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Harpacticoid copepods—their symbiotic associations and biogenic substrata: a review

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Abstract

Members of the order Harpacticoida are primarily free-living and benthic but some lineages have adopted alternative modes of life which involve a major habitat shift or dependence on a host. Since the first discovery of a harpacticoid associated with an invertebrate host about 150 years ago, a total of 172 species, representing 84 genera and 17 families, have been shown to live in symbiotic partnership with other organisms. The steady addition of new taxa during the last 35 years testifies to the widespread and previously underestimated occurrence of symbiosis in the group. Harpacticoids have entered into associations with Cyanobacteria, Protozoa, macroalgae, grasses, fish hosts, marine tetrapods (including whales, sea turtles and manatees) and at least eleven invertebrate phyla. At present, 86 independent colonizations of marine and freshwater host organisms can be identified but this number is a minimum estimate and is expected to increase as certain host groups will be more properly sampled. In contrast to the Cyclopoida and Siphonostomatoida, which have been extremely successful in developing associations with cnidarians, sponges, echinoderms and ascidiaceans, members of the Harpacticoida have a marked predilection for crustacean hosts. Except for a few species that can be classified as genuine parasites, the precise nature of the relationship between most associated harpacticoids and their hosts has yet to be elucidated but can probably be defined as commensalistic, where the benefit to the copepod may be nutritional or protective. Most are ectosymbiotic but some live as endocommensals in microhabitats which provide considerable protection from predation. The success of symbiotic harpacticoids in freshwater is limited with the few species known to be associated with freshwater hosts typically representing isolated forays into a symbiotic lifestyle from an otherwise free-living lineage. The scattered literature on symbiotic harpacticoids is compiled and presented by host group. Dichotomous keys are provided for the identification of most species while accidental and doubtful records are discussed where appropriate.

The genus *Idomenella* T. Scott, 1906a (Pseudotachidiidae), previously a junior subjective synonym of *Dactylopodella* Sars, 1905a, is reinstated to accommodate *Dactylopodella rostrata* (T. Scott, 1893), *D. janetae* Hicks, 1989, *Xouthous coronatus* (T. Scott, 1894b), *X. antarcticus* (Giesbrecht, 1902), *X. intermedius* (Lang, 1934) and *Idomenella paracoronata* **sp. nov.** *Kioloaria* Harris, 1994 (Porcellidiidae) is adopted as the valid replacement name for the preoccupied *Acutiramus* Harris, 2014a. The name of a second porcellidiid genus, *Murramia* Harris, 1994, lacks the mandatory type fixation and is made available here by adopting the original name but taking the present authorship and date. The generic name *Ellucana* Sewell, 1940 is currently unavailable and must instead be attributed to Coull (1971b). *Laophonte commensalis* Raibaut, 1962a is fixed as the type of *Raibautius* **gen. nov.** in the family Laophontidae, *Tegastes cnidicus* Humes, 1981b as the type of *Aglaogastes* **gen. nov.** in the Tegastidae, and *Canuella (Canuella) indica* Krishnaswamy, 1957 as the type of *Indicanuella* **gen. nov.**

A number of new names are proposed for species that had previously been misidentified: *Diarthrodes septemtrionalis* **sp. nov.** for *D. roscoffensis* (Monard, 1935b) *sensu* Kornev & Chertoprud (2008), *Kioloaria jejuensis* **sp. nov.** for *Porcellidium brevicaudatum* Thompson & Scott, 1903 *sensu* Kim & Kim (1996), *Xouthous andamanensis* **sp. nov.** for *X. maldivae* [*sic*] Sewell, 1940 *sensu* Wells & Rao (1987), *X. wellsi* **sp. nov.** for *X. laticaudatus* (Thompson & Scott, 1903) *sensu* Wells (1967), *X. namibiensis* **sp. nov.** for *X. pectinatus* (Scott & Scott, 1898) *sensu* Kunz (1963), and *Idomenella paracoronata* **sp. nov.** for *Idomene coronata* (T. Scott, 1894b) *sensu* Sars (1909a). The inadequately described *Amenophia ovalis* Brady, 1910 is relegated to a *species inquirenda* in *Amenophia* Boeck, 1865. *Idomene australis* Brady, 1910, *I. pusilla* Brady, 1910, *Dactylopusia ferrieri* T. Scott, 1912 and *I. kabylica* Monard, 1936 are ranked *species incertae sedis* in the Pseudotachidiidae. *Dactylopus bahamensis* Edwards, 1891 is tentatively considered as *species incertae sedis* in the Dactylopusiidae. *Canuellina onchophora* Por, 1967 and *C. nicobaris* Wells & Rao, 1987 are transferred to the genus *Ellucana* Coull, 1971b while *Ellucana secunda* Coull, 1971b is assigned to the genus *Canuellina* Gurney, 1927. *Xylora calyptogenae* Willen, 2006 is sunk as a junior subjective synonym of *X. bathyalis* Hicks, 1988a. The incorrect original spellings of *Parathalestris pacificus* Chislenko, 1971, *P. infestus* Ho & Hong, 1988, *Tripartisoma ovalis* Avdeev, 1983, *T. trapezoidalis* Avdeev, 1983, *Amplipedicola pectinatus* Avdeev, 2010 and *Sunaristes japonicus* Ho, 1986a are amended to reflect agreement in gender with their respective generic names.

Key words: Crustacea, Copepoda, symbiotic relationships, commensalism, inquilinism, phoresis, pholeteros, biogenic substrata

Introduction

Members of the order Harpacticoida are best known for their ubiquity, diversity and hyperabundance in marine sediments, from the intertidal zone to the deepest hadal trenches, spanning a vertical range in excess of 10,000 m (Wolff 1960; Belyaev 1989). Harpacticoid copepods hold a similar position of preeminence in fresh and inland saline continental waters (Boxshall & Defaye 2008; Galassi *et al.* 2009) where they can be found in nearly every habitat and situation where sufficient moisture and organic matter are present (Reid 2001). Some species are no longer associated with the ancestral benthic environment and have exploited alternative habitats such as the open pelagic (Boxshall 1979; Huys & Böttger-Schnack 1994; Huys & Conroy-Dalton 2000) or the ephemeral habitat at the ice-water interface of polar and subpolar ice (Kern & Carey 1983; Dahms *et al.* 1990). Though relatively few species are known to be commensals, parasites or otherwise associated, recent discoveries suggest that the true diversity of harpacticoids associated with invertebrate hosts has yet to be revealed. Since interest in symbiotic harpacticoids has traditionally not paralleled interest in either cyclopoids or siphonostomatoids, it is reasonable to expect that many more species will be discovered in the future. In particular, a full appreciation of their diversity awaits a more scrutinous examination of certain marine host groups such as decapod crustaceans, scleractinian corals and ascidiaceans. For example, Harpacticoida have historically been considered to be only rarely associated with cnidarian hosts, but the recent discovery of several species from hydrozoans and corals (Humes 1981a, 1981b, 1984, 1985, 1991, 1992) indicates that harpacticoids may be more frequent associates than previously believed.

Harpacticoid copepods associated with invertebrate hosts were first discovered about 150 years ago when Hesse (1867) described *Sunaristes paguri* from the apical whorls of the gastropod shells inhabited by the common hermit crab *Pagurus bernhardus* (Linnaeus, 1758). The first harpacticoid from a vertebrate host was reported by Aurivillius (1879a) who described *Balaenophilus unisetus* from the baleen plates of a Northern blue whale landed at a whaling station in northern Norway. Out of approximately 1,200 described harpacticoid species Lang (1948: 1586) was able to list only five whose symbiotic association with vertebrate or invertebrate hosts could be regarded as proven. Gotto (1979) reviewed the literature on copepods associated with marine invertebrates and listed about 33 harpacticoids which habitually partner other organisms. At present more than 50 species, all of them new, have been described from invertebrate hosts in the last 35 years.

The number of comprehensive regional reviews of symbiotic harpacticoids is relatively limited, including synoptic treatments covering the British Isles (Leigh-Sharpe 1935; Gotto 1993, 2004), The Netherlands (Faasse 2003), the Mediterranean (Soyer 1968), Cuba (Varela & Lalana 2015), Mexico (Morales-Serna *et al.* 2012), Nosy Bé, Madagascar (Humes 1995) and Korea (Kim 1998). Other contributions have attempted to summarize knowledge on harpacticoid copepods associated with particular host groups such as sponges (Huys 1990a), sea anemones (Humes 1982), sipunculans (Illg 1975), molluscs (Monod & Dollfus 1932), cephalopods (Hochberg 1983, 1990), decapods (Hendricks & Fiers 2010), hermit crabs (Williams & McDermott 2004; McDermott *et al.* 2010), land crabs (Bright & Hogue 1972), lobsters (Shields *et al.* 2006), spiny lobsters (Shields 2011), echinoderms (Barel & Kramers 1977; Jangoux 1987; Huys 1988a), sea cucumbers (Changeux 1961; Humes 1980) and starfish (Humes 1986). The present paper reviews our current knowledge of harpacticoid copepods living in association with metazoan hosts (both invertebrate and vertebrate), macroalgae, grasses, Cyanobacteria and protozoans. Accidental and doubtful records are discussed where appropriate.

How many species? A review of the literature found a total of 172 harpacticoid species to be associated with other organisms (Appendix 1). These species are distributed among 17 different families and 84 genera (Tables 1–3). The representation of species varied greatly among families, with a disproportionate number of species belonging to the Laophontidae (26) and Tisbidae (25) (Table 2). Other families that contain a substantial number of symbionts include the Canuellidae (17), Pseudotachidiidae (15), Ameiridae (14), Porcellidiidae (11) and Tegastidae (11). The Laophontidae also contained the highest number of genera (15), followed in generic representation by the Tisbidae (13) and Canuellidae (10). Symbiotic lineages vary in size from an entire subfamily, such as the Cholidyinae (Tisbidae) and Donsiellinae (Pseudotachidiidae), to several unrelated clusters of genera within a family, such as the Laophontidae, or a single monotypic genus (Hamondiidae). A single species of the Tachidiidae and Hamondiidae, families otherwise containing exclusively free-living members, has entered into a symbiotic relationship with an invertebrate host.

A total of 234 metazoan species, representing 132 genera, have so far been recorded as hosts (Table 2), and 25 species in 17 genera of marine macroalgae (Table 1) are known to be infested by harpacticoids. The Tisbidae (39), Laophontidae (38), Porcellidiidae (33) and Canuellidae (29) utilize more hosts than any other family.

Ecological radiation and colonization events. Harpacticoids have shifted into a symbiotic mode of life at different points of their complex evolutionary history. Some degree of dependence between harpacticoid guests and their larger hosts has evolved multiple times independently in tropical, subtropical, and temperate habitats. A tabular representation underscores the widespread occurrence of symbiosis in the group, having established relationships with Cyanobacteria, Protozoa, macroalgae, grasses, fish hosts, marine tetrapods (including whales, sea turtles and manatees) and at least eleven invertebrate phyla (Table 1). At present eighty-six independent colonizations of marine and freshwater host organisms can be identified (Table 3) but this number is a minimum estimate and is expected to increase as certain host groups will be more properly surveyed. Nearly half of these colonizations involve crustacean hosts, including crayfish, lobsters, anomurans, brachyurans, palinurids, axiideans, amphipods, isopods and barnacles (Table 3). Other invertebrate host groups that have recurrently been colonized by harpacticoid copepods include cnidarians, echinoderms and molluscs, each with seven independent colonization events. In contrast to the Cyclopoida and Siphonostomatoida, which have been extremely successful in developing associations with cnidarians, sponges, echinoderms and ascidiaceans, members of the Harpacticoida have a marked predilection for crustacean hosts. Currently, 92 species representing 43 genera and ten families, are known to live in association with approximately 120 species of crustaceans.

TABLE 1. Numbers of harpacticoid copepod species associated with other organisms, including number of independent colonization events per host group [* includes unidentified sponge utilized by *Hamondia superba*; † includes unidentified polychaetes associated with *Amphiascus giesbrechti*; # includes unidentified Cirroteuthidae utilized by *Cholidyella intermedia*; host species indicated by "sp." only not included; unconfirmed records enclosed by square brackets]. Note that grand total of copepod genera and species is lower than the summation of numbers for each host category since some have been reported from more than one host group.

	Number of host genera	Number of host species	Number of copepod genera	Number of copepod species	Number of colonization events
Cyanobacteria	1	N/A	4	4	1
Protozoa	1	1	1	1	1
Macroalgae	17	25	7	17	6
Grasses	1	1	1	1	1
Invertebrate hosts					
Porifera	3*	4*	2	3	2
Cnidaria	16	22	8	12	7
Platyhelminthes	1	2	1	1	1
Annelida	3†	3†	3	3	3
Sipuncula	1	1	1	1	1
Mollusca	19#	34#	14	19	7
Bryozoa	6	6	3	4	3
Chaetognatha	[1]	[1]	[1]	[1]	1
Crustacea	62	119	43	92	38
Echinodermata	8	9	7	8	7
Tunicata	5	9	3	5	3
Fish hosts	1	1	1	1	1
Marine tetrapods	5	9	1	2	3
Total	151	247	84	171	86

TABLE 2. Number of symbiotic copepod genera/species on metazoