleosome, termed the ***Nebenkörper*** or **parasome** (Sprague et al., 1969; Perkins & Castagna, 1971). *Paramoeba perniciosa* has two morphologies: a small form that is spherical, 3 to 7 μm long, and a large form that is lobose, 10 to 25 μm long (Sawyer, 1969; Johnson 1977b; Couch, 1983). The small form occurs in the haemolymph in late stages of infection (fig. 71-12.15), whereas the large form dwells in the connective tissues of the antennal gland, endothelial, and nerve tissues (Johnson, 1977b).

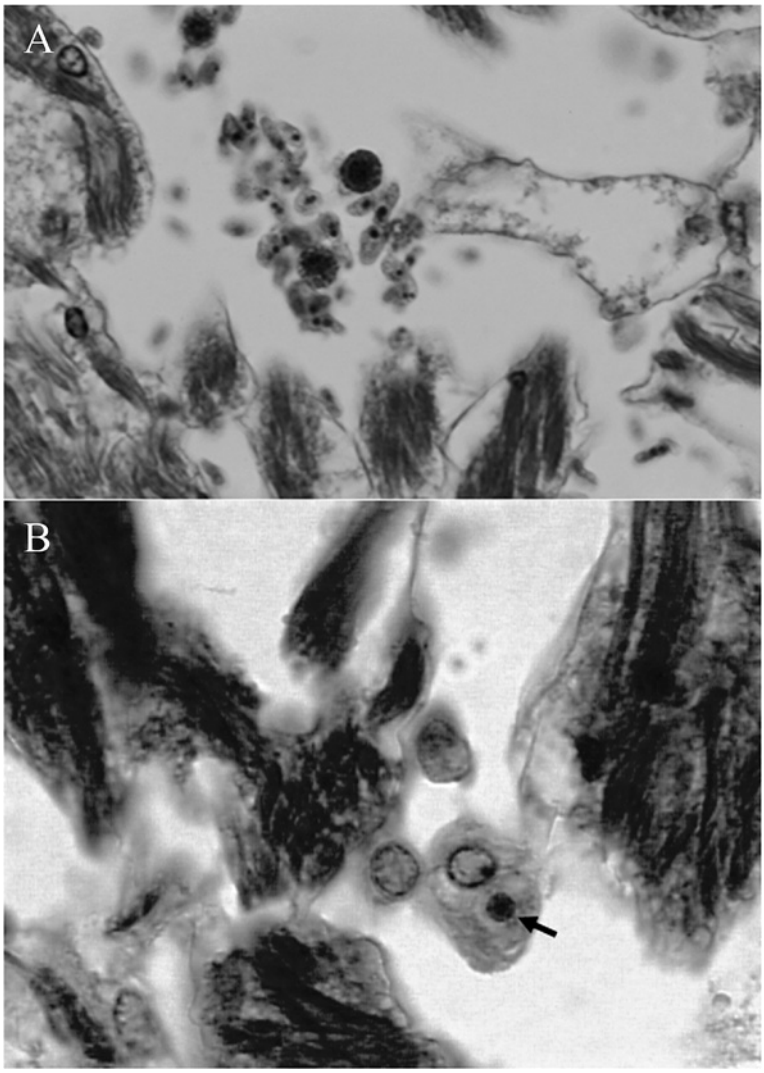

Fig. 71-12.15. *Paramoeba perniciosa* in the heart of *Callinectes sapidus*: A, small forms free in circulating haemolymph in the lumen of the heart; note the binucleate appearance of the small trophonts; B, large form showing the regular nucleus and the parasome or symbiont nucleus (arrow). [Photos by J. D. Shields.]

Crabs infected with the amoeba often develop a grey sternum and the disease is known colloquially as "gray-crab" disease in the endemic region of the Delmarva Peninsula, U.S.A. (Sprague & Beckett, 1966; Sprague et al., 1969). The amoeba can cause mortalities in high salinity waters but crabs with light and moderate infections exhibit few signs of disease. Heavily infected crabs are often moribund and often die shortly after capture (Johnson, 1977b). During an epizootic, estimated losses due to the parasite were 30% of the population (Newman & Ward, 1973). Amoebae do not generally occur in the haemolymph until late in the course of the infection (Sawyer et al., 1970). Haemolymph from heavily infected crabs is cloudy and does not clot (Sprague et al., 1969; Sawyer et al., 1970; Johnson, 1977b). Infected crabs show several physiological changes and alterations of the haemolymph. These changes could be due to proteolytic activity of the parasite, from the loss of serum fibrinogen, or from the loss of hyalinocytes that carry clotting factors (Pauley et al., 1975).

Paramoeba perniciosa has been reported from several hosts, including *Callinectes sapidus*, *Carcinus maenas*, and *Cancer irroratus* (see Sawyer, 1976; Campbell, 1984), but *Callinectes sapidus* is considered the primary host. The parasite has been reported from *Callinectes sapidus* from Long Island Sound south to the Atlantic coast of Florida (Newman & Ward, 1973; Johnson, 1977b), but not in the Gulf of Mexico (Overstreet, 1978). Prevalence ranged from 3 to 30% from South Carolina to Florida (Newman & Ward, 1973). The mode of transmission of *Paramoeba perniciosa* remains unknown, but cannibalism does not result in transmission (Newman & Ward, 1973; Couch, 1983). Cysts have not been observed in any species of *Paramoeba* (Couch, 1983). Because mortalities peak in late spring, transmission can occur during ecdysis or in postmoult when the carapace is soft (Newman & Ward, 1973; Couch, 1983) and the amoeba apparently overwinters in crabs (Johnson, 1977b).

Ciliophora. – **Ciliates** are common symbionts on the cuticle, appendages, and gills of crustaceans. One class, Oligohymenophorea, has several representatives from different taxa: apostomes, peritrichs, and scuticociliates. The apostomes are a highly specialized order of symbionts that encyst on the host cuticle, excyst to feed on exuvial fluids within the old instar of their crustacean hosts (Bradbury & Trager, 1967), and then swarm onto the new instar and encyst until the next moult. With a few exceptions, the apostomes are not pathogenic. The scuticociliates have several parasitic taxa, including some serious pests of fishes; however, only a few have been identified as facultative parasites of crabs and lobsters (Miller et al., 2013; Small et al., 2013). The peritrichs are fouling organisms and occur on many crustaceans, including freshwater crayfish, copepods, and crabs. Because they live on the external habitus of their hosts, the peritrichs are strongly influenced by environmental conditions as well as the moult cycle of the host. Phyllopharyngea, species of which are colloquially known as **suctorians** because of their highly modified feeding apparatus, has several species that attach to the gills and exoskeletons of their crustacean hosts (Fernández-Leborans & Tato-Porto, 2000a). They are considered commensals on crustacean hosts.

— *Peritrich ciliates.* – **Peritrichs** occur as epibionts on the gills, carapace, eggs, and other external surfaces of their hosts. They are often stalked and frequently found in colonies between the gill lamellae of their hosts. Most peritrichs are considered commensals, but at very high intensities, they foul their hosts and can cause disease. They are not invasive and do not penetrate through the host's cuticle, but can block lamellae and may interfere with respiration or excretion through the gills (Couch, 1967; Couch & Martin, 1982), but this remains to be determined experimentally. Heavy infestations can potentially increase the stress level of an infested crab. Physiological work with the stalked barnacle *Octolasmis lowei* indicates that heavily infested crabs are in a functional state equivalent to crabs stressed by exercise (Gannon & Wheatley 1992, 1995). Perhaps high intensity infestations of ciliates result in a similar condition on affected crabs. Approximately 270 peritrichs have been identified as ectocommensals on crustaceans; of these only 10 have been reported from brachyurans (Fernández-Leborans & Tato-Porto, 2000a). In a survey of the ciliates from decapods of the Mediterranean, 10 brachyuran species were examined for epibiotic ciliates and the diversity was surprisingly low, with only four genera represented (Fernández-Leborans, 2003). More details on the biology of these ciliates can be found in Couch (1967), Bradbury (1994), and Morado & Small (1995).

— *Apostome ciliates.* – **Apostome ciliates** include both external and internal symbionts of invertebrates. They lack a buccal apparatus and have unusual arrangements of their kineties; both features separate them from other hymenophorean ciliates. With few exceptions, they are commensals on crustaceans and feed on the exuvial fluids that remain within the exuvia of the moulted host. They live most of their lives as encysted **phoronts** on the exoskeleton and gills of their hosts. The cyst wall is weakly permeable (Chatton & Lwoff, 1935; Landers, 2010) and, prior to host moulting and presumably cued by **moulting hormones** of the host, the phoronts develop into **tomonts**. The tomonts undergo division to produce **trophonts**, which excyst to feed on exuvial fluids produced during host **ecdysis**. At least 37 species have been described, with five reported from crabs (Bradbury, 1994; Landers, 2004; Landers et al., 2006; Chantangsi et al., 2013); they are typically host generalists (Bradbury, 1994).

Unlike most apostomes found on crabs, *Synophrya hypertrophica* is pathogenic and causes black spot disease in the gills of infected hosts (fig. 71-12.16). The trophont is histophagous and burrows through the soft cuticle of the gill lamellae after a crab has moulted (Johnson & Bradbury, 1976). The damaged area becomes melanized by the host's response, giving it the appearance of black spots. The ciliate feeds on haemolymph and tissues until it encysts as a tomont (Johnson & Bradbury, 1976; Bradbury, 1994). As with other apostomes, *Synophrya hypertrophica* is a generalist infecting portunids, calappids, parthenopodids, dromiids, grapsids, palicids, pilumnids, raninids, and even albuneid anomurans and several shrimp hosts (Johnson & Bradbury, 1976; Bradbury, 1994). The parasite occurs in hosts from high salinities (Haefner & Spacher, 1985).

— *Scuticociliates.* – **Scuticociliates** have free living and parasitic taxa. The parasitic taxa infect a wide range of marine animals, including molluscs, echinoderms, crustaceans, and fishes, and range from facultative to obligate parasites. They can cause significant

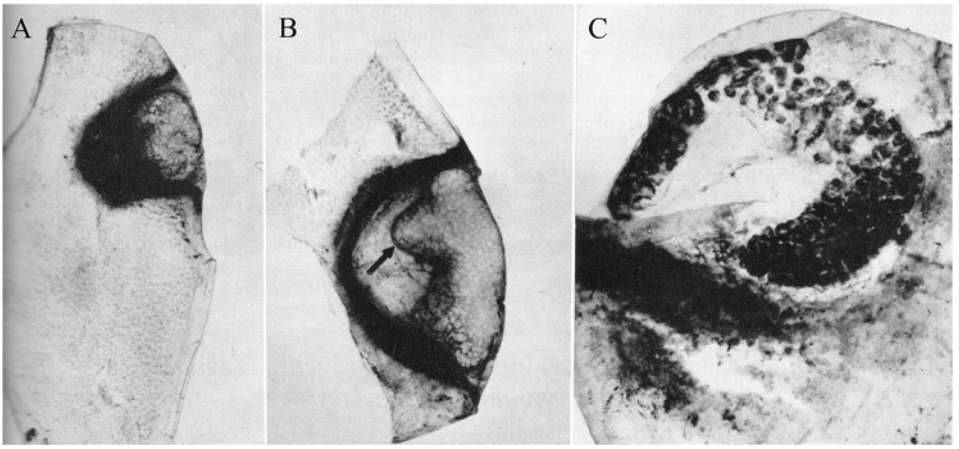

Fig. 71-12.16. Trophonts of *Synophrya hypertrophica* within the gill lamellae of crabs (protargol stain): A-B, lamellae from *Ovalipes ocellatus* exhibiting dense, melanotic reaction around large ciliates (360 and 570 μm, respectively); the cyst wall (arrow) is some distance from the reaction tissues; C, lamella from *Macropipus* sp. with small trophonts (20 μm) escaping from a cyst. [After Johnson & Bradbury, 1976.]

pathology, mortality and, in some cases, castration in their hosts. Scuticociliate infections in crustaceans have a long but sparse record that was reviewed by Morado & Small (1995). Four species in crabs are now recognized: *Mesanophrys maggii* in *Carcinus maenas* from the Mediterranean, *Mesanophrys carcini* in *Cancer pagurus* from Brittany, France, *Mesanophrys pugettensis* in *Metacarcinus magister* from the west coast of the U.S.A., and *Mesanophrys chesapeakensis* in *Callinectes sapidus* from the east coast of the U.S.A. Morphological differences among species are highly variable, however, and may not warrant species level recognition (Wiackowski et al., 1999).

Scuticociliate infections in brachyurans are very rare in natural settings. Prevalence levels were less than 1% in *Carcinus maenas* (see Morado & Small, 1995) and *Callinectes sapidus* (see Messick & Small, 1996). Outbreaks have nevertheless been associated with crabs held under laboratory or commercial conditions (Grolière & Leglise, 1977; Armstrong et al., 1981; Small et al., 2013). These facultative parasites require a portal of entry for transmission (Miller et al., 2013) and are not transmitted by feeding on infected tissues as they do not survive gastric fluids (Loughlin et al., 1998). Infections of the starfish pathogen *Orchitophrya stellarum* in *Callinectes sapidus* are associated with low winter temperatures (Miller et al., 2013; Small et al., 2013).

Experimental studies show that infections progress quickly, often killing crabs within 7-10 days. Infected crabs exhibit lethargy and poor clotting of the haemolymph. Inoculation studies indicate that the ciliates have a very rapid rate of growth in host tissues, and that host haemocytes decline precipitously during infections (Cain & Morado, 2001; Miller et al., 2013). Ciliates can invade connective, heart, muscle, thoracic ganglion, and haematopoietic tissues (fig. 71-12.17) (Messick & Small, 1996) and infiltration of the nerves can result in infection-induced autotomy (Miller et al., 2013).

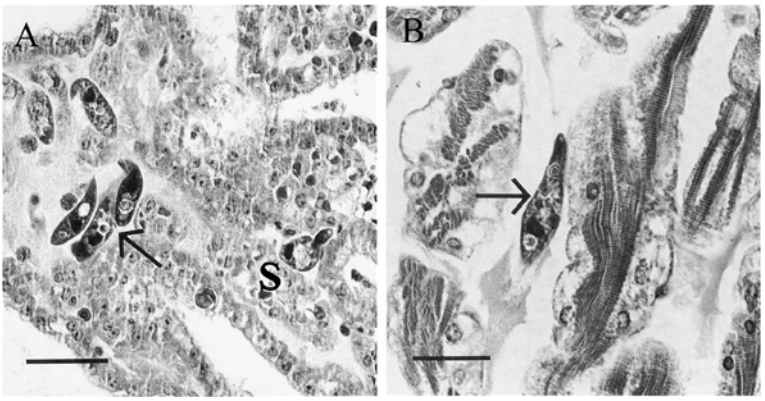

Fig. 71-12.17. *Mesanophrys chesapeakensis* in tissues of *Callinectes sapidus*: A, ciliates in the haemal sinus of the antennal gland with apparent ingested haemocytes (arrow); ciliates in oblique section (S) stain darker than surrounding tissue (bar = 35 μm); B, ciliate between the myocardial fibres of thoracic muscle with ingested tissues (arrow) (bar = 20 μm). [After Messick & Small, 1996.]

— *Suctorian ciliates.* – Little is known about **suctorian** infestations on crabs, but they are commensals and rarely occur in heavy infestations. There are 124 species of suctorians found on crustaceans, with seven reported from crabs, and three of these identified at the species level (Fernández-Leborans & Tato-Porto, 2000b). *Acineta* sp. has a small, disk-shaped holdfast that can often be observed on the gill lamellae of infested hosts (Shields, 1992). The holdfast can remain present after the ciliate has died, leaving a record of its presence on host instars.

Dinoflagellata (Dinophyta). – Dinoflagellates share affinities with Apicomplexa and Ciliata and together with a few other protist taxa, comprise Alveolata (Cavalier-Smith, 1993; Keeling et al., 2005; Parfrey et al., 2010). Dinoflagellata has been treated as both an animal and plant taxon. The higher taxa within the group therefore have a dual system of nomenclature, depending on whether a zoological or botanical system is followed (ordinal names indicated with an asterisk follow the botanical scheme). Over 2000 species of dinoflagellates have been described and approximately 140 of these are parasitic (Coats, 1999). Four orders within the phylum containing approximately 35 genera possess parasitic taxa, and two of these orders, Blastodinida (Blastodiniales*), and Syndinida (Syndiniales*) consist entirely of parasitic taxa. Blastodinida and Syndinida have a number of taxa that parasitize crustaceans, but only one genus, *Hematodinium*, in Syndinida infects crabs (Shields, 1994). Given the importance of these parasites as pathogens in commercially valuable crabs and lobsters, there have been several reviews of their biology including those of Meyers (1990), Shields (1994), Stentiford & Shields (2005), Morado (2011), and Small (2012).

There are only two described species in *Hematodinium* due to the lack of distinctive morphological characters. The type species, *Hematodinium perezi* was described from *Carcinus maenas* and *Liocarcinus depurator* from France (Chatton & Poisson, 1931) and

Hematodinium australis was described from *Portunus pelagicus* and *Scylla serrata* from Australia (Hudson & Shields, 1994). Based on morphological characters, *Hematodinium perezi* has been reported in portunid crabs from Europe (Chatton & Poisson, 1931), North America (Newman & Johnson, 1975; Messick & Shields, 2000), and possibly China (Li et al., 2008, 2013b; Xu et al., 2010). Although these specimens are morphologically similar, they can be separated into three genotypes based on DNA sequence data. *Hematodinium perezi* genotype I occurs in portunid crabs in Europe, genotype II in portunids and other decapods in China, and genotype III in portunids and other decapods from the U.S.A. (Small et al., 2012). It is likely that these genotypes will be considered distinct species when additional sequence data are known. There is also ample evidence that *Hematodinium* sp. or the *Hematodinium*-like infections in cold-water hosts, i.e., *Chionoecetes* spp. and the Norway lobster *Nephrops norvegicus*, are different from the *Hematodinium perezi* clade and likely comprise a new genus, species, or species complex in their boreal hosts (Hamilton et al., 2010; Small et al., 2012).

Two life cycles have been described, one for the *Hematodinium*-like species from *Nephrops norvegicus* by Appleton & Vickerman (1998) and the other for *Hematodinium perezi* genotype III from *Callinectes sapidus* by Li et al. (2011a). Both life cycles have a propensity for rapid proliferation because **asexual division** occurs in several life history stages, including the filamentous trophont, the amoeboid trophont, and sporont stages (figs. 71-12.18, 71-12.19). The presence of trichocysts is indicative of the sporont and spore stages (Gaudet et al., 2014, 2015). Sexual reproduction has not been observed, but based on microsatellite data, the parasites are haplo-diploid with strong evidence for **sexuality** in their life cycle (Pagenkopp et al., 2014).

Transmission of *Hematodinium* spp. remains unknown. Walker et al. (2009) transmitted infections to a few crabs via **cannibalism** over a very short period but Li et al. (2011b) and Butler et al. (2014) ruled out cannibalism and scavenging as possible modes of transmission. Several well-studied systems show distinct cycles of infection with a *Hematodinium*-like organism in relation to moulting, but the mode of entry into the host is not clear (Meyers et al., 1987; Eaton et al., 1991; Messick & Shields, 2000; Stentiford et al., 2001; Shields et al., 2005, 2007). Sharp autumnal peaks in the prevalence of *Hematodinium* overlap with settlement and moulting of juvenile crabs (Messick & Shields, 2000; Shields, 2003). **Dinospores** are thought to be a transmissive stage of the parasite (Frischer et al., 2006). Sexual transmission has been suggested as a mode of transmission in Tanner crabs, *Chionoecetes bairdi* (Oregoniidae), based on the finding of parasites in the seminal fluids of a few males (Meyers et al., 1996); however, this does not explain the high prevalence observed in juvenile crabs, nor does it explain the low prevalence observed in adults.

At least 38 decapods, including several brachyurans, are known to harbour *Hematodinium* or *Hematodinium*-like infections (see Stentiford & Shields, 2005; Small, 2012). Many decapods could be at risk of infection because these parasites exhibit low host specificity. They can infect several species of amphipods as well as different decapod taxa (Johnson, 1986b; Pagenkopp et al., 2012).

Several fisheries have suffered economic losses due to outbreaks, including those for *Chionoecetes bairdi*, *Chionoecetes opilio* (see Meyers et al., 1987, 1990; Shields et al.,

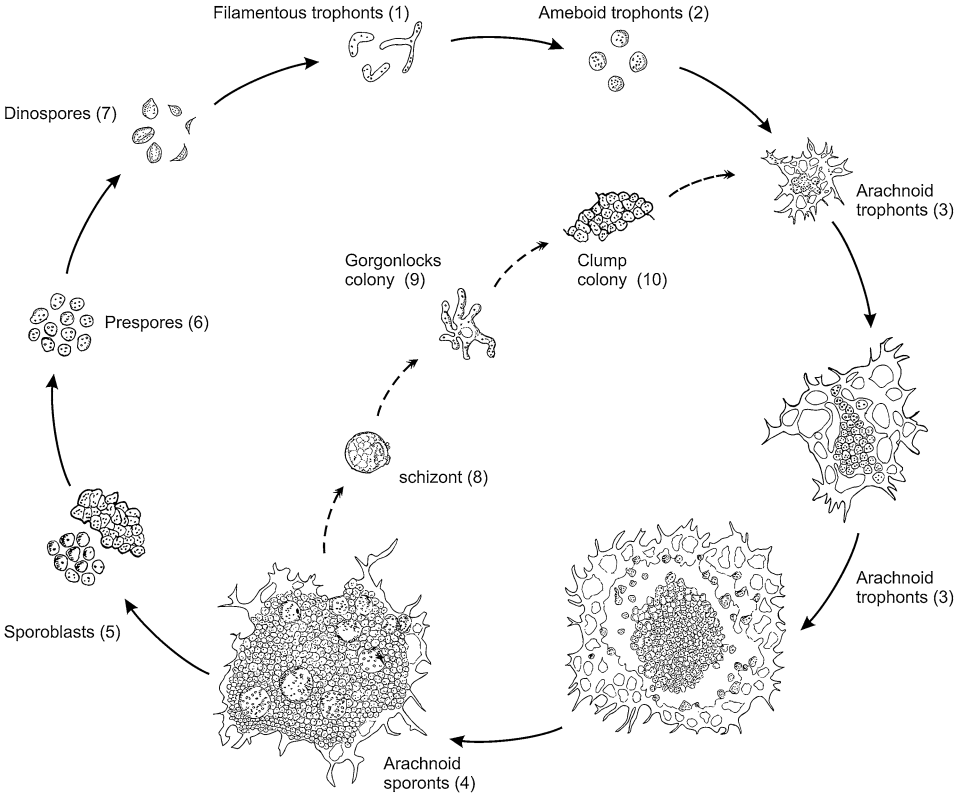

Fig. 71-12.18. Life cycle of *Hematodinium perezi* from *Callinectes sapidus*: filamentous trophonts (1) appear in the haemolymph of early infections and undergo merogony to form amoeboid trophonts (2); arachnoid trophonts (3) attach to tissues from the haemal sinuses and grow to form arachnoid sporonts (4) that either develop sporoblasts (5), which become prespores (6) and dinospores (7), or develop into a presumptive schizont (8) that generates gorgonlocks (9) and clump colonies (10). Dinospores are presumbably infectious to new hosts, but this remains to be determined. [After Li et al., 2011.]

2005, 2007; Mullowney et al., 2011), *Callinectes sapidus* (see Messick & Shields, 2000; Lee & Frischer, 2004), *Necora puber* (see Wilhelm & Mialhe, 1996), *Maja squinado* (Majidae), *Cancer pagurus* (see Latrouite et al., 1988; Chualáin et al., 2009; Smith et al., 2013b), *Nephrops norvegicus* (see Stentiford & Shields, 2005), and several decapods in culture in China (Xu et al., 2007, 2010; Li et al., 2013b). Patently infected Tanner and snow crabs (*Chionoecetes bairdi* and *Chionoecetes opilio*) develop a condition known as **bitter crab disease** (**BCD**), rendering them unmarketable (Meyers et al., 1987; Taylor & Khan, 1995). Physiological and biochemical disruptions to the muscles and other organs substantially alter the metabolism of several infected host species (see Stentiford & Shields, 2005).

Diagnosis of *Hematodinium*-infections is typically done using fresh haemolymph smears stained with neutral red (0.3%), from prepared histological slides (fig. 71-12.20), or

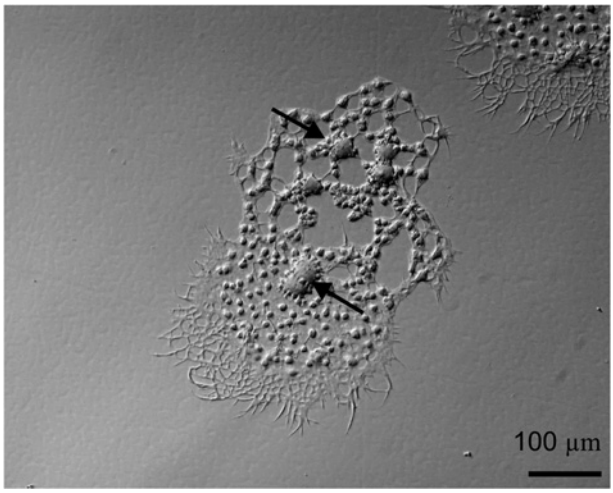

Fig. 71-12.19. Arachnoid sporont of *Hematodinium perezi* from *Callinectes sapidus* showing the development of germinative centres that exhibit budding (arrows), which leads to rapid asexual proliferation in the host (bar = 100 μm). [After Li et al., 2011.]

in the case of snow crabs and Norway lobsters, from altered body coloration indicative of advanced infections (Stentiford & Shields, 2005). Molecular studies with *Hematodinium* spp. initially focused on detection using the polymerase chain reaction (PCR) for genus-specific probes (Hudson & Adlard, 1994; Gruebl et al., 2002; Hamilton et al., 2007; Small et al., 2007). Additional tools were developed for detection in environmental samples (Frisher et al., 2006; Hamilton et al., 2011), for real-time PCR in environmental samples (Li et al., 2010; Hanif et al., 2013), comparative diagnostics (Chualáin & Robinson, 2011), and a novel application of high performance liquid chromatography (Troedssson et al., 2008), as well as development of microsatellite markers for **population genetics** (Pagenkopp et al., 2014). A novel dinoflagellate/viral nucleo-protein technique was more recently developed for visualizing the parasite in host haemolymph (Gornik et al., 2013).

Given their potential as pathogens in fishes and cultured populations of decapods, these parasites warrant further attention, particularly in studies of their life cycles, transmission pathways, and effects on host populations. Modelling studies indicate, for example, that the presence of the parasite in depleted stocks can seriously impede efforts to rebuild crab populations (Siddeek et al., 2010).

Apicomplexa: gregarines and coccidians. – The phylum Apicomplexa is grouped within Alveolata as they share affinities with dinoflagellates and ciliates. All members of Apicomplexa have at some point in their life cycle a characteristic apical complex that is used for host cell invasion. They show a high diversity in vertebrate hosts, and two genera, *Plasmodium* and *Babesia*, contain pathogens of particular importance to humans and livestock. Within Apicomplexa, the **gregarines** and **coccidians** both use crustaceans as hosts. They have very different host-parasite associations, however, with the gregarines having direct as well as indirect life cycles (mollusc intermediate hosts,

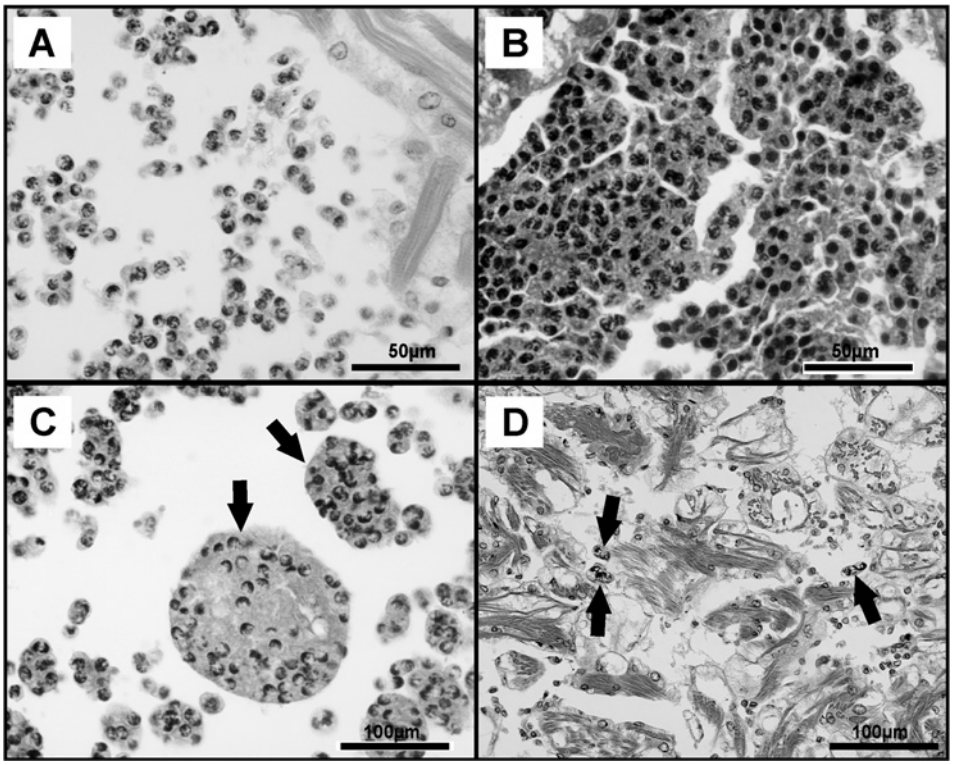

Fig. 71-12.20. *Hematodinium* sp. in the tissues of *Chionoecetes opilio*: A, single and small multinucleate stages in the heart; B, presumptive arachnoid sporont in the hepatopancreas; note the characteristic condensed chromatin in the cells of the parasite; C, clump colonies in the heart; D, light infection of multi-nucleated filamentous trophonts (arrows) in heart tissue. [After Wheeler et al., 2007.]

crustacean definitive hosts) and coccidians having only indirect life cycles (crustacean intermediate hosts and cephalopod definitive hosts).

Gregarines are typically found in the digestive tract of their invertebrate hosts, but they can be found in other tissues with a lumen. They infect a variety of invertebrates and are common in annelids, molluscs, and arthropods. At least 97 species infect crustaceans, with 43 species reported from brachyurans, and many species reported from other crustaceans (Bradbury, 1994; Clopton, 2002). Eight genera are known from brachyurans: *Caridohabitans*, *Cephaloidophora*, *Nematopsis*, *Paraophioidena*, *Pachyporospora*, *Stephanospora*, *Thiriotia*, and *Uradiophora*. Members of Porosporidae, which include *Nematopsis* in crabs, have indirect life cycles and use molluscs as intermediate hosts (see Clopton, 2002). Only one indirect life cycle, that of *Nematopsis ostrearum*, has been fully elucidated (Prytherch, 1940). Other families of gregarines have a direct, or single host, life cycle. Following Bradbury's (1994) exhaustive review, several species have been described from crabs, including species of *Nematopsis* in grapsoid and ocypodoid crabs from India (Prasadan & Janardanan, 2001), *Cephaloidophora rhithropanopei* from xanthids from the Black Sea

(Belofastova, 1996), and *Thiriotia pugettiae* from *Pugettia gracilis* (Epialtidae) (Rueckert et al., 2011). Gregarines can be highly host specific, with specificity at the species or genus level (Bradbury, 1994), but transfection studies are rarely undertaken to clarify host range (Clopton, 2002).

Unlike other sporozoans, **merogony** is absent in the life cycle of gregarines; they use **gamogony** and **sporogony** for proliferation (Clopton, 2002). The **sporozoite** is freed from the **sporocyst** in the digestive tract of the host and penetrates a host cell with its apical complex. The organelle then develops into a complex holdfast known as a **mucron** or **epimerite**, depending on the taxon. The developing **gamont** is extracellular, with its septate body free in the lumen feeding osmotrophically on the contents of the gut. The gamonts can form long chains in the gut with different cells in the chain representing male or female gametes. Two gamonts will pair in a presexual union known as **syzygy**. A cyst wall forms around the mating pair, they fuse to form a zygote, and gymnospores complete sporogony.

Coccidians parasitize a variety of vertebrates and invertebrates. They are **heteroxenous**, having a two-host life cycle, with merogony occurring in the intermediate host and gamogony and sporogony in the definitive host. They live intracellularly and often show specificity for certain host tissues such as blood cells, gut epithelia, fat bodies, and salivary glands. At least 10 species are known from crustaceans, with four in *Aggregata* reported from brachyurans, including several species of portunids, majids, dromiids, goneplacids, and ocypodoids (Vivarès & Rubio, 1969; Vivarès, 1972; Bradbury, 1994). All species found in crabs use cephalopods as definitive hosts. The life cycle of *Aggregata eberthi* was described by Leger & Duboscq (1906) and re-examined by Gestal et al. (2002). Although the taxonomic characterization of species of *Aggregata* has proceeded with the development of molecular tools for work in cephalopod hosts (Gestal et al., 2010; Castellanos-Martínez et al., 2013), little work has been done on these parasites in their intermediate crab hosts.

Metazoans

Brachyurans have a broad diversity of **metazoan symbionts**, with representatives from seven phyla. The range of symbionts is too large for a comprehensive review of all taxa; we therefore focus on some of the most recent reviews and provide examples highlighting the nature of these host-symbiont associations. The importance of marine crustaceans as **vectors** for helminths was reviewed by Busch et al. (2012).

Helminths

Phylum Platyhelminthes.

— *Turbellaria.* – Most **turbellarians** are free-living, but some are symbiotic and use arthropods as hosts. Well-known examples include the commensals *Bdelloura candida* on the horseshoe crab, *Limulus polyphemus* (Chelicerata: Merostomata), and *Stylochus zebra* on hermit crabs (Williams & McDermott, 2004; McDermott et al., 2010). Few turbellarians have been reported from brachyurans. The best known of these are species of

Temnocephalida found on freshwater decapods, mostly crayfish, but some species can use crabs and shrimps as well (Cannon & Joffe, 2001).

Temnocephalids are highly specialized turbellarians with oral tentacles and a posterior attachment organ (sucker). The order shows a subtropical Gondwanian distribution throughout South America, Australia, and Asia, but not Africa (Gelder, 1999). *Temnosewellia semperi* lives as a commensal on the surface of the freshwater crab *Stoliczia rafflesi* (Potamidae) from Malaysia (Rohde, 1966) and species of potamids from China (Lee, 1936). It has also has been reported on *Eriocheir japonica* (Varunidae) from Japan, *Geothelphusa miyazakii* (Potamidae) from Taiwan, and several other freshwater potamid crabs in Southeast Asia (see Gelder, 1999; Kawakatsu et al., 2007). Only one other species of *Temnosewellia* is known as a primary brachyuran symbiont: *Temnosewellia vietnamensis* on *Villopotamon thaii* (Potamidae) from Vietnam (Damborenea & Brusa, 2009). Another species, *Temnocephala brevicornis*, occurs on an unidentified pseudothelphusid freshwater crab from El Salvador (Kraus, 1954) and *Temnocephala lutzi* infests *Callinectes bocourti* in freshwater habitats from Brazil (Peralta et al., 2005). These worms are capable of host switching because *Temnosewellia chaeropsis* was introduced into South Africa with its crayfish host, *Cherax tenuimanus*, and was later found infesting an indigenous crab host, *Potamonautes warreni* (Potamonautidae) (Avenant-Oldewage, 1993).

Several monocoelid turbellarians have been reported from brachyurans, but they have not been well studied and their status as parasites in unclear. *Peraclistus oophagus* occurs in the egg clutches as well as on the body of *Chionoecetes opilio* and *Hyas araneus* (Oregoniidae) in the northwestern Atlantic and on *Hyas araneus* from the northeastern Atlantic (Fleming & Burt, 1978). The worm had a prevalence of 90.9% on ovigerous *Hyas araneus* from the Barents Sea, was only found on ovigerous crabs, and was considered an egg predator (Dvoretsky, 2012). Two monocoelids, *Ectocotyla hirudo* and *Ectocotyla multitesticulata*, occur on the gills and in the branchial chambers of *Chionoecetes opilio* and *Hyas araneus* from the northwestern Atlantic (Fleming & Burt, 1978; Fleming et al., 1981). Prevalence on gills and egg masses of *Chionoecetes opilio* ranged from 8.8 to 90% (Brattey et al., 1985). A commensal planoceroid turbellarian had a relatively low prevalence in the gills of *Portunus pelagicus* (see Shields, 1992).

Turbellarians in the order Fecampiida are internal parasites of crustaceans. Only one is known from brachyurans. *Fecampia erythrocephala* develops internally within the haemocoel of *Carcinus maenas* and *Cancer pagurus* from Europe (Kuris et al., 2002). In brachyurans it infects small juveniles less than 10 mm carapace width but infects large, mature hosts in hermit crabs and shrimps (Kuris et al., 2002). Prevalence ranged from 4-7% in juvenile *Carcinus maenas* and *Cancer pagurus*. The worm grows to a large size within the host, eventually killing the crab upon emergence of the mature worm (Southward, 1950). In this respect they are considered **parasitoids** because they kill their hosts. Worms lay a diagnostic parchment-like cocoon on macroalgae and under rocks. Some habitat differences were observed with worms preferring crabs in less disturbed substrates and higher salinities (Kuris et al., 2002).

— *Trematoda.* – Digenean, or digenetic, **trematodes** are a class of Platyhelminthes known as **flukes**. They are relatively common parasites in crabs and use them as second intermediate hosts. As **trophically transmitted parasites**, trematodes do not typically kill their intermediate hosts, but in order for completion of the life cycle, the intermediate hosts have to be ingested by the definitive hosts (Lafferty & Kuris, 2002). Trematodes encyst as **metacercariae**, or resting cysts, in the tissues of crab hosts. Most trematodes have complex life cycles that usually include at least two hosts ("Digenea" refers to having two hosts), although some have an abbreviated life cycle with only a molluscan host (Poulin & Cribb, 2002). The first intermediate host is, with few exceptions, a mollusc, usually a gastropod, and it is within the molluscan host that **asexual reproduction** occurs, ultimately producing a **cercaria**, an infectious larval stage. The parasites typically exhibit high host specificity for their first intermediate hosts (Cribb et al., 2001) but are often less specific in their second intermediate hosts for which they can use invertebrates, fishes, or amphibians. In some species, cercariae encyst on vegetation and skip the second intermediate host. Crabs often serve as the second intermediate host, or occasionally as an additional intermediate host. With few exceptions, vertebrates are the **definitive hosts**, where **maturation** and **sexual reproduction** occur. Adult trematodes are usually hermaphroditic, have an absorptive tegument, a blind alimentary tract, and anterior and posterior suckers. Paragonimidae and Microphallidae are families with well-known representatives that use crabs as intermediate hosts. Digenean parasites of crustaceans were reviewed previously by Overstreet (1983).

Paragonimus westermani and species within the *Paragonimus skrjabini* complex are lung flukes that are pathogenic in **humans** (see Blair et al., 1999). These parasites are endemic in southeast Asia and parts of Africa where they use large cats and other carnivores as definitive hosts. The parasites use freshwater snails (Cerithioidea and Rissooidea) as first intermediate hosts and crustaceans as second intermediate hosts (Yokogawa, 1965). At least 50 different crustaceans, including many freshwater crabs, have been identified as interemediate hosts for *Paragonimus westermani* and species in the *Paragonimus skrjabini* complex (Blair et al., 1999). Crabs obtain infections by exposure to infectious cercariae or by eating infected snails (Noble, 1963; Shibahara, 1991). Humans are infected by eating raw or poorly prepared crabmeat in such delicacies as drunken crab or shrimps (live animals marinated in wine before eating), or when raw crabmeat contaminates food or fingers prior to cooking. The worms undergo extensive migration from the human intestine into the lungs where they become encapsulated and mature, releasing eggs into the lungs that are transported up air passages and swallowed or are coughed up in the sputum. Completion of the life cycle takes place when eggs from the sputum or faeces contaminate water sources and release **miracidia** that penetrate appropriate snail hosts.

Two commercially important crab hosts, *Eriocheir sinensis* and *Eriocheir japonica*, are also important **vectors** to humans. Prevalence levels in these crabs ranged from 0 to more than 59% (Cho et al., 1991; Odermatt et al., 2007; Kim et al., 2009; Doanh et al., 2012). Crabs can transmit infections as artisanal foods, or they can serve as natural reservoirs for the parasite, with recent examples including the potamids *Indochinamon*

tannanti, *Indochinamon lipkei*, and *Vietopotamon aluoiense* from Vietnam (Doanh et al., 2007, 2012; Habe et al., 2013), *Larnaudia larnaudii* from Thailand (Waikagul, 2007), *Maydelliathelphusa lugubris* from India (Tandon et al., 2007), and *Liberonautes latidactylus* from Liberia (Sachs & Cumberlidge, 1990). Two species of *Paragonimus* use *Indochinamon tannanti* in Vietnam, and the worms can be distinguished by the size of their metacercariae (Doanh et al., 2007). Several species of shrimps and crayfish also serve as intermediate hosts in Asia and Africa. A similar parasite, *Paragonimus kellicotti* uses crayfish as intermediate hosts in the U.S.A. (Procop, 2009), whereas *Paragonimus mexicanus* uses the pseudothelphusid crab *Hypolobocera aequatorialis* in Ecuador, in some cases with high prevalence levels (Vieira et al., 1992). Human cases of **paragonimiasis** resulting in fatalities have been caused by all these species.

Microphallid digeneans frequently parasitize crabs as second intermediate hosts after developing in snails from intertidal and nearshore estuarine and marine habitats. *Microphallus primas* was the first **digenean** to be reported from a crab (McIntosh, 1865); it occurs in the hepatopancreas of *Carcinus maenas* from the U.K. (Stunkard, 1957; Threlfall, 1968). Worms enter as cercariae into the crab's gill chamber and create a portal of entry using a penetration cyst and stylet (Saville & Irwin, 2005). Two microphallids (*Microphallus claviformis* and *Maritrema subdolum*) occur in *Carcinus maenas* from Denmark and Germany, where the parasites are patchy, but the prevalence can be over 60% with intensities of over 1000 metacercariae per crab. Introduced populations of *Carcinus maenas* in non-native areas (South Africa and Australia) do not contain these parasites (Zetlmeisl et al., 2011). The microphallids *Gynaecotyla adunca* and *Probolocoryphe uca* use *Uca pugilator* and other *Uca* spp. as intermediate hosts. The former species is known as a host generalist in vertebrates and uses shore birds and several fishes as definitive hosts (Cable & Kuns, 1951). The latter species is only known as metacercariae (Schell, 1985), but excystment experiments indicate an avian host is likely (Dunn et al., 1990). Methods for the culture of *Gynaecotyla adunca* after excystment from *Uca pugnax* have been developed (West et al., 2014) and temperature has been shown to influence the emergence of cercariae from snails and the resulting transmission to second intermediate hosts (Koprivnikar et al., 2014). *Probolocoryphe uca* has a broad distribution and has been reported from *Nanosesarma minutum* (Sesarmidae) from Kuwait (Al-Kandari & Al-Bustan, 2010). Experiments with *Probolocoryphe lanceolata*, a species found in birds and marsh rice rats, *Oryzomys palustris* (Mammalia: Cricetidae), in Florida, indicate that host suitability in *Uca* spp. has a physiological basis (Smith et al., 2007). On the west coast of North America, *Hemigrapsus oregonensis* and *Hemigrapsus nudus* are second intermediate hosts for *Maritrema laricola*, which uses gulls (Aves: Laridae) as definitive hosts (Ching, 1963). Species of *Hemigrapsus* also harbour *Maritrema* sp. and *Microphallus* sp. in Japan (Blakeslee et al., 2009; McDermott, 2011). *Uca rapax* is the second intermediate host for *Microphallus sabanensis*, which uses birds as definitive hosts in Venezuela (Diaz et al., 2004). The varunids *Cyrtograpsus angulatus* and *Neohelice granulata* serve as hosts for *Maritrema bonaerense*, *Maritrema orensense*, *Levinseniella cruzi*, and *Odhneria* sp. in Argentina. These parasites show partitioning of the microhabitat within their hosts (Alda et al., 2011). *Macrophthalmus abbreviatus* (Macrophthalmidae) is the second intermediate

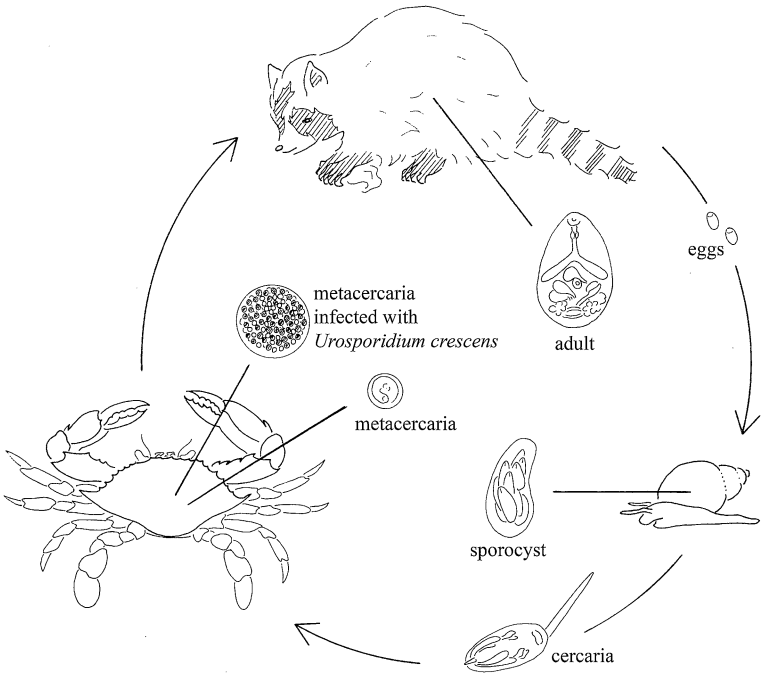

Fig. 71-12.21. Life cycle of *Microphallus basodactylophallus*. Eggs from adult worms leave the raccoon host via faeces. The snail host consumes the eggs which develop into sporocysts and produce cercariae that leave the snail and penetrate a crab host to encyst as metacercariae. The crab is eaten by a raccoon, the metacercariae excyst and develop into mature worms. Also depicted in the crab is an enlarged metacercaria infected by the hyperparasite *Urosporidium crescens*. [After Overstreet, 1978.]

host for *Microphallus koreana* in South Korea, with birds as experimental definitive hosts (Guk et al., 2008). *Gynaecotyla squatarolae* also occurs in *Macrophthalmus abbreviatus* as well as in *Macrophthalmus japonicus* (Macrophthalmidae) (Seo et al., 2007; Lee et al., 2010). Several crabs are hosts for *Maritrema* sp. and *Microphallus* sp. in New Zealand (see below).

One microphallid will serve to illustrate the autecology of infection in crabs (fig. 71-12.21). *Microphallus basodactylophallus* is found encysted as metacercariae in *Callinectes sapidus* along the Atlantic and Gulf coasts of the U.S.A. (Strong & Cable, 1972). The parasite uses several species of hydrobiid snails as first intermediate hosts. *Callinectes sapidus*, *Uca minax* (Ocypodidae), *Uca pugnax*, and *Uca longisignalis* act as second intermediate hosts and, when eaten, transmit the parasites to the definitive hosts, raccoons, *Procyon lotor* (Mammalia: Procyonidae), and marsh rice rats (Heard & Overstreet, 1983). Cercariae enter the gill chamber of the crab host, form ephemeral penetration cysts on the gills, and use their stylets to create a portal of entry into the host. The cercariae migrate into muscle, hepatopancreas, connective or nervous tissues, and encyst as metacercariae. The haplosporidan hyperparasite *Urosporidium crescens* can infect the metacercariae, causing them to hypertrophy and fill with the brown-black spores of the protozoan

(fig. 71-12.14), which can lead to the condition known as pepper spot disease (see above). Other microphallids use *Callinectes sapidus* as an intermediate host, such as *Microphallus nicolli*, which forms large cysts in connective tissues (Heard & Overstreet, 1983), and *Microphallus diodontis*, which occurs at the base of the gills. Another microphallid, *Levinseniella capitanea*, infects the hepatopancreas and ovary, where the large cysts (about 1 mm) can be seen with the naked eye (Overstreet & Perry, 1972); this parasite apparently uses a fish as a definitive host (see Overstreet, 1983).

Metacercarial infections in crustaceans can occur at surprisingly high intensities. *Microphallus szidati* ranged from 2 to 802 worms in the hepatopancreas of *Neohelice granulata*, and at high intensities, necrosis and changes to glycogen levels were observed (Robaldo et al., 1999). Focal necrosis and tissue displacement is quite common around metacercariae (Stentiford & Feist, 2005). Infections in the nervous tissues of the host can damage the nerves, leading to **ataxia** and possibly **lethargy** (Sparks & Hibbits, 1981). Using multiple regression techniques, no differences were observed in **serotonin** or **dopamine** levels in *Macrophthalmus hirtipes* (Macrophthalmidae) infected with helminths such as *Maritrema* sp., *Profilicollis* sp. (Acanthocephala) or nematodes (Poulin et al., 2003). Infections of *Maritrema novaezealandense* were thought to increase host mortality in the varunids *Austrohelice crassa* and *Hemigrapsus sexdentatus*, the hymenosomatid *Halicarcinus varius*, and *Macrophthalmus hirtipes* (see Koehler & Poulin, 2010; Koehler et al., 2011). Blinded studies using fish predators could be a suitable avenue for continued examination of this issue in crustaceans.

— *Cestoda.* – Cestodes, or **tapeworms**, are entirely parasitic, lack a gut, or digestive tract, have an absorptive tegument, and are typically hermaphroditic. Species have indirect or direct life cycles; those with indirect life cycles use invertebrates and vertebrates as intermediate hosts. All adult tapeworms use vertebrates as definite hosts. Tapeworms occur in crabs as juvenile stages known as **metacestodes** (Overstreet, 1983). Metacestodes of most cestode taxa have a diagnostic inverted **scolex**, or **holdfast organ** that will evaginate upon ingestion by the definitive host and the adult tapeworm will use the scolex to attach to host tissue within the intestine or spiral valve of their vertebrate host. The orders Tetraphyllidea, Trypanorhyncha, and Lecanicephalidea have representatives that use crabs as intermediate hosts, and all three orders use elasmobranchs (Pisces: Chondrichthyes: Elasmobranchii) as definitive hosts. Cestodes are more commonly found in shrimp hosts (Overstreet, 1983) but when found in crabs, infections can reach high intensities (Shields, 1992; Gurney et al., 2004) that are typically focal in nature (Smolowitz et al., 1992; Gurney et al., 2004). In heavy infections, crabs can show alterations in their digestive physiology such as decreases in **trypsin** and **lipase** activity (Gurney et al., 2006).

Because adult morphology is used to identify cestodes to species, very few cestodes from crabs have been identified beyond genus, making it difficult to elucidate the life cycles of those found in elasmobranchs (Jensen & Bullard, 2010). A similar conundrum regarding species identifications occurs in the metacestodes that use fishes, where separate terminology has been used for metacestodes, e.g., "*Scolex polymorphus*". Metacestodes are sometimes recorded in surveys of the parasites of shrimps or crabs, and they are usually encysted within the connective tissues, viscera, and skeletal muscles. Most re-

ports are anecdotal, such as an undescribed trypanorhynch that has been observed once in *Pinnixa chaetopterana* (Pinnotheridae) from North Carolina (McDermott, 2009), an undescribed trypanorhynch and tetraphyllid reported in *Carcinus maenas* from Spain (Kuris et al., 2005; Blakeslee et al., 2009), and an undescribed trypanorhynch that uses *Hemigrapsus oregonensis* from California (J. D. Shields, unpublished). Two trypanorhynchs, *Dollfusiella martini* and *Trimacracanthus aetobatidis*, infect *Carcinus maenas* introduced to Australia, with high prevalence levels from some locations (Kuris & Gurney, 1997; Zetlmeisl et al., 2011). A lecanicephalid, *Polypocephalus moretonensis*, and an undescribed congener live in the ventral nerve ganglia of *Portunus pelagicus* in Australia, sometimes reaching high intensities (Butler, 1987; Shields, 1992; Brockerhoff & Jones, 1995). *Prochristianella* sp. infects *Callinectes sapidus* (see Shields & Overstreet, 2007) and a "*Rhynchobothrium*" sp. can also use the blue crab (DeTurk, 1940), but both species are rare in this host. An unidentified tetraphyllidean has been observed in *Callinectes similis* (Portunidae) from Mississippi, U.S.A. (Overstreet, 1978) and possibly in *Achelous spinimanus* (Portunidae) and *Callinectes ornatus* (Portunidae) from North Carolina (DeTurk, 1940).

Phylum Nemertea. – Nemerteans, or ribbon worms, superficially resemble flatworms but are distinguished by the presence of a **rhynchocoel**, a body cavity housing a proboscis used in prey capture. Several nemerteans are symbionts of invertebrates. Carcinonemertidae within the monostyliferous Hoplonemertea consists of two genera (*Carcinonemertes* with 15 species and *Ovicides* with 5 species) all of which are obligate egg predators of palinurid lobsters, anomurans, and brachyurans (Jensen & Sadeghian, 2005).

Species of *Carcinonemertes* are filiform in shape and have a greatly reduced, slightly extrusible proboscis that is used to puncture eggs. They have separate sexes, but cases of **hermaphroditism** and **parthenogenesis** have been reported in both genera (Roe, 1986; Shields & Segonzac, 2007). Fertilization of the eggs is internal but can also occur during oviposition. Eggs are laid in mucous sheaths attached on setae in the egg clutches of their hosts. Egg sheaths are mostly elongated and visible to the naked eye, and can hold hundreds of eggs, but smaller species have microscopic egg sheaths (Kajihara & Kuris, 2013). Larval nemerteans hatch in synchrony with hatching of the host embryos (Humes, 1942; Roe, 1988; Shields & Kuris, 1990). Newly hatched larvae exhibit positive **phototaxis** and can swim for several days (Humes, 1942; Davis, 1965). Larvae that settle on appropriate hosts develop into juveniles, which in some cases live in the limb axillae of their hosts, absorbing **amino acids** that leak through the thin host cuticle (Roe et al., 1981). Nemerteans can be lost during host ecdysis (Humes, 1942; Hopkins, 1947), or move to the new instar (Wickham et al., 1984), where they show little to no reduction in prevalence between moults (Shields, 1992; Shields & Wood, 1993).

Species of *Carcinonemertes* are highly adapated to the embryogenesis of their respective hosts (Shields & Kuris, 1990). Species such as *Carcinonemertes carcinophila* and *Carcinonemertes mitsukurii* that live on portunids have a short duration (10-14 days) of embryogenesis, settle on ovigerous females, develop rapidly, migrate into the branchial

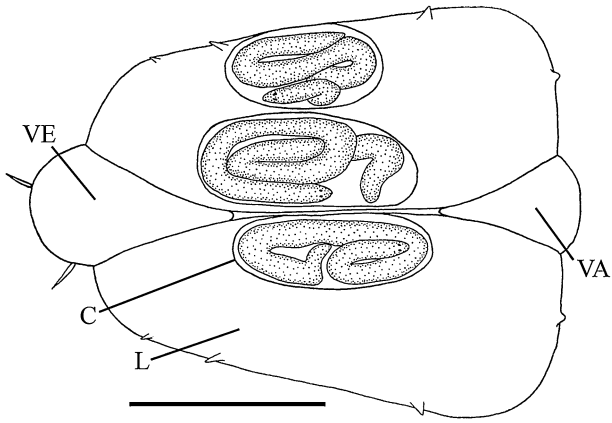

Fig. 71-12.22. *Carcinonemertes carcinophila* encapsulated in a mucous sheath on the gill lamella of *Callinectes sapidus* (bar = 2 mm). Abbreviations: C, capsule; L, lamella; VA, afferent blood vessel; VE, efferent blood vessel. [After Humes, 1942.]

chamber of the host, where they secrete a mucous cyst (fig. 71-12.22) and then lie dormant until the female lays eggs. Species such as *Carcinonemertes errans* and *Carcinonemertes epialti* that typically live on cancrids and varunids have a moderate duration (40-90 days) of embryogenesis, settle on male and female crabs, develop as juveniles on the limb apodemes, axillae, and abdomens (pleons) of their hosts, and move into the clutch during oviposition (Wickham, 1980). Larvae of *Carcinonemertes errans* are present in the Coos Bay Estuary (Oregon, U.S.A.) during August through November. After settlement on the exoskeleton of *Metacarcinus magister* they move to the abdomen of hosts and metamorphose into juveniles within 48 hours (Dunn & Young, 2013, 2014). Juvenile *Carcinonemertes errans* can transfer from male to female hosts upon mating (Wickham et al., 1984), and this could be the case for those on portunids as well, as there are records of male crabs with infestations (Humes, 1942). Species such as *Carcinonemertes regicides* and *Carcinonemertes wickhami* that typically infest crabs and lobsters that have long brood periods (3-9 months), settle and mature directly on ovigerous hosts, but generally die or leave their host after eclosion.

At least three species of *Carcinonemertes* are generalists that use several species of crabs among disparate families. Two of these, *Carcinonemertes carcinophila* and *Carcinonemertes mitsukurii*, are frequently found on portunids, but have been reported on species in other families as well; similarly, *Carcinonemertes epialti* favours varunids, cancrids, and majids, but it has also been reported on portunids (see Wickham & Kuris, 1985). Other species appear to be more host specific, possibly because of their close association with the reproductive cycles of their hosts. In particular, *Carcinonemertes pinnotheridophila* lives intertwined in the branchial chamber and the sternal segments of its pea crab host (McDermott & Gibson, 1993). Several species have been described from bythograeid crabs from **hydrothermal vent sites** (Shields & Segonzac, 2007). They could have colonized these hosts from shallow water relatives, as their life history patterns

are more like those species on cancrids, but molecular work is needed to address their **evolutionary relationships**.

Epizootics of *Carcinonemertes regicides* and *Carcinonemertes errans* have been implicated in declining stocks of *Metacarcinus magister* and the anomuran *Paralithodes camtschaticus* (see Wickham, 1979; Hobbs & Botsford, 1989; Kuris et al., 1991). *Carcinonemertes errans* can reach prevalence levels of 100% and intensities of over 800 worms per crab in *Metacarcinus magister* from offshore waters (McCabe et al., 1987; Dunn & Young, 2013) and could have important impacts on the *Metacarcinus magister* fishery. *Carcinonemertes errans*, however, exhibits a spatiotemporal gradient, with *Metacarcinus magister* hosts in estuaries having lower prevalence and intensity on crabs than those in nearshore waters. Estuaries can thus act as **refugia** from this parasite (McCabe et al., 1987; Dunn & Young, 2013). Epizootics of *Carcinonemertes* spp. are associated with intense **fishing pressure** (Shields, 2012). The presence of nemertean worms and their seasonality should be considered when examining underlying causes of poor recruitment or lost fecundity in crabs or lobsters.

Phylum Nematomorpha. – Nematomorpha is a small phylum of pseudocoelomate worms commonly known as Gordian, or horsehair, worms. They are **protelean parasitoids**, meaning that the larvae are parasitic, or protelean, and a single nematomorph can kill its host (= **parasitoid**). The larvae are endoparasites of arthropods and after a period of development they rupture from the body of the hosts, giving rise to free-living adults that are typically long and thread-like. *Nectonema* comprises five species, all of which infect crustaceans, but only two are found in brachyurans. Adults of *Nectonema* spp. have a reduced digestive tract and do not feed (Ward, 1892). Digestion in the larval form occurs through a carrier-mediated transport system across the cuticle and intestine (Skaling & MacKinnon, 1986).

Nectonema agile has a broad host range, infecting decapods from the North Atlantic Ocean. It infects shrimps, pagurids, and galatheids as well as brachyurans, including cancroids, grapsoids, and portunoids (see Poinar & Brockerhoff, 2001). *Nectonema zealandica* infects *Hemigrapsus sexdentatus* from New Zealand (Poinar & Brockerhoff, 2001). An unidentified species of *Nectonema* was reported from four specimens of the atelecyclid *Erimacrus isenbeckii* from Japan (Oku et al., 1983), and another unidentified species is prevalent in coral-dwelling xanthoids on the Great Barrier Reef (J. D. Shields, unpublished). Two species, *Nectonema svenskundi* and *Nectonema melanocephalum*, are only known from free-living adults (Poinar & Brockerhoff, 2001), their crustacean hosts remain to be determined.

Nematomorphs cause significant pathological changes to their hosts. Hosts typically die when nematomorphs mature and leave them. Parasitic castration is thought to occur in crustacean hosts, but data on castration are mostly lacking for brachyuran hosts. A few male *Cancer irroratus* from the Bay of Fundy, where prevalence levels approached 50%, possessed atrophied gonads (Leslie et al., 1981). As with most parasitoids, the typical mode of infection was usually one nematomorph per host, but some crabs had as many as nine parasites.

Phylum Acanthocephala. – Acanthocephala is a small phylum of strictly parasitic, pseudocoelomate, "thorny-headed" worms. They have indirect life cycles and use arthropods as first intermediate hosts. The intermediate host must ingest the infectious eggs to become infected and the parasites are then trophically transmitted to vertebrate definitive hosts (fishes, birds, mammals). Acanthocephalans often use **paratenic**, or transport, hosts that are ingested by definitive hosts. These worms can cause considerable pathology in accidental hosts. They provide some of the best-studied examples of behavioural manipulation by parasites (see Moore, 2002; Lafferty & Shaw, 2013), including brachyuran hosts (Latham & Poulin, 2001). The larvae in arthropods can be difficult to identify, but the inverted proboscis of the **cystacanth** (a fully developed juvenile) changes little upon maturation and can be used to identify the worms to the genus level. Acanthocephalans have been reported from decapods; in particular they are common in mole crabs (Goulding & Cohen, 2014), but they also occur in brachyurans.

Three genera of acanthocephalans use brachyurans as intermediate hosts: *Profilicollis*, *Hexaglandula*, and *Arhythmorhynchus*. The taxonomy of *Profilicollis* and its tortuous relationship with the genus *Polymorphus* was reviewed by Nickol et al. (1999) and García-Varela et al. (2013). Those species using crustaceans as intermediate hosts are considered to be in the genus *Profilicollis* based on the **cytochrome oxidase 1** gene (García-Varela & Pérez-Ponce de León, 2008; García-Varela et al., 2013).

Profilicollis botulus uses a number of different crustacean hosts and has a broad geographic distribution. Brachyuran hosts include *Carcinus maenas* from northern Europe and Cape Cod, Massachusetts, U.S.A. (Thompson, 1985a; Nickol et al., 1999; Christiansen et al., 2009), *Necora puber* from Scotland (Nickol et al., 1999), *Hemigrapsus oregonensis* from British Columbia (Ching, 1989), *Hyas araneus* and other decapods from the Barents Sea (Uspenskaya, 1960; Sparks, 1987; Jansen et al., 1998), *Cancer irroratus* and *Carcinus maenas* from eastern Canada (Brattey et al., 1985; Brattey & Campbell, 1986) and non-native *Hemigrapsus sanguineus* from Cape Cod (Christiansen et al., 2009). The parasite can be quite common in these hosts: a prevalence of 62% was reported from *Hemigrapsus oregonensis* from British Columbia (Ching, 1989), and 80% from *Hyas araneus* from Scotland (Nickol et al., 1999). *Profilicollis botulus* was probably misidentified as *Profilicollis major* occurring in *Cancer irroratus* from Maine (Schmidt & MacLean, 1978; Sawyer et al., 1984; Brattey et al., 1985).

The life cycle of *Profilicollis botulus* has been described. **Acanthellae** and cystacanths are embedded in the wall of the host gut, encysted in the spongy connective tissues surrounding various organs, or free in the haemocoel (Brattey & Campbell, 1986). When the crab is eaten, the parasites excyst in the intestine of the vertebrate host, in this case a bird such as a diving duck (Aves: Anatidae) (Thompson, 1985a; Ching, 1989; Mayer et al., 2003). Eggs are passed in the faeces of the definitive host and are then ingested by the crab intermediate host. The parasites are also found in sea otters, *Enhydra lutris nereis* (Mammalia: Mustelidae), which act as non-competent hosts, and have been implicated in mortalities of these hosts (Mayer et al., 2003).

Profilicollis sphaerocephalus uses several brachyuran hosts, including the varunids *Brachynotus spinosus*, *Cyclograpsus granulosus*, *Paragrapsus gaimardii*, *Paragrapsus*

laevis, *Paragrapsus quadridentatus*, and the geryonid *Nectocarcinus integrifrons* from Victoria and Tasmania, Australia (Pichelin et al., 1998). *Profilicollis antarcticus* and *Profilicollis novaezelandensis* use *Macrophthalmus hirtipes*, *Hemigrapsus sexdentatus*, *Hemigrapsus crenulatus*, and *Austrohelice crassa* in New Zealand (Latham & Poulin, 2001; Brockerhoff & Smales, 2002). *Profilicollis antarcticus* has also been reported from *Hemigrapsus crenulatus* from southern Chile (Pulgar et al., 1995). *Profilicollis chasmagnathi* uses *Neohelice granulata* from Uruguay (Holcman-Spector et al., 1977a, b), as well as *Cyrtograpsus angulatus* and *Neohelice granulata* from Argentina (Martorelli, 1989; Alda et al., 2011; La Sala et al., 2012); it uses the stilt (*Himantopus melanurus*; Aves: Recurvirostridae) as the avian definitive host. Acanthocephalans can have broad geographic distributions because of the migration behaviours of their definitive hosts, as exemplified by the wide distribution of *Profilicollis altmani* in North and South America (Goulding & Cohen, 2014).

Two other acanthocephalans use brachyurans: *Hexaglandula corynosoma* infects *Uca spinicarpus* (Ocypodidae) from Mexico (Guillén Hernández et al., 2008), and *Uca spinicarpus* and *Uca rapax* from the southeastern U.S.A. (Nickol et al., 2002). Yellow-crowned night herons (*Nyctanassa violacea*; Aves: Ardeidae) are the definitive hosts for this worm in Mexico (Guillén Hernández et al., 2008). *Arhythmorhynchus frassoni* infects *Uca spinicarpus* and *Uca rapax*, and clapper rails (*Rallus crepitans*; Aves: Rallidae) act as definitive hosts for this species in the southeastern U.S.A. (Nickol et al., 2002). Raccoons (*Procyon lotor*) can serve as accidental hosts (Richardson, 2014). Cystacanths of *Arhythmorhynchus* sp. have been observed in *Uca minax* and *Uca pugnax* from Chesapeake Bay (J. D. Shields, unpublished).

Acanthocephalans can cause remarkable physiological and behavioural changes in crustaceans including castration, changes to pigmentation, and alterations in behaviour that increase their risk of predation (Nickol, 1985; Moore & Gotelli, 1990; Kolluru et al., 2011). Some brachyurans show altered **burrowing behaviour** when harbouring high loads of acanthocephalans. Latham & Poulin (2002) found that *Macrophthalmus hirtipes* parasitized by *Profilicollis* spp. foraged in the open more often than non-parasitized individuals, providing evidence of increased risk to predation by bird definitive hosts. Such changes in behaviour were not found in parasitized individuals of *Hemigrapsus crenulatus*. Acanthocephalans can cause significant physiological alterations in crabs, including changes in oxygen consumption (Haye & Ojeda, 1998), dopamine levels (Rojas & Ojeda, 2005), and serotonin levels (Poulin et al., 2003; Pérez-Campos et al., 2012). Infected crabs show changes in burrow guarding behaviours (Latham & Poulin, 2002) and mating success, but they do not undergo changes in coloration (Latham & Poulin, 2001). Intensity of infection often shows a strong relationship with host size (Liat & Pike, 1980; Thompson, 1985a), and heavy infections can lead to reduced fecundity and increased host mortality (Latham & Poulin, 2002). Given the potential for high transmission rates to shore birds (Thompson, 1985b), the ecology of these parasites has led to insights regarding **food web** properties in larger **ecosystems** (Thompson et al., 2005).

Phylum Nematoda. – Nematodes, or **roundworms**, comprise a large phylum of free-living and parasitic taxa. They have a rigid but flexible cuticle, a complete digestive tract, and a **pseudocoelom** that maintains a hydrostatic musculo-skeletal system. They also exhibit **eutely** and most species are **dioecious**, although a few exhibit **parthogenesis**. Nematodes have a complex array of variations in their life histories, host relationships, and transmission patterns. In different taxa, eggs with developing larvae can either be eaten by hosts, can hatch as **L1**, **L2**, or even **L3 larvae** serving as infectious stages, or the eggs themselves can develop as **microfilaria** stages which use arthropods as vectors. Larval stages moult successively as L1 through L4 stages to adults. The parasitic taxa are mostly trophically transmitted and larvae often use **paratenic**, or transport, hosts to reach their final definitive hosts. In some cases the larvae undergo extensive migrations in their definitive hosts before developing as adults in their final tissue of preference. The **evolution** of nematode life histories, including those in invertebrates, was reviewed by Adamson (1986) and Blaxter et al. (2000). A number of nematode species use crustaceans as intermediate and definitive hosts. Some unidentified larval nematodes are suspected to have successfully infected introduced populations of *Carcinus maenas* and *Hemigrapsus sanguineus*, but such findings are rare (Torchin et al., 2001; Blakeslee et al., 2009). An overview of the various host-parasite associations with crustaceans was given in Overstreet (1983) and Busch et al. (2012) and the systematics of the nematode taxa can be found in Anderson (2000).

— *Ascaridida.* – The ascaridoid nematode *Anisakis simplex*, or "**sushi worm**", is an accidental pathogenic parasite in humans. The nematode uses euphausiids as the first intermediate host, a variety of invertebrates and fishes as paratenic hosts, and marine mammals as definitive hosts (Smith & Wootten, 1978). This parasite can be very rare in its first intermediate hosts (including amphipods, euphausiids, galatheids, and mysids); hence, there are very few reports of it from decapods. Sparse records of *Anisakis* sp. larvae indicate its presence in *Hyas araneus* from the Barents Sea, but at very low prevalence levels (Uspenskaya, 1963). An L3 of *Anisakis* sp. was found in the viscera of a single *Cancer plebejus* (Cancridae) from Chile (George-Nascimento et al., 1994). Squid and teleost fishes are important transport hosts for this nematode (Smith & Wootten, 1978).

The L3 larvae of another ascaridoid, *Hysterothylacium reliquens*, infect a broad number of invertebrates, including *Callinectes sapidus* from the Gulf of Mexico (Deardorff & Overstreet, 1981a). Invertebrates and several fishes serve as paratenic hosts for this parasite (Overstreet, 1983). *Callinectes sapidus* acquires the infection from a copepod intermediate host or another paratenic host. The nematode matures in a broad range of fish definitive hosts (Deardorff & Overstreet, 1981b). A congener, *Hysterothylacium aduncum*, infects a number of invertebrates and fishes (see Margolis & Arthur, 1979). It was reported from unidentified crab **zoea** and **megalopa** stages off eastern Canada (Jackson et al., 1997). The parasite was not reported from that region in other decapods (Brattey et al., 1985); however, given its broad range, it is possible that it could use other decapods as transport hosts. An unidentified ascaridoid nematode was reported from the portunid *Ovalipes catharus* from New Zealand (Miller et al., 2006).

— *Spirurida.* – Several spirurid nematodes use crabs as intermediate or paratenic hosts, including freshwater and marine taxa; however, few spirurids use crabs as definitive hosts. The L3 of the acuariid *Ancyracanthopsis winegardi* lives in the haemocoel of *Uca* spp. from Louisiana (Wong & Anderson, 1990). The adult can be found in several species of shore birds. The acuariid *Skrjabinoclava inornatae* also uses *Uca* spp. as intermediate hosts and willets, *Tringa semipalmata* (Aves: Scolopacidae), as definitive hosts (Wong et al., 1989); prevalence of this parasite was 52% in Louisana. Larval acuariids can be difficult to identify to species because they have few defining morphological characters. They have been reported in intertidal crabs from the Southern Hemisphere including *Uca uruguayensis* (Ocypodidae), *Neohelice granulata*, and *Cyrtograpsus angulatus* from Argentina (Cremonte et al., 2007; La Sala et al., 2009; Alda et al., 2011).

A few larval physalopterids (Physalopteridae) have been reported from crabs. *Proleptus obtusus* uses *Carcinus maenas* as intermediate hosts and elasmobranchs are the definitive hosts (Lloyd, 1920, 1928). The larval stages occur in the haemocoel of the crab (Perez-Calderon, 1986), but are not known from most populations of this widely distributed host. This parasite was not observed in a histological survey of *Carcinus maenas* from six locations in the U.K. (Stentiford & Feist, 2005), nor in surveys of this host from the U.S.A. (Blakeslee et al., 2009) or South Africa (Zeltmeisl et al., 2011), but *Proleptus* sp. was reported in this host from Australia (Zetlmeisl et al., 2011). A larval *Proleptus* sp. was reported in the viscera and muscles of *Cancer plebejus* from Chile (George-Nascimento et al., 1994) where it reached a prevalence of 17%. The definitive host was thought to be the catshark, *Schroederichthys chilensis* (Pisces: Scyliorhinidae).

Members of Cystidicolidae use insects and crustaceans as intermediate hosts and shorebirds and some teleosts as definitive hosts (Anderson, 2000). *Ascarophis* has been reported from several decapods including brachyurans (Uzmann, 1967; Brattey & Campbell, 1986). The L3 encysts within the viscera and haemocoel of their crustacean hosts. *Ascarophis morrhuae* was reported in *Carcinus maenas* from Brittany, France (Petter, 1970). Another *Ascarophis* sp. occurs in *Hemigrapsus oregonensis* from California (Poinar & Kuris, 1975). Four different morphological types of *Ascarophis* sp. occur in several decapods, including one brachyuran, *Pugettia producta* (Epialtidae), from California and Washington state (Poinar & Thomas, 1976). Other records include *Ascarophis* sp. in *Macrophthalmus hirtipes* from New Zealand (Moravec et al., 2003), and in *Uca uruguayensis*, *Neohelice granulata*, and *Cyrtograpsus angulatus* from Argentina (Cremonte et al., 2007; La Sala et al., 2009; Alda et al., 2011). These nematodes are probably more common than indicated by the number of records, as they can be difficult to find and properly identify.

There are a few records of spirurid nematodes using crabs as definitive hosts. These include adults of the thelazioid (Thelazioidea: Rhabdochonidae) *Heptochona praecox* living in the hepatopancreas of the freshwater crab *Ceylonthelphusa rugosa* (Parathelphusidae) from Sri Lanka (Poinar & Kannangara, 1972). A larval spirurid was also found encysted in the hepatopancreas of *Oziotelphusa ceylonensis* (Parathelphusidae) from Sri Lanka (Kannangara, 1972). A spirurid was reported in freshwater crabs from India (Pearse, 1932), but neither the host nor the parasite were identified.

— *Rhabditida.* – Rhabditids are common soil nematodes that feed on bacteria. They have ***dauer* larvae** capable of arrested development that attach to invertebrates and use **phoresy** to disperse to new habitats (Anderson, 2000). Species in one genus have symbiotic relationships with brachyurans. *Crustorhabditis* spp. live on the mouthparts, egg masses, and within the branchial chambers of ocypodids (Chitwood, 1935; Riemann, 1970; Sudhaus, 1974).

— *Monhysterida.* – Monhysterids are mostly free-living nematodes with species in terrestrial, marine, and freshwater environments. Several species are known as symbionts of crustaceans, and some have parasitic relationships with amphipods (Poinar et al., 2010). Monhysterids are gill-dwelling symbionts of gecarcinids (Baylis, 1915; Riemann, 1968, 1970). Two species have been reported from *Callinectes* sp. from the Caribbean (Riemann, 1970).

Phylum Annelida

Annelids are segmented, coelomate worms. They are not common symbionts of brachyurans because crabs can preen themselves, and worms such as polychaetes are components of the diets of many predatory crabs (Seitz et al., 2005).

Clitellata: Oligochaeta. – Branchiobdellida is an order of highly modified oligochaetes within Clitellata (containing oligochaetes and leeches) (Martin, 2001). Branchiobdellids provide a good example of why some symbiotic relationships are better thought of as a continuum since intermediate intensities of the worms appear to benefit hosts by removing debris from gills, whereas high intensities can have negative impacts (Brown et al., 2012). Branchiobdellids have a close symbiotic relationship with their freshwater crustacean hosts, particularly crayfish. They are obligate ectosymbionts that have oral and ventral suckers, 15 body segments, no seta or chaetae, and unpaired gonopores (Holt, 1968). They are hermaphroditic and deposit cocoons on their hosts. There are approximately 140-150 species of branchiobdellids in 22 genera, four subfamilies and one family (Gelder et al., 2002; Gelder, 2010).

A few branchiobdellids have been reported from pseudothelphusids (Holt, 1973). The best example is *Cambarincola vitreus*, which occurs on the gills and carapace of *Callinectes sapidus* (see Holt, 1968), but *Cambarincola mesochoreus* and *Cambarincola pamelae* have been identified from that host as well (Overstreet, 1983; Gelder et al., 2002; Gelder & Messick, 2006). Infestations occur in low salinity waters (Overstreet, 1983) and a prevalence of 100% was noted from the upper Chesapeake Bay in salinities less than 3 psu (Gelder & Messick, 2006). Most branchiobdellids feed on detritus, small protozoans, algae, and other microorganisms (Jennings & Gelder, 1979; Overstreet, 1983). They are not parasitic and they do not feed on host eggs; however, their effects on hosts when found at high densities should be investigated (Brown et al., 2012). An unidentified branchiobdellid was reportedly found on *Cancer borealis*, probably collected from low salinity waters near Portland, Maine, U.S.A. (see Gelder et al., 2002).

Clitellata: Hirudinea. – **Leeches** (subclass Hirudinea) have an oral and ventral sucker, true body segmentation (32 **postoral somites**), a flattened body, and no chaetae (Govedich et al., 2005). They can be free-living predators or parasitic blood suckers on fishes and other vertebrates. Leeches generally do not parasitize crabs, but some use crabs as phoretic hosts for transportation or as sites for depositing their cocoons. Leeches have been reported on crabs from habitats ranging from hydrothermal vents and deep-water fjords to estuarine and freshwater systems.

The deep-sea *Bathybdella sawyeri* was found on the chelipeds of the bythograeid *Cyanagraea praedator* from hydrothermal vents on the South East Pacific Rise (Burreson & Segonzac, 2006), where it parasitizes fishes and lays cocoons on hard surfaces such as bivalves and crabs. The piscicolid leech *Notostomum cyclostomum* uses *Chionoecetes bairdi* from deep-water fjords in British Columbia (Sloan et al., 1984). The prevalence on these hosts varied from 22-100% depending on location, and there were few correlations with depth, sex, or shell condition of the host. The leech deposits its cocoons on the carapace and limbs of the crabs and uses the host for dispersal. The gut contents of the leeches from these hosts contained meals of fish blood (Sloan et al., 1984; Khan & Paul, 1995); therefore, they are not considered parasites of crabs. The piscicolid *Platybdella olriki* has a relatively low prevalence on *Hyas araneus* from Newfoundland; it lays its cocoons on the legs and carapace of the crab host (Khan & Paul, 1995). The leech is a vector for a pathogen of flatfishes (Khan, 1982, 1984).

Johanssonia arctica is a common inhabitant on *Chionoecetes opilio*, *Hyas coarctatus* (Oregoniidae), and *Hyas araneus* (Oregoniidae), as well as on the pycnogonid *Nymphon stroemi* (Chelicerata: Pycnogonida) from the North Atlantic (Meyer & Khan, 1979; Khan, 1991). The biology of the worm was elucidated by Khan (1982). It lives up to 2.5 years, can lay an average of 62 cocoons per lifetime, lives at −1 to 2°C, and feeds 8 to 9 times per lifetime on different fish hosts (fig. 71-12.23). The worm can be quite common on *Chionoecetes opilio* in summer months (Khan, 1991) and prevalence is higher in waters deeper than 160 m (Khan, 1991; Savoie et al., 2007; Dvoretsky & Dvoretsky, 2010).

Myzobdella lugubris is a piscicolid leech found on *Callinectes sapidus*. It has a wide geographic range and can be found on a number of different crustacean hosts (Sawyer et al., 1975). In shallow, low salinity (less than 15 psu) estuarine habitats, these leeches feed on fishes and can build up to quite large numbers on the external, oral, and pharyngeal tissues of individual fish. In autumn, the leeches drop off their fish hosts, and move to the benthos to find blue crab hosts (Sawyer et al., 1975). Male *Callinectes sapidus* have a higher prevalence because female crabs migrate to higher salinity waters where the leeches cannot survive. Cocoons are laid on the posterior margin of the infested crab (Daniels & Sawyer, 1975).

Myzobdella lugubris has two different morphologies depending on whether it is on a crab or fish host (Sawyer et al., 1975; Overstreet, 1983). On a fish host, immature leeches are approximately 1 cm long, with a reddish gut engorged with fish blood. On a crab host, mature leeches can reach up to 4 cm long and have a green or tan coloration. These two forms were once considered separate species. *Callinectes sapidus* from the Gulf of Mexico can also harbour *Cystobranchus vividus* (see Overstreet, 1983). Unlike *Myzobdella lugubris*, this leech does not depend on the crab to deposit cocoons.

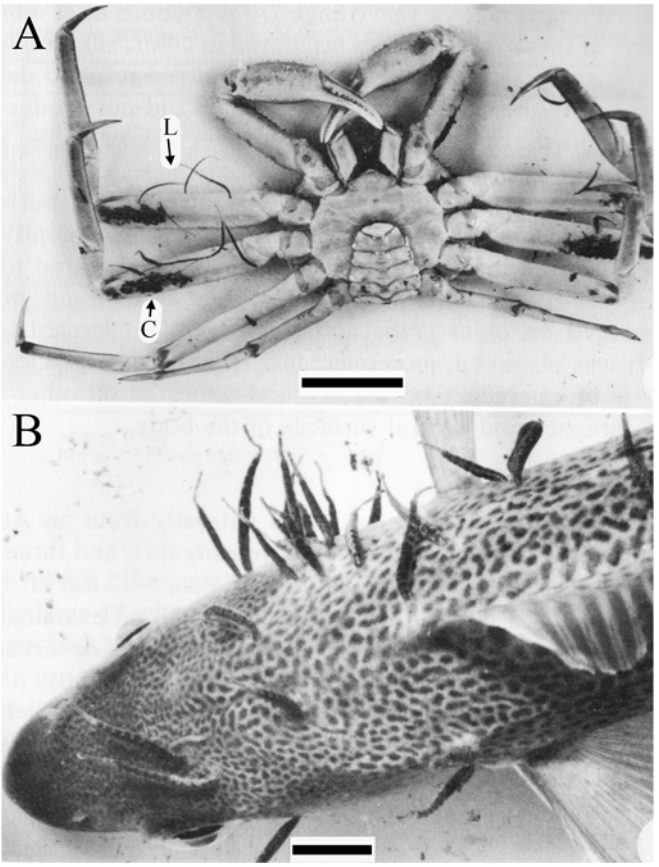

Fig. 71-12.23. A, Leeches, *Johanssonia arctica* (L) and their cocoons (C), on the limbs of *Chionoecetes opilio* from Newfoundland; B, engorged leeches on a cod, *Gadus morhua* (bar = 5 cm). [After Khan, 1982.]

The portunids *Callinectes toxotes* and *Callinectes arcuatus* are the hosts of an unidentified species of *Myzobdella* along the Pacific coast of Colombia (Norse & Estevez, 1977). *Myzobdella platensis* has been shown to harbour **haemocyanin** and **haemocytes** from its host, *Callinectes bocourti*, from Brazil (Zara et al., 2009). The gut contents were probed with anti-haemocyanin antibodies and anti-crab haemolymph antibodies to show positive evidence of parasitism. Leeches can sometimes be found around lesions on *Callinectes sapidus*, but there is no evidence that *Myzobdella lugubris* feeds on its crab host (Overstreet, 1983).

A few associations are also known from freshwater crabs. The leech *Paraclepsis vulnifera* occurs on "*Paratelphusa*" spp. from Sri Lanka (Kannangara, 1972). While no data were given on its prevalence, it was reportedly common and widely distributed (Fernando, 1960; Kannangara, 1972). The glossiphonid leech *Marsupiobdella africana* infects and matures on the clawed frog, *Xenopus laevis* (Amphibia: Pipidae), in South Africa but uses *Potamonautes perlatus* (Potamonautidae) as a phoretic host (Badets & Du

Preez, 2014). The leech either deposits young directly onto frog hosts, or lays cocoons on the crab host to protect the eggs from snail predation. The intensity of worms on crab hosts can be quite high, with over 75-100 worms per host.

Polychaeta. – Many polychaetes live in symbiosis with hermit crabs, mostly due to their use of gastropod shells (see Williams & McDermott, 2004), but a few use brachyurans as hosts. Iphitimidae is a small family of eunicoid worms that are entirely symbiotic, inhabiting the branchial chambers of their decapod hosts, mostly brachyurans. The best known is *Iphitime cuenoti*, a commensal often found in the branchial chambers of crabs from the North Atlantic and Mediterranean (Hartnoll, 1962). It has been reported from *Liocarcinus depurator*, *Liocarcinus corrugatus* (Portunidae), *Necora puber*, *Carcinus maenas*, *Cancer pagurus*, *Hyas araneus*, *Macropipus tuberculatus* (Portunidae), *Macropodia tenuirostris* (Inachidae), and *Maja squinado* (see Comely & Ansell, 1989; Martin & Brityaev, 1998). Several related species have also been reported in commensal relationships with brachyurans. Commensal dorvilleid polychaetes, *Ophryotrocha* spp. can be abundant in the branchial chambers of deep-water geryonids (Gaston & Benner, 1981; Pfannenstiel et al., 1982; Martin et al., 1991).

PHYLUM ARTHROPODA

Crustacea.

— *Copepoda.* – Nicothoidae is a family of highly specialized **siphonostomatoid copepods** that parasitize a broad range of crustacean hosts, with a few rare reports on crabs. These small, cryptic parasites are found in the egg masses or branchial chambers of their hosts, where they eat eggs or suck haemolymph from their hosts depending on where they reside (Lemercier, 1963). Two genera, *Nicorhiza* and *Rhizorhina*, are sometimes referred to as **mesoparasitic** with adult females anchored to their host by a rootlet system that penetrates host tissues. Nicothoids are considered egg mimics in that their egg sacs and bodies resemble host eggs, presumably making it more difficult for their host to remove them during preening (Bowman & Kornicker, 1967; Ohtsuka et al., 2005). Few nicothoids have been described from decapods, albeit their cryptic nature, small size, similarity to host eggs, and habitat (host broods) make them difficult to find.

Choniosphaera cancrorum occurs on the egg masses of *Cancer irroratus* and *Cancer borealis* from the northwestern Atlantic (Connolly, 1929). *Choniosphaera maenadis* has been reported from *Carcinus maenas* from Maine, U.S.A. (Johnson, 1957) as well as the North Sea (Bloch & Gallien, 1933) and Irish Sea (Gotto, 1970). The eggs, **nauplii**, and **copepodids** of the parasite can often be found in the egg masses of the host. The copepodids live in the branchial chamber and move to the egg masses where they feed on host eggs and mature (Connolly, 1929; Bloch & Gallien, 1933; Johnson, 1957). The copepodite is probably the transmissive or infectious stage (Johnson, 1957). This parasite has been suggested as a potential **biological control** agent for *Carcinus maenas*, but its prevalence can be too low in natural populations of its host to warrant much interest (Glude, 1955; Kuris et al., 2005) and host specificity would need to be carefully examined.

Choniosphaera indica occurs on the eggs and within the branchial chambers of *Portunus* spp. from India (Gnanamuthu, 1954) and Australia (Shields, 1992). In *Portunus*

pelagicus from Moreton Bay, Australia, prevalence was 7% on all females, 57.7% on ovigerous females, and none on male crabs (Shields, 1992). Prevalence of the parasite was as high as 85.2% and ranged up to 1821 female copepods on a single ovigerous host (Shields & Wood, 1993). Mean egg mortality due to the parasite was estimated at 2.4%, but reached as high as 19.6% of the clutch. Seasonality fluctuated in relation to the breeding cycle of the crab host. This parasite has not been found on *Scylla serrata* (see Hudson & Lester, 1994; Kvingedal et al., 2006).

Choniomyzon libiniae occurs in the eggs of *Libinia spinosa* (Epialtidae) from Brazil (Santos & Björnberg, 2004). All stages of the parasite, including three copepodid stages, occur within the egg mass of the host. Larval stages of *Choniomyzon* often occur in the branchial chamber of nonovigerous female hosts. *Choniosphaera* and *Choniomyzon* are the only genera in Nicothoidae whose larvae hatch as a nauplius stage (Boxshall & Halsey, 2004; Wakabayashi et al., 2013).

The harpacticoid copepods (Harpacticoida) comprise a very large and diverse group. Most are free-living, but many are specialized symbionts in a wide variety of benthic invertebrates including decapods. Several harpacticoids have been described as symbionts on decapods, primarily hermit crabs and semi-terrestrial grapsoids (see Huys, 2001; Boxshall & Halsey, 2004). Many copepods can be found on the surfaces and egg masses of decapods; some are likely just transiting over the "host" and are accidentally found in washings of the surface of the host. Hendrickx & Fiers (2010), however, indicated that at least 40 species of harpacticoid copepods belonging to eight families have some form of obligate relationship with their decapod hosts. In particular, species in Cancrincolidae have a highly specialized relationship with their semi-terrestrial crab hosts, requiring the moisture in their host's branchial chamber for survival and requiring host breeding migrations for dispersal (Humes, 1958; see Huys et al., 2009). Cancrincolids live within the branchial chambers of semi-terrestrial crabs in the families Grapsidae, Sesarmidae, Varunidae, and Gecarcinidae (Huys et al., 2009). They are a sister group to Ameiridae, harpacticoid commensals of crayfishes (Fiers, 1990), and there is some evidence that both families attempted incursions into low salinity habitats via their hosts (Huys et al., 2009). Their biology is difficult to study because the host must be sacrificed in order to find the symbionts; hence, little is known about their ecology and life history. They likely have more specializations with respect to their host-symbiont associations that are yet to be discovered. In *Cardisoma guanhumi*, for example, egg production of *Cancrincola jamaicensis* is synchronized with that of the host, and Wilson (1913) posited that hatching and larval development must all be accomplished while the crab is at sea as there were no eggs present in the oviducts of copepods on crabs returning from the sea. Members of this family are likely parasitic and have mouthparts adapted for attachment and sucking on the gill lamellae (Wilson, 1913), but it is not known whether they are **haematophagous** or are detritus feeders. Their gut contents could be examined with stable isotope analysis, as has been done for other parasitic copepods (Dean et al., 2011).

— *Rhizocephala.* – Rhizocephalans are highly specialized barnacles that parasitize other crustaceans. They have a complicated but direct life cycle that in most cases involves a short, free-living naupliar stage, an infectious **cyprid** larva, and internal forms that

define their systematics. They are sometimes termed **mesoparasites**, because they span the host's internal environment where the nutrient absorbing system of **rootlets** (**interna**) is found, and the external environment where the reproductive body (**externa**) is present. Rhizocephalans provide classic examples of **parasitic castrators**, causing severe impacts on host physiology, reproduction (including **feminization**), and behaviour through action of hormonal influence (Høeg et al., 2005). Although rhizocephalans cannot be externally observed in early infections, their presence can often be detected by gross modification of host secondary sexual characteristics. Miocene tumidocarcinids (ca. 5-23 Mya) are suspected as having been parasitized by rhizocephalans, based on feminized pleonal segments (Feldmann, 1998). Excellent reviews of the order were provided by Høeg & Lützen (1985), Høeg (1995), and Høeg et al. (2005).

Rhizocephala constitutes a **monophyletic group** and is most closely related to thoracican barnacles (Høeg, 1992; Billoud et al., 2000; Pérez-Losada et al., 2002; Glenner & Hebsgaard, 2006; Glenner et al., 2010). There is some debate about the **phylogeny** within Rhizocephala. Based on features of the cypris larva, Rhizocephala can be divided into two groups: Akentrogonida, with cyprids that directly inject female inoculum into the host, and Kentrogonida, with sexually dimorphic cyprids that metamorphose into a **kentrogon** stage and inject a **vermigon** into the host. Glenner et al. (2010), however, showed the akentrogonids formed a monophyletic grouping nested within a **paraphyletic grouping** of kentrogonids.

Rhizocephalans release free-swimming nauplius larvae that develop into cyprids (all akentrogonids and most kentrogonids) or hatch cyprids directly (a few kentrogonids) (Høeg, 1990, 1995; Walker et al., 1992; Glenner, 2001; Høeg et al., 2005; Glenner & Hebsgaard, 2006; Glenner et al., 2010). Cyprids move through the water column and settle on appropriate crustacean hosts to begin the parasitic phase of their life cycle (fig. 71-12.24). Female cyprids inject female inoculum into the host (**akentrogonids**) or metamorphose into a kentrogon stage that injects the vermigon (**kentrogonids**) (fig. 71-12.24D). The female grows, forming a branched nutrient-absorbing system termed the interna, which grows and ultimately produces the reproductive body (externa) that emerges from the abdomen of the host during moulting (fig. 71-12.24H, I). Male cyprids are attracted to the virgin externa and either a **trichogon** male stage invades and blocks the female receptacles with its shed cuticle (kentrogonids) or the trichogon stage is lacking and the developing mantle cavity is invaded by male generative cells (akentrogonids) (fig. 71-12.24L, M). After implantation of male cells in the ovary, the externa matures, producing eggs that are fertilized internally and develop in the mantle cavity (Høeg et al., 2005). These hatch and are released into the water as non-feeding nauplius or cyprid larvae, depending on the taxon. The cues for detection and settlement on hosts by rhizocephalans have been investigated and host specificity of some rhizocephalans has been experimentally tested (Boone et al., 2003, 2004; Pasternak et al., 2004a, b; Kuris et al., 2007). Most brachyuran kentrogonids produce a single externa from one interna, as in *Sacculina carcini*, although in some cases multiple infections in a single crab can give rise to multiple externae. Some kentrogonids and all akentrogonids in crabs undergo asexual reproduction and have multiple externae arising from a single interna, as in *Polyascus polygenea* and *Thompsonia japonica*.

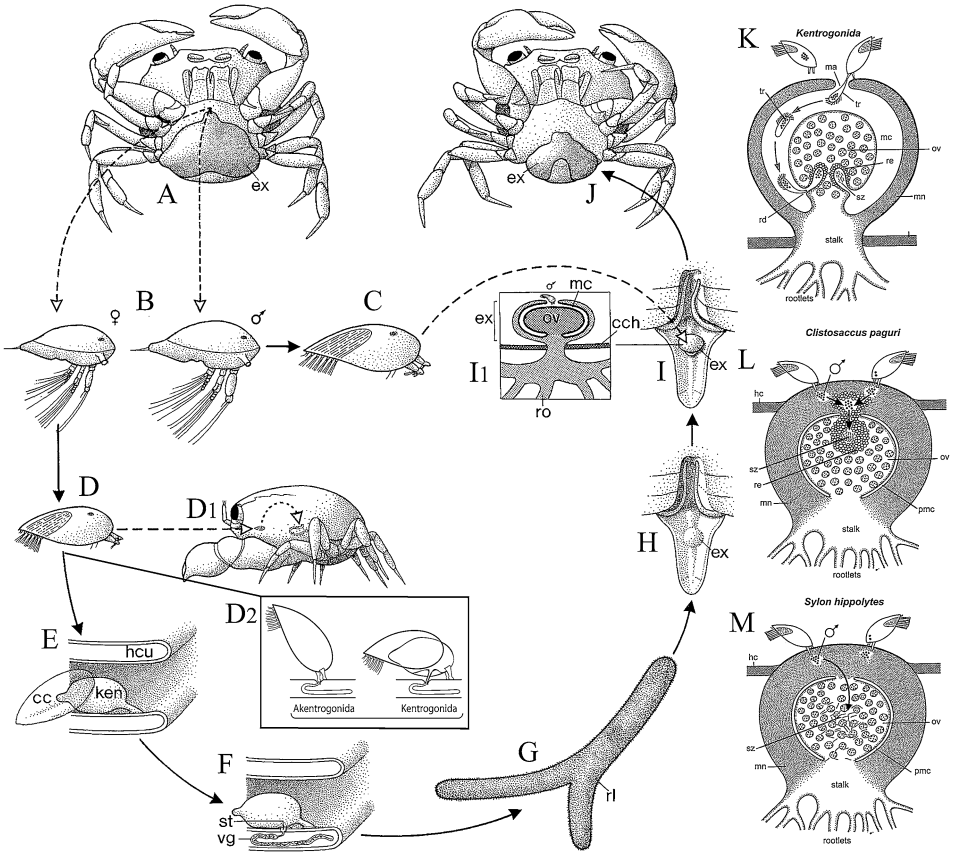

Fig. 71-12.24. Rhizocephalan life cycle: A-J, life cycle of the akentrogonid rhizocephalan *Loxothylacus panopaei* parasitizing the brachyuran *Rhithropanopeus harrisii*; A, externa (ex) underneath the abdomen; B, male and female nauplius larvae are released and develop into cyprids; C, male cyprids settle on the mantle of recently emerged virgin externa (I); D, female cyprids settle on host gill lamella (D_1); D_2, cyprids of Akentrogonida inject the parasitic material directly into the haemolymph of the host, using one of their antennules; in Kentrogonida, the kentrogon larva develops a stylet that penetrates the host and injects the vermigon into the haemolymph of the host; E, kentrogon (ken) has developed and has attached to host gill lamellae (hcu, cuticle of the gills; cc, carapace of the cyprid); F, stylet penetrates the gills and injects a vermigon into the host (st, stylet; vg, vermigon); G, vermigon grows into a rootlet (branching) system of the internal parasite; H, virgin externa (ex) begins to show through the integument of the host abdomen; I, externa has emerged on the host abdomen; further development requires settlement of male cyprids; I_1, vertical section through the externa as depicted in I (amc, mantle cavity; ov, ovary; cch, cuticle of the host; ro, rootlet); J, after settlement of males, the externa (ex) will mature and produce larvae; K, in Kentrogonida male cyprids settle at the open mantle aperture of the virgin externa, metamorphose into trichogons and implant into the two receptacles opening into the mantle cavity; L, in the akentrogonid *Clistosaccus paguri* (parasite of hermit crabs) the male cyprids settle on the surface of the externa, penetrate the integument with one of the antennules, and inject male cells that travel through the connective tissue of the mantle and into the receptacle, then initiate spermatogenesis; M, in the akentrogonid *Sylon hippolytes* (parasite of prawns), settlement and implantation of males

Of the 284 species of Rhizocephala, 190 infect brachyurans. Both Kentrogonida and Akentrogonida have representatives in crabs. Kentrogonida includes more species (244) than Akentrogonida (40), although it is likely that akentrogonid diversity is severely underestimated as most species have a highly derived sac-like morphology that hampers traditional morphological species recognition. Within the kentrogonids, Sacculinidae contains most of the known rhizocephalan species (184 of 284) with 129 of the species in the paraphyletic genus *Sacculina*. Species in *Sacculina* are almost universally referred to as exclusive parasites of brachyurans (Walker, 2001). As indicated by authors like Glenner et al. (2003) and Boyko & Williams (2009), however, the monophyly of *Sacculina* is in question, partly based on species described from non-brachyuran hosts: two species from anomurans (Albuneidae and Galatheidae) and one from a gebiidean shrimp (Upogebiidae). In the latter case, molecular analysis of externae from upogebiid hosts shows that the monophly of *Sacculina* is not supported (H. Glenner, pers. comm.).

Rhizocephalans in crabs show the highest diversity within the East Asian Sea (EAS, 77 species), followed by the northwestern Pacific Ocean (NWP, 36 species), and Caribbean Sea (CAR, 22 species) (fig. 71-12.25A) (ecoregions based on Kelleher et al., 1995). Patterns of diversity for kentrogonids and akentrogonids are similar, although no akentrogonids are known from brachyurans in the Caribbean. Regions appearing to lack rhizocephalans (or containing low numbers of these parasites) may be an artifact of limited sampling, as suitable hosts exist in all marine regions.

The majority of kentrogonids on brachyurans, 138 species of sacculinids, parasitize heterotreme crabs, most commonly in Majidae, Portunidae, and Xanthidae. Almost all those on thoracotreme hosts are in Grapsoidea (25 of 30 species). Only four species parasitize podotremes, in Dromiidae and Raninidae. Nine species of akentrogonids are known from brachyuran hosts, mostly in Portunoidea and Xanthoidea. Most rhizocephalans have been reported from shallow waters but specimens have been collected from as deep as 5200 m (Lützen, 1985).

Rhizocephalans can have a high prevalence in some host populations, such as 100% reported for *Sacculina carcini* in some populations of *Carcinus aestuarii* from Mediterranean lagoons (see Øksnebjerg, 2000). Prevalence often varies over short spatial and temporal scales, with sheltered sites having the highest abundance (Werner, 2001). Few commercial fisheries have high prevalence levels of rhizocephalans, but they have been reported from lithodid and portunid crab fisheries (Sloan, 1984; Hawkes et al., 1986; Hochberg et al., 1992; Walker et al., 1992; Shields & Wood, 1993; Alvarez & Calderon, 1996). Stunted hosts are too small for sale and are often culled back into the water, leaving them to accumulate in the fishing grounds (Meyers, 1990). Environmental factors such as

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is the same as in *Clistosaccus*, but a female receptacle is lacking and the male cells implant in the ovary where spermatogenesis occurs (Hc, host cuticle; ma, mantle aperture; mc, mantle cavity; mn, mantle; ov, ovary; pmc, primordial mantle cavity; tr, trichogon; rd, receptacle duct; re, receptacle; sz, spermatozoa). [A-J, After Glenner, 2001; D inset, after Glenner & Hebsgaard, 2006; J-L, after Glenner et al., 2010.]

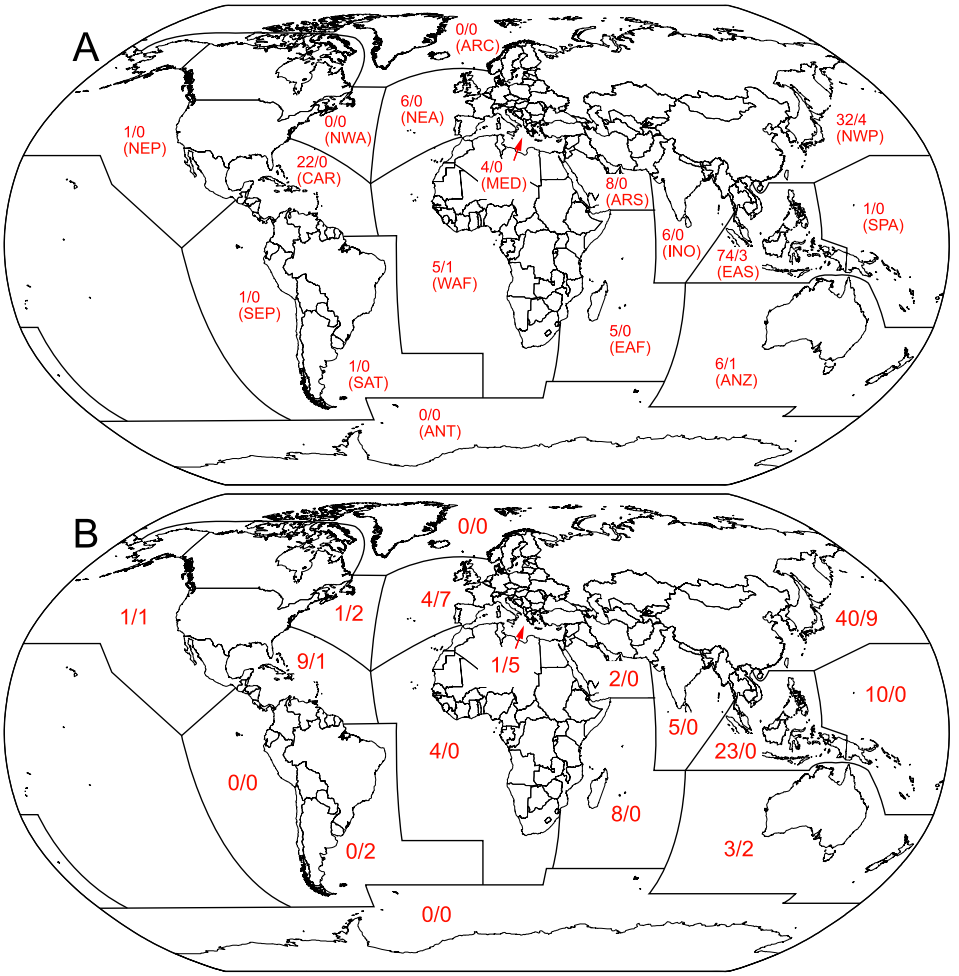

Fig. 71-12.25. Biogeographic distribution of parasitic isopods and parasitic barnacles associated with brachyuran hosts; numbers of species shown within marine ecoregions. A, Distribution of rhizocephalans (of Kentrogonida/ of Akentrogonida); B, distribution of bopyroids (of Bopyridae/ of Entoniscidae). Ecoregional abbreviations, shown in parentheses in part A (ANT, Antarctic; ANZ, Australia/New Zealand; ARC, Arctic; ARS, Arabian Sea; CAR, Wider Caribbean; EAF, East Africa; EAS, East Asian Sea; INO, Central Indian Ocean; MED, Mediterranean; NEA, North East Atlantic; NEP, North East Pacific; NWA, North West Atlantic; NWP, North West Pacific; SAT, South Atlantic; SEP, South East Pacific; SPA, South Pacific; WAF, West Africa). Only described parasite species included. Ecoregions based on Kelleher et al. (1995).

salinity, temperature, and water masses constrained by physiography are important modulators of prevalence (Sloan, 1984; Reisser & Forward, 1991; Walker & Lester, 1998; Boone et al., 2004; Costa et al., 2013). Host factors such as sex, size, moulting frequency, moult stage, and migratory behaviour also show correlations with prevalence (Veillet, 1945; Høeg, 1984; Lützen, 1984; Høeg & Lützen, 1995; Tindle et al., 2004; Costa et al., 2013).

Host **grooming behaviour** has been shown to be an important factor in *Lernaeodiscus porcellanae* parasitizing intertidal porcelain crabs (Ritchie & Høeg, 1981; Høeg & Ritchie, 1985, 1987). Hosts living in high energy environments have more damage to their grooming appendages, which in turn makes the crabs more susceptible to infection, whereas those in sheltered habitats have less damage and lower prevalence levels. This finding was tested experimentally (Sloan et al., 2010). In some host-parasite systems, low prevalence levels are overcome by long-lived parasites that can have extended reproduction over several years (Høeg, 1982).

Rhizocephalans can cause a remarkable range of physical and behavioural pathologies in their host crabs. In most cases, infected hosts show **castration**, **anecdysis** (in those infected by kentrogonids), stunting, and increased mortality. The internal rootlets can penetrate organs or surround nerves and organs and alter their function (Chassard-Bouchard & Hubert, 1976). Castration can occur through direct damage of the **sex-determining organ** (i.e., the **androgenic gland**) (Zerbib et al., 1975; Rubiliani & Payen, 1979), through interruption of hormones (Andrieux, 1974; Rubiliani, 1983, 1985), or through the metabolic cost of infection. Behavioural changes include increasing docility and male homosexual behaviours (Bishop & Cannon, 1979; Shields & Wood, 1993). Feminization of males can result from the destruction of the androgenic gland (Zerbib et al., 1975; Rubiliani & Payen, 1979), leading to morphological modifications to the body causing their secondary sexual characters to become more like those of females (Giard, 1886; Veillet, 1945; see Kristensen et al., 2012). Rhizocephalans can indirectly cause sterile matings, with loss of fecundity, and competition with phenotypically identical parasites (Shields & Wood, 1993). In spite of the significant influence on host physiology, *Sacculina carcini* was not found to alter consumption rates of *Carcinus maenas* on blue mussels and appeared to have minimal impacts on their feeding biology (Larsen et al., 2013).

Introduced crabs tend to lack rhizocephalan parasites that are normally found in their native ranges. For example, in its native range (Russia southward to Hong Kong and Japan) *Hemigrapsus sanguineus* is parasitized by *Polyascus polygenea*, where the parasite can reach prevalence levels of over 80% and behaviourally manipulates its hosts (Takahashi et al., 1997; Takahashi & Lützen, 1998; Korn et al., 2005). *Hemigrapsus sanguineus* has not been documented with rhizocephalans in its introduced ranges along the east coast of the U.S.A. and Europe (McDermott, 2007, 2011; Blakeslee et al., 2009). Similary, *Carcinus maenas* is parasitized by *Sacculina carcini* in its European native range and can reach prevalence levels of over 75%, but this host has not been found with rhizocephalans in its introduced populations in North America, Africa, or Australia (Torchin et al., 2001; Blakeslee et al., 2009; Zetlmeisl et al., 2011). Rapid spread of both crab species could be due in part to ecological release from parasitism experienced by these hosts (Torchin et al., 2001, 2003).

There are, however, cases of rhizocephalans being accidentally introduced along with their brachyuran hosts. For example, *Heterosaccus dollfusi* was not found in the Mediterranean until three decades after its only host, *Charybdis longicollis* (Portunidae), was recorded as introduced. This rhizocephalan has not been shown to reduce populations

of this crab in the Mediterranean (Galil & Innocenti, 1999; Innocenti & Galil, 2007). There is a single record of a rhizocephalan occuring in an introduced population of *Callinectes sapidus* in Greece; however, the identity of this parasite is in question (Øksnebjerg, 2000). It could either be *Loxothylacus texanus*, the parasite of *Callinectes sapidus* in its native range, or an example of host switching of a rhizocephalan from another Mediterranean brachyuran. *Loxothylacus panopaei* is a parasite of at least nine species of panopeid crabs and was introduced to the Chesapeake Bay from the Gulf of Mexico (see Kruse & Hare, 2007) and has since spread to as far north as Long Island, New York state (Freeman et al., 2013). *Loxothylacus panopaei* has been documented to impact host populations (Alvarez et al., 1995). Although these findings suggest that rhizocephalans could be used in combating invasive hosts, their potential as biocontrol agents requires detailed studies on host specificity of the parasites (Murphy & Goggin, 2000; Goddard et al., 2005; Kuris et al., 2005, 2007).

— *Thoracica.* – Brachyurans are often infested with commensal barnacles, ranging from facultative commensals such as the balanomorph *Chelonibia patula* to obligate symbionts such as the gooseneck barnacles *Octolasmis* spp. (Pearse, 1952). Species of *Octolasmis* cement themselves to the gills, gill lamellae, and gill cleaners of various crabs and lobsters. They are often host generalists using the crab or lobster host as a substrate (Young, 1991; Jeffries & Voris, 1996). One species, *Octolasmis hoeki*, is a highly calcified species, and can occur outside the gill chamber. Infestations of *Octolasmis lowei* on *Callinectes sapidus* and other decapods have been well studied (see Gannon, 1990; Key et al., 1997; Jeffries & Voris, 2004). Individuals can possess several hundred barnacles in their gills and, in heavy infestations, *Octolasmis lowei* can become pathogenic to a crab. Gannon & Wheatly (1992, 1995) examined the physiological responses to the barnacle at different intensities and found that infested crabs had elevated heart and ventilation rates. Crabs with extremely heavy infestations were sluggish (Overstreet, 1978). Species of *Octolasmis* can reinfest crabs quickly after ecdysis. Shields (1992) found individuals of *Octolasmis* spp. on postmoult *Portunus pelagicus* at the same prevalence of infestation as on concurrent intermoult crabs, but with lower intensities of infection. A pulsed mode of colonization has been described for *Octolasmis cor* on newly moulted specimens of *Scylla serrata* (see Jeffries et al., 1989), and a trickle mode of colonization for *Octolasmis lowei* on *Callinectes sapidus* (see Voris & Jeffries, 2001).

— *Amphipoda.* – There are surprisingly few records of amphipods associated as ectosymbionts of decapods, and even fewer on brachyurans. Ischyroceridae has two species associated with crabs and both appear to be host generalists, or perhaps simply facultative visitors to the egg masses of their hosts. *Jassa kjetilanna* occurs cryptically on the body of the spider crab *Eurypodius latreillii* (Inachidae), and an unidentified spider crab from near the Falkland Islands (Vader & Krapp, 2005). *Ischyrocerus commensalis* occurs within the egg masses of several decapods from the eastern Pacific. It has been observed in the egg masses of *Romaleon antennarium* (Cancridae), *Chionoecetes opilio*, and *Hyas araneus* off Newfoundland (Steele et al., 1986). The amphipods can be voracious egg predators in artificial laboratory settings, and they are often found on the external margins

of the egg masses of their ovigerous hosts and show clear signs of eating eggs (Kuris et al., 1991). Dvoretsky & Dvoretsky (2010), however, found no evidence that *Ischyrocerus commensalis* was an egg predator of red king crabs based on fieldwork. Commensal or egg-predatory amphipods are likely more common on decapods, but they can leave their host upon capture or can only occur on them when they are ovigerous, making them more difficult to find.

— *Isopoda.* – Epicaridean isopods are obligate endo- and ectoparasites of other crustaceans and comprise almost 8% of the described isopods (updated from Williams & Boyko, 2012). They share a long **evolutionary history** with brachyurans, dating back to at least the Late Jurassic (163.5-157.3 Mya), as evidenced by characteristic swellings of the gill chambers (Klompmaker et al., 2014). Two superfamilies, Bopyroidea (3 families) and Cryptoniscoidea (10 families), have species that use crustaceans as intermediate or definitive hosts, but only Bopyridae, Entoniscidae, and one species of Cryptoniscidae use decapods as definitive hosts (Trilles, 1999; Martin & Davis, 2001; Williams & Boyko, 2012; Boyko et al., 2013). They have distinctive mouthparts that are modified as a **suctorial cone** for feeding on haemolymph of their hosts. Epicarideans have three larval stages (**epicaridium**, **microniscus**, **cryptoniscus**) and a two-host life cycle (fig. 71-12.26). Epicaridium larvae hatch from eggs within the marsupium of the female isopod and are released into the water column where they externally infest copepod intermediate hosts. The larvae metamorphose into microniscus larvae on the copepod host and feed on the haemolymph. The microniscus then leaves the copepod and becomes a cryptoniscus larva that infests a definitive host and transforms into a juvenile (**bopyridium**). The juvenile matures in its final location on the definitive host, usually in the branchial chamber. The first isopod to settle on a host will mature into a female, with any subsequent isopods settling on the same host becoming dwarf males. Bopyrids found in the branchial chambers of brachyurans often cause the chamber to become inflated as they and their hosts moult to grow. Unlike rhizocephalans, epicarideans rarely inhibit moulting in their hosts, albeit the frequency of moulting can be reduced (Van Wyk, 1982; O'Brien & Van Wyk, 1985). The conspicuous swellings caused by bopyrids make parasitized crabs relatively easy to distinguish.

Entonisicidae is a small family comprising 37 species that are unusual internal parasites of decapods. The majority of entoniscid species (28 of 37) have been described from brachyurans. Entoniscids have highest diversity in the northwestern Pacific (NWP, 10 species on all hosts, 9 of which are brachyurans) and northeastern Atlantic (NEA, 8 species on all hosts, 7 of which are brachyurans) (fig. 71-12.25B; Williams & Boyko, 2012). They are most commonly found in portunids and xanthids. Female entoniscids are highly modified endoparasites, often with the appearance of a tumor or worm-like body, and may not be recognizable as isopods by the casual observer (Williams & Boyko, 2012). Dwarf males, however, retain the isopod *Bauplan* and the cryptoniscus larvae are typical of epicarideans; males and larvae often co-occur within the marsupium of a female. Entoniscids grow without moulting although their hosts often continue to moult (Chaix & Veillet, 1981). Female entoniscids develop an **exit pore** through the exoskeleton of their hosts for larval release into the external environment.

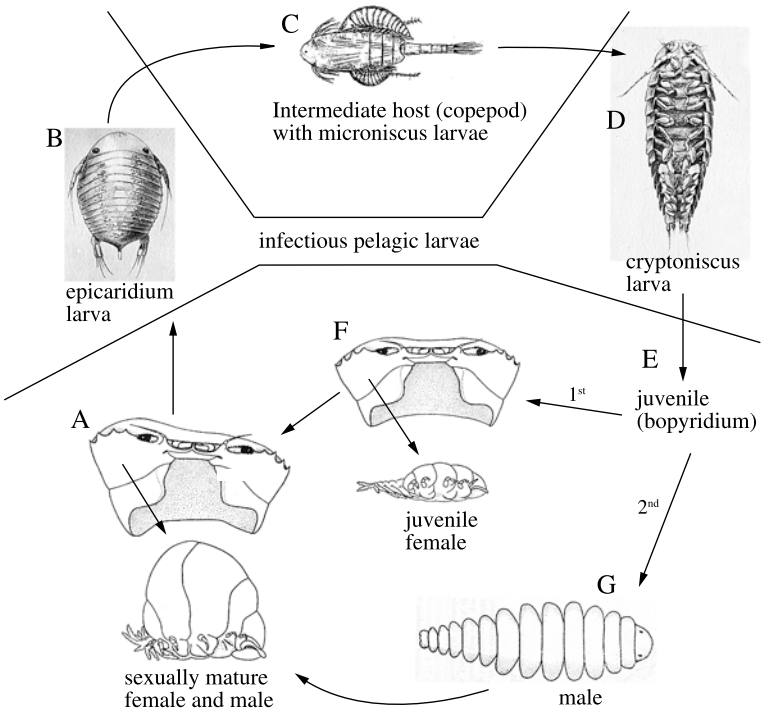

Fig. 71-12.26. Bopyrid life cycle: *Cancricepon elegans* parasitizing the host crab *Pilumnus* sp. A, Sexually mature female from the gill chamber of the definitive host, bump in host carapace evident; after fertilization by a male isopod, the female releases epicaridium larvae; B, epicaridium larvae move through the water column and parasitize calanoid copepods as intermediate hosts; C, copepod intermediate host with two microniscus larvae; the microniscus larva will metamorphose into a cryptoniscus larva; D, cryptoniscus larva settles onto a definitive host and transforms into a juvenile bopyrid; E, first juvenile isopod (bopyridium) to parasitize a host becomes female; F, juvenile female; G, subsequent isopods become male(s) and live on the female. [A, F, After Bourdon, 1968; B, D, after Bonnier, 1900; C, after Sars, 1899.]

Cryptoniscoidea contains 157 species in 10 families, but only *Danalia hapalocarcini* is a direct parasite of a brachyuran. This species pierces the cuticle of the dorsal carapace of the coral gall crab *Hapalocarcinus marsupialis* (Cryptochiridae). Nine other cryptoniscoid species, most in *Danalia*, are hyperparasitic on rhizocephalans infesting brachyurans. They can be difficult to identify as they resemble small rhizocephalans protruding from their hosts.

Bopyridae contains most (74%) of the known epicaridean species (595 of 799). Most species of bopyrids are parasitic in shrimps and anomurans; however, taxa in the subfamilies Pseudioninae (232 species) and Keponinae (94 species) parasitize brachyurans as well as axiioid and gebiidean shrimps and palinuran lobsters. Most Keponinae (81 of the 94 species) pararasitize brachyurans, whereas only 14 species of Pseudioninae do so, with most (13 of 14) being species of *Gigantione*. Bopyrids show their highest diversity in the northwestern Pacific (NWP, 123 species), East Asian Sea (EAS, 116 species),

Caribbean (CAR, 79 species), and Central Indian Ocean (INO, 44 species); those parasitizing brachyurans show highest diversity in the NWP (40 species), EAS (23 species), South Pacific (SPA, 10 species), and CAR (9 species) (fig. 71-12.25). Most bopyrids of brachyurans parasitize heterotreme crabs (most commonly Leucosiidae, Majidae, Portunidae, and Xanthidae). Those on thoracotreme hosts are mostly in Sesarmidae and Pinnotheridae. Only six species parasitize podotreme hosts, mostly in Dromiidae. Regions appearing to lack epicarideans (or containing low numbers of these parasites) may be an artifact of limited sampling. Most epicarideans are restricted to fairly shallow water; the deepest record from a brachyuran appears to be 500-750 m for a bopyrid on *Chaceon quinquedens* off the Republic of Congo (Bourdon, 1971).

Prevalence of bopyrids generally ranges from less than 1% to approximately 25% of hosts infested (Cericola & Williams, 2015). In brachyuran hosts prevalence levels are similar; for example, approximately 9-30% of *Pachygrapsus transversus* (Grapsidae) from Bermuda are infested with *Leidya bimini* (see McDermott, 1991) and approximately 9-14% of *Pilumnus hirtellus* (Pilumnidae) with *Cancricepon elegans* on the Atlantic coast of France (Bourdon, 1968). These parasites are capable of producing large broods of over 8000 and 21 000 epicaridium larvae for *Leidya bimini* and *Cancricepon elegans*, respectively (Bourdon, 1968; McDermott, 1991). Bilateral infestation of both branchial chambers is known for a number of bopyrid species, including *Cancricepon elegans*, where it can be quite common at up to approximately 19% (Bourdon, 1968). Although simultaneous infestations of branchial and abdominal bopyrids are known in shrimp and anomuran hosts (Trilles, 1999), this has not been documented for any brachyuran. However, **dual infestations** of bopyrids and entoniscids, as well as rhizocephalans and entoniscids, are known to occur in brachyurans (Veillet, 1945; Bourdon, 1968). Bopyrids are often parasitic castrators of hosts, apparently through energy drain (Bourdon, 1968). Some bopyrids cause reduced reproduction by females but may not interfere with male reproductive ability (Van Wyk, 1982; O'Brien & Van Wyk, 1985).

Of the best-studied invasive brachyurans (*Carcinus maenas*, *Callinectes sapidus*, *Eriocheir sinensis*, *Hemigrapsus sanguineus*, *Rhithropanopeus harrisii*) only two (*Carcinus maenas* and *Rhithropanopeus harrisii*) are parasitized by epicarideans (the entoniscid *Portunion maenadis* and the bopyrid *Cancricepon choprae*, respectively) in their native ranges (Markham, 1975; Torchin et al., 2001); neither of these parasites have been reported to occur in introduced populations.

Chelicerata: Acarina. – Few mites are found as marine parasites, but several taxa use crustaceans or their burrows as habitats. Host-parasite associations are quite diverse, spanning the gamut from phoretic to parasitic. Mites show a remarkable diversity in aquatic habitats with records from a number of crustaceans (Bartsch, 1989). In a study of the mite fauna on introduced *Eriocheir sinensis* in Poland and Germany, Normant et al. (2013) listed 22 species of halicarid and oribatid mites reported from decapods. The seven species of mites found on *Eriocheir sinensis* were considered facultative commensals, albeit at least three species had males, females, larvae, and nymphs present, indicative of reproduction on the host. At least two freshwater mites, *Gecarcinolaelaps*

cancer and *Rhizoglyphus* sp., occur on the gills of the terrestrial crab *Gecarcinus lateralis* (Gecarcinidae) from the Caribbean (Pearse, 1929; Bright & Hogue, 1972; Casanueva & Johnston, 1995), but their relationships with the host have not been well established. Several brackish water and marine mites have been reported from marine brachyurans, including records from *Peltarion spinulosum* (Atelecyclidae), *Libinia* spp., *Menippe nodifrons* (Menippidae), and *Maja squinado*, but their relationships with these hosts remain unknown (see Normant et al., 2013).

Insecta: Diptera. – The relationships between flies and brachyurans highlights the disparate symbioses that occur at the interface between terrestrial and aquatic environments. Some relationships are not truly symbiotic as in the case of several dozen species of mosquitoes, including species of *Aedes*, *Anopheles*, and *Culex*, that use crab burrows as incidental sites for development (see Bright & Hogue, 1972). Species of *Deinocerites*, 18 species with a neotropical distribution, however, are only found in association with burrows made by species of crabs in Gecarcinidae, Ocypodidae, and Pseudthelphusidae (see Adames, 1971). Some species of *Deinocerites* have affinities for different burrow sizes generated by different species of crabs. The larvae of *Deinocerites* have a well-developed subantennal pouch with expansion of the basal and apical lobes of the mandible that is suggestive of a specialized relationship with the crab burrow, but the nature of this relationship is unknown (Belkin & Hogue, 1959; Adames, 1971).

Blackflies in the *Simulium neavei*-complex exhibit an obligate relationship with freshwater crabs (Lewis et al., 1960; Williams, 1968, 1991; Crosskey, 1990). Blackfly larvae inhabit fast-flowing streams with adjacent dense forest canopies and use the carapace of the crab host as a site of attachment. The larvae are thought to derive protection from predation, improve their orientation in the fast-moving current, and minimize damage from exposure while on the crab (Corbet, 1961). Flies in the *Simulium neavei*-complex only associate with crabs (Raybould et al., 1978). Phoretic hosts include the potamonautids *Potamonautes loveni* from highland streams of Kenya (Crosskey, 1990; Williams, 1991), *Potamonautes aloysiisabaudiae* and *Potamonautes niloticus* from Uganda (Crosskey, 1990; Garms et al., 2009), and *Sudanonautes africanus* in Cameroon (Disney, 1971). The distribution and abundance of fly larvae and pupae can vary with host size, with intermediate-size crabs possessing the most fly larvae (Disney, 1971). In areas where species in the *Simulium neavei*-complex are vectors of **river blindness**, freshwater crabs are monitored for the presence or absence of fly larvae to evaluate the effectiveness of insecticide-based control efforts (Katabarwa et al., 2014).

Three phylogenetically distinct species of *Drosophila* have distinct obligate commensal relationships with land crabs (Carson, 1974). *Drosophila carcinophila* lives on the mouthparts and around the opening of the antennal gland (**renal pore**) of *Gecarcinus ruricola* (Gecarcinidae) from the Caribbean (Wheeler, 1960; Carson, 1967). *Drosophila endobranchia* lives on *Gecarcinus ruricola* and *Gecarcinus lateralis* from Cuba and the Cayman Islands (Carson & Wheeler, 1968). *Lissocephala powelli* is a drosophilid found on *Gecarcoidea lalandii* (Gecarcinidae), *Cardisoma carnifex* (Gecarcinidae), *Geograpsus crinipes* (Grapsidae), as well as the anomuran *Birgus latro* from Christmas Island in the

Indian Ocean (Carson & Wheeler, 1973). Eggs can be found on the crab hosts while the larvae and adults apparently feed on the microflora on the surface of their host (Stensmyer et al., 2008). Carson (1974) discussed the remarkable **evolution** and **adaptations** of these unusual fruit flies. Both *Drosophila carcinophila* and *Drosophila endobranchia* were initially considered as derived from different **ancestors**, and were used as examples of **parallel evolution** within the genus; however, they are now known to be from the same subgenus of *Drosophila* based on molecular evidence (Stensmyr et al., 2008). It remains remarkable that three distinct species from two genera separated by enormous geographical distances evolved such similar relationships with their land crab hosts.

FOULING COMMUNITIES OF CRABS

Brachyurans can host a diverse **fouling community** comprised of members from many different phyla. The **epibiont communities** found on many species of brachyurans have been catalogued (Abelló et al., 1990; Gili et al., 1993; McGaw, 2006; McDermott, 2007; Savoie et al., 2007; also see Chapter 71-11 in this volume). Bacterial, algal, protistan, and metazoan phyla have all been identified as members of the fouling community. Many **fouling organisms** (oysters, mussels, barnacles, corals) are incidental or have a weak phoretic relationship with the crab host, but a few such as the bryozoan *Triticella elongata*, have obligate relationships (Key et al., 1999). Crabs offer a hard substrate for settlement, and their carapace offers a biologically active surface; therefore, crabs can represent a significant component of the hard surface available for colonization in mud and sand habitats. Studies of the fouling community have examined basic biological and ecological questions such as the host moulting (as ephemeral habitats), longevity, community succession, migration, and differences in the spatial patterns between host sexes. Issues such as the presence or absence of a terminal moult for *Callinectes ornatus* and *Callinectes danae* (Portunidae) have been addressed through the study of the fouling community (Negreiros-Fransozo et al., 1995) as well as moult stage for *Chionoecetes opilio* (see Benhalima et al., 1998a). Fouling organisms generally have little effect on their host. Crabs that are heavily fouled by barnacles such as *Octolasmis* spp., however, can experience increased weight, drag, and impaired swimming ability, and thus have greater metabolic demands (Gannon & Wheatley, 1992, 1995). Crab species with terminal moults or those infected with kentrogonid rhizocephalans, which result in host anecdysis, are often more heavily fouled (Overstreet, 1978; Shields, 1992). Abelló et al. (1990), Becker & Wahl (1996), Key et al. (1996, 1997, 1999), Shields & Overstreet (2007), and Savoie et al. (2007) have reviewed aspects of the fouling communities on various crab hosts. Becker & Wahl (1996) provide evidence that crabs have evolved **behavioural defences** (burying, exposure to air) that reduce epibiont loads. In contrast, some brachyurans have behavioural and morphological modifications to encourage fouling. In particular, decorator crabs (Majoidea) actively select a variety of different organisms as **camouflage** to escape detection of predators (Wicksten, 1980; Stachowicz & Hay, 2000; see Chapter 71-11 in this volume).

SIGNIFICANCE OF PARASITISM AND DISEASES OF BRACHYURANS AND DIRECTIONS FOR FUTURE RESEARCH

The sheer diversity seen in the phyla covered herein highlights the myriad associations possible between parasites, symbionts, and pathogens with their brachyuran hosts. These symbionts are an integral part of **crab populations**. Through their interactions with their hosts, pathogens and parasites affect crab fecundity, growth rates, and mortality. In turn, host factors such as moulting, maturation, migration, and behaviour affect the growth, survival, and dispersion of their parasites. Crab hosts can be especially vulnerable to infection during ecdysis, oviposition, and dormancy, when they are incapable of moving away or have weakened defences. Likewise, their parasites have remarkable adaptations for transmission during susceptible host states. Adaptations range from simply migrating onto the new instar (nemerteans, leeches, some bopyrids) to those that have synchronized reproduction such that transmissive stages readily find a new host (peritrich and apostome ciliates), and to those parasites that interfere with hormonal control of ecdysis to enable their own survival and reproduction (rhizocephalans).

The study of these host-parasite associations can provide insights into the biology and ecology of the brachyuran hosts. For example, bacterial shell disease is associated with poor water quality and pollution; barnacles show relationships with host moulting, longevity, and migration patterns; leeches and branchiobdellid annelids can indicate host origin and **water quality** conditions; and parasites that use crabs as intermediate hosts (trematodes, cestodes, nematodes, and acanthocephalans) indicate transmission pathways, trophic structure, and connectivity within the **ecosystem**. We can also speculate on the differences in **parasite fauna** between marine and freshwater crabs. In comparing this fauna, we can see that very different **niches** on and within these hosts have been exploited in disparate ways. Such diverse niches are suggestive of very different **selection pathways** leading to the establishment of such specialized associations. We speculate that the extensive **catadromous migrations** of the host, or host **colonization** of freshwater habitats, could have resulted in part from **selection pressures** induced by the myriad fouling organisms and pathogenic parasitic diseases in marine systems. Perhaps the migration into freshwater systems was a means to reduce **disease pressure**. New associations were thus formed in crabs migrating into freshwater ecosystems. Why these patterns have evolved is intriguing. Addressing such **evolutionary questions** on **host-symbiont relationships** will enhance our understanding of how such intimate associations develop in invertebrate hosts. Although until recently largely overlooked by ecologists, parasites have critical roles in influencing food webs and are thus in need of expanded study, including those impacting crab hosts. Greater understanding of host-parasite associations involving crabs also has important ecological, medical, and **food safety** implications, particularly with the expanding emphasis on the culture and harvest of crabs and other crustaceans as food (Stentiford et al., 2012).

ACKNOWLEDGMENTS

This is Contribution #3429 from the Virginia Institute of Marine Science. This work was partly funded by NSF OCE 0723662 to J. D. Shields. We thank J. F. Morado for kindly giving the TEM archives of P. T. Johnson to J. D. Shields.

APPENDIX

Taxa at species level mentioned in this chapter with authorities and year of description. Binomina of Bacteria are not included in this list: providing authorities and dates for those is considered outside the scope of the current series focused on Crustacea

ARTHROPODA

CHELICERATA

Gecarcinolaelaps cancer (Pearse, 1929)
Limulus polyphemus (Linnaeus, 1758)
Nymphon stroemi Krøyer, 1844

CRUSTACEA

Amphipoda

Ischyrocerus commensalis Chevreux, 1900
Jassa kjetilanna Vader & Krapp, 2005

Anomura

Birgus latro (Linnaeus, 1767)
Paralithodes camtschaticus (Tilesius, 1815)

Astacidea

Cherax tenuimanus (Smith, 1912)
Homarus americanus H. Milne Edwards, 1837
Nephrops norvegicus (Linnaeus, 1758)

Brachyura

Achelous spinimanus (Latreille, 1819)
Aratus pisonii (H. Milne Edwards, 1837)
Armases cinereum (Bosc, 1802)
Austrohelice crassa (Dana, 1851)

Brachynotus spinosus (H. Milne Edwards, 1853)

Callinectes arcuatus Ordway, 1863
Callinectes bocourti A. Milne-Edwards, 1879
Callinectes danae Smith, 1869
Callinectes ornatus Ordway, 1863
Callinectes rathbunae Contreras, 1930
Callinectes sapidus Rathbun, 1896
Callinectes similis Williams, 1966
Callinectes toxotes Ordway, 1863
Cancer borealis Stimpson, 1859
Cancer irroratus Say, 1817
Cancer pagurus Linnaeus, 1758
Cancer plebejus Poeppig, 1836
Cancer productus Randall, 1840
Carcinus aestuarii Nardo, 1847

Carcinus maenas (Linnaeus, 1758)
Cardisoma carnifex (Herbst, 1796)
Cardisoma guanhumi Latreille, 1828
Ceylonthelphusa rugosa (Kingsley, 1880)
Chaceon quinquedens (Smith, 1879)
Charybdis japonica (A. Milne-Edwards, 1861)
Charybdis longicollis Leene, 1938
Chionoecetes bairdi Rathbun, 1924
Chionoecetes opilio (Fabricius, 1788)
Chionoecetes tanneri Rathbun, 1893
Chiromantes haematocheir (De Haan, 1833)
Cyanagraea praedator Saint Laurent, 1984
Cyclograpsus granulosus H. Milne Edwards, 1853
Cyrtograpsus angulatus Dana, 1851

Erimacrus isenbeckii (Brandt, 1848)
Eriocheir japonica (De Haan, 1835)
Eriocheir sinensis H. Milne Edwards, 1853
Eurypodius latreillii Guérin, 1825

Gecarcinus lateralis (Guérin, 1832)
Gecarcinus ruricola (Linnaeus, 1758)
Gecarcoidea lalandii H. Milne Edwards, 1837
Geograpsus crinipes (Dana, 1851)
Geothelphusa miyazakii (Miyake & Chiu, 1965)

Halicarcinus varius Dana, 1851
Hapalocarcinus marsupialis Stimpson, 1859
Hemigrapsus crenulatus (H. Milne Edwards, 1837)
Hemigrapsus nudus (Dana, 1851)
Hemigrapsus oregonensis (Dana, 1851)
Hemigrapsus penicillatus (De Haan, 1835)
Hemigrapsus sanguineus (De Haan, 1835)
Hemigrapsus sexdentatus (H. Milne Edwards, 1837)
Hyas araneus (Linnaeus, 1758)
Hyas coarctatus Leach, 1816
Hypolobocera aequatorialis (Ortmann, 1897)

Indochinamon lipkei (Ng & Naiyanetr, 1993)
Indochinamon tannanti (Rathbun, 1904)

Larnaudia larnaudii (A. Milne-Edwards, 1869)
Liberonautes latidactylus (De Man, 1903)
Libinia emarginata Leach, 1815
Libinia spinosa H. Milne Edwards, 1834
Liocarcinus corrugatus (Pennant, 1777)
Liocarcinus depurator (Linnaeus, 1758)

Macrophthalmus abbreviatus Manning & Holthuis, 1981
Macrophthalmus hirtipes (Jacquinot, in Hombron & Jacquinot, 1846)
Macrophthalmus japonicus (De Haan, 1835)
Macropipus depurator (Linnaeus, 1758)
Macropipus tuberculatus (Roux, 1830)

Macropodia tenuirostris (Leach, 1814)
Maja brachydactyla Balss, 1922
Maja squinado (Herbst, 1788)
Maydelliathelphusa lugubris (Wood-Mason, 1871)
Menippe mercenaria (Say, 1818)
Menippe nodifrons Stimpson, 1859
Metacarcinus anthonyi (Rathbun, 1897)
Metacarcinus magister (Dana, 1852)

Nanosesarma minutum (De Man, 1887)
Necora puber (Linnaeus, 1767)
Nectocarcinus integrifrons (Latreille, 1825)
Neohelice granulata (Dana, 1851)
Nepinnotheres pinnotheres (Linnaeus, 1758)

Ocypode platytarsis H. Milne Edwards, 1852
Ovalipes catharus (White, in White & Doubleday, 1843)
Ovalipes ocellatus (Herbst, 1799)
Oziotelphusa ceylonensis (Fernando, 1960)

Pachygrapsus transversus (Gibbes, 1850)
Panopeus herbstii H. Milne Edwards, 1834
Paragrapsus gaimardii (H. Milne Edwards, 1837)
Paragrapsus laevis (Dana, 1851)
Paragrapsus quadridentatus (H. Milne Edwards, 1837)
Peltarion spinulosum (White, 1843)
Pilumnus hirtellus (Linnaeus, 1761)
Pinnixa chaetopterana Stimpson, 1860
Pinnotheres pisum (Linnaeus, 1767)
Portunus pelagicus (Linnaeus, 1758)
Portunus trituberculatus (Miers, 1876)
Potamonautes aloysiisabaudiae (Nobili, 1906)
Potamonautes loveni (Colosi, 1924)
Potamonautes niloticus (H. Milne Edwards, 1837)
Potamonautes perlatus (H. Milne Edwards, 1837)
Potamonautes warreni (Calman, 1918)
Pugettia gracilis Dana, 1851
Pugettia producta (Randall, 1840)

Rhithropanopeus harrisii (Gould, 1841)
Romaleon antennarium (Stimpson, 1856)

Scylla paramamosain Estampador, 1949
Scylla serrata (Forskål, 1775)
Sesarma reticulatum (Say, 1817)
Stoliczia rafflesi (Roux, 1936)
Sudanonautes africanus (A. Milne-Edwards, 1869)

Uca burgersi Holthuis, 1967
Uca longisignalis Salmon & Atsaides, 1968
Uca minax (LeConte, 1855)
Uca pugilator (Bosc, 1802)
Uca pugnax (Smith, 1870)

Uca rapax (Smith, 1870)
Uca spinicarpus Rathbun, 1900
Uca uruguayensis Nobili, 1901
Ucides cordatus (Linnaeus, 1763)

Vietopotamon aluoiense Dang & Hô, 2002
Villopotamon thaii Dang & Hô, 2003

Cirripedia
Chelonibia patula (Ranzani, 1818)
Clistosaccus paguri Lilljeborg, 1860
Heterosaccus dollfusi Boschma, 1960
Lernaeodiscus porcellanae Müller, 1862
Loxothylacus panopaei (Gissler, 1884)
Loxothylacus texanus Boschma, 1933
Octolasmis cor (Aurivillius, 1892)
Octolasmis hoeki (Stebbing, 1894)
Octolasmis lowei (Darwin, 1852)
Polyascus polygenea (Lützen & Takahashi, 1997)
Sacculina carcini Thompson, 1836
Sylon hippolytes Sars, 1870
Thompsonia japonica Häfele, 1911

Copepoda
Cancrincola jamaicensis Wilson, 1913
Choniomyzon libiniae Santos & Björnberg, 2004
Choniosphaera cancrorum Connolly, 1929
Choniosphaera indica Gnanamuthu, 1954
Choniosphaera maenadis (Bloch & Gallien, 1933)

Dendrobranchiata
Fenneropenaeus merguiensis (De Man, 1888)
Penaeus monodon Fabricius, 1798

Isopoda
Cancricepon choprae (Nierstrasz & Brender-à-Brandis, 1925)
Cancricepon elegans Giard & Bonnier, 1887
Danalia hapalocarcini Fize, 1955
Leidya bimini Pearse, 1951
Portunion conformis Muscatine, 1956
Portunion maenadis (Giard, 1886)

INSECTA
Drosophila carcinophila Wheeler, 1960
Drosophila endobranchia Carson & Wheeler, 1968
Lissocephala powelli Carson & Wheeler, 1973
Simulium neavei Roubaud, 1915

NON-ARTHROPODA
ACANTHOCEPHALA
Arhythmorhynchus frassoni (Molin, 1858)
Hexaglandula corynosoma (Travassos, 1915)
Profilicollis altmani (Perry, 1942)

Profilicollis antarcticus Zdzitowiecki, 1985
Profilicollis botulus (Van Cleave, 1916)
Profilicollis chasmagnathi (Holcman-Spector, Mañé-Garzón & Dei-Cas, 1977)
Profilicollis major (Lundstrom, 1942)
Profilicollis novaezelandensis Brockerhoff & Smales, 2002
Profilicollis sphaerocephalus (Bremser, in Rudolphi, 1819)

ANNELIDA
Bathybdella sawyeri (Burreson, 1981)
Cambarincola mesochoreus Hoffman, 1963
Cambarincola pamelae Holt, 1984
Cambarincola vitreus Ellis, 1919
Cystobranchus vividus Verrill, 1872
Iphitime cuenoti Fauvel, 1914
Johanssonia arctica (Johansson, 1898)
Marsupiobdella africana Goddard & Malan, 1912
Myzobdella lugubris (Leidy, 1851)
Myzobdella platensis (Cordero, 1933)
Notostomum cyclostomum (Johansson, 1898)
Paraclepsis vulnifera Harding, 1924
Platybdella olriki (Malm, 1865)

APICOMPLEXA
Aggregata eberthi (Labbé, 1895)
Cephaloidophora rhithropanopei Belofastova, 1996
Nematopsis ostrearum Prytherch, 1938
Thiriotia pugettiae Rueckert, Simdyanov, Aleoshin & Leander, 2011

BRYOZOA
Triticella elongata (Osburn, 1912)

CERCOZOA
Haplosporidium cadomensis Marchand & Sprague, 1979
Haplosporidium littoralis Stentiford, Bateman, Stokes & Carnegie, 2013
Haplosporidium louisiana (Sprague, 1963)
Mikrocytos mackini Farley, Wolf & Elston, 1988
Paramarteilia canceri Feist, Hine, Bateman, Stentiford & Longshaw, 2009
Paramikrocytos canceri Hartikainen, Stentiford, Bateman, Berney, Feist, Longshaw, Okamura, Stone, Ward, Wood & Bass, 2014
Urosporidium crescens De Turk, 1940

CILIOPHORA
Mesanophrys carcini (Grolière & Leglise, 1977)
Mesanophrys chesapeakensis Messick & Small, 1996
Mesanophrys maggii Wiackowski, Hryniewiecka-Szyfter & Babula, 1999
Mesanophyrs pugettensis Morado & Small, 1994
Orchitophrya stellarum Cépède, 1907
Synophrya hypertrophica Chatton & Lwoff, 1926

DINOFLAGELLATA (DINOPHYTA)
Hematodinium australis Hudson & Shields, 1994
Hematodinium perezi Chatton & Poisson, 1931

FUNGI
Exophiala cancerae De Hoog, Vicente, Najafzadeh, Badali, Seyedmousavi & Boeger, 2011
Fonsecaea brasiliensis Vicente, Orélis-Ribeiro, Najafzadeh, Sun, Guerra, Miesch, Ostrensky, Meis, Klaassen, De Hoog & Boeger, 2012
Fusarium solani (Martius, 1842)
Rhizophydium littoreum Amon, 1984
Trichomaris invadens Hibbits, Hughes & Sparks, 1981

KINETOPLASTIDA
Perkinsiella amoebae Hollande, 1980
Procryptobia sorokini (Zhukov, 1975)
Trypanosoma murmanense Nitikin, 1927

MICROSPORIDIA
Abelspora portucalensis Azevedo, 1987
Ameson metacarcini Small, Meyer, Stentiford, Dunham, Bateman & Shields, 2014
Ameson michaelis (Sprague, 1970)
Ameson pulvis (Pérez, 1905)
Enterospora canceri Stentiford, Bateman, Longshaw & Feist, 2007
Hepatospora eriocheir (Wang & Chen, 2007)
Nadelspora canceri Olson, Tiekotter & Reno, 1994
Nosema sapidi Sprague, 1970
Ormieresia carcini Vivarès, Bouix & Manier, 1977
Plistophora cargoi Sprague, 2007
Thelohania grapsi Prowazek, 1910
Thelohania maenadis Pérez, 1904

NEMATODA
Ancyracanthopsis winegardi Wong & Anderson, 2011
Anisakis simplex (Rudolphi, 1809)
Ascarophis morrhuae Van Beneden, 1871
Heptochona praecox (Poinar & Kannangara, 1972)
Hysterothylacium aduncum (Rudolphi, 1902)
Hysterothylacium reliquens (Norris & Overstreet, 1975)
Proleptus obtusus Dujardin, 1845
Skrjabinoclava inornatae Wong & Anderson, 1988

NEMATOMORPHA
Nectonema agile Verrill, 1879
Nectonema melanocephalum Nierstrasz, 1907
Nectonema svenskundi Bock, 1908
Nectonema zealandica Poinar & Brockerhoff, 2001

NEMERTEA
Carcinonemertes carcinophila (Kölliker, 1845)
Carcinonemertes epialti Coe, 1902
Carcinonemertes errans Wickham, 1978
Carcinonemertes mitsukurii Takakura, 1910
Carcinonemertes pinnotheridophila McDermott & Gibson, 1993
Carcinonemertes regicides Shields, Wickham & Kuris, 1989
Carcinonemertes wickhami Shields & Kuris, 1990

PLATYHELMINTHES
Bdelloura candida (Girard, 1850)
Dollfusiella martini (Beveridge, 1990)
Ectocotyla hirudo Levinsen, 1879
Ectocotyla multitesticulata Fleming & Burt, 1978
Fecampia erythrocephala Giard, 1886
Gynaecotyla adunca (Linton, 1905)
Gynaecotyla squatarolae (Yamaguti, 1934)
Levinseniella capitanea Overstreet & Perry, 1972
Levinseniella cruzi Travassos, 1921
Maritrema bonaerense Etchegoin & Martoreli, 1997
Maritrema laricola Ching, 1963
Maritrema novaezealandense Martorelli, Fredensborg, Mouritsen & Poulin, 2004
Maritrema orensense Cremonte & Martorelli, 1998
Maritrema subdolum Jägerskiöld, 1909
Microphallus basodactylophallus (Bridgman, 1969)
Microphallus claviformis (Brandes, 1888)
Microphallus diodontis (Siddiqi & Cable, 1960)
Microphallus koreana Guk, Chai, Sohn, Kim, Sim & Seo, 2008
Microphallus nicolli (Cable & Hunninen, 1938)
Microphallus primas (Jägerskiöld, 1908)
Microphallus sabanensis Díaz, Bashirullah & Hernández, 2004
Microphallus szidati Martorelli, 1986
Paragonimus kellicotti Ward, 1908
Paragonimus mexicanus Miyazaki & Ishii, 1968
Paragonimus skrjabini Chen, 1959
Paragonimus westermani Kerbert, 1878
Peraclistus oophagus (Friedmann, 1924)
Polypocephalus moretonensis Butler, 1987
Probolocoryphe lanceolata (Holliman, 1961)
Probolocoryphe uca (Sarkisian, 1957)
Scolex polymorphus Rudolphi, 1819
Stylochus zebra (Verrill, 1882)
Temnocephala brevicornis Haswell, 1892
Temnocephala lutzi Monticelli, 1913
Temnosewellia chaeropsis Hett, 1925
Temnosewellia semperi (Weber, 1889)
Temnosewellia vietnamensis Damborenea & Brusa, 2009
Trimacracanthus aetobatidis (Robinson, 1959)

OOMYCOTA
Aphanomyces astaci Schikora, 1906
Atkinsiella dubia (Atkins, 1954)
Atkinsiella hamanaensis Bian & Egusa, 1980
Atkinsiella okinawaensis Nakam & Hatai, 1995
Haliphthoros milfordensis Vishniac, 1958
Lagenidium callinectes (Couch, 1942)
Lagenidium scyllae Bian, Hatai, Lio-Po & Egusa, 1979
Leptolegnia marina (Atkins, 1954)
Pythium thalassium Atkins, 1955
Salilagenidium thermophilum (Nakamura, Nakamura, Hatai & Zafran, 1995)

RHIZOPODA
Paramoeba perniciosa Sprague, Beckett & Sawyer, 1969

STRAMENOPILES
Enteromyces callianassae Lichtwardt, 1961
Taeniella carcini Léger & Duboscq, 1911

VERTEBRATA
Pisces: Chondrichthyes
Schroederichthys chilensis (Guichenot, 1848)

Pisces: Osteichthyes
Gadus morhua Linnaeus, 1758

Amphibia
Xenopus laevis Daudin, 1802

Aves
Himantopus melanurus Vieillot, 1817
Nyctanassa violacea (Linnaeus, 1758)
Rallus crepitans Gmelin, 1789
Tringa semipalmata (Gmelin, 1789)

Mammalia
Enhydra lutris (Linnaeus, 1758)
Enhydra lutris nereis (Merriam, 1904)
Oryzomys palustris (Harlan, 1837)
Procyon lotor (Linnaeus, 1758)

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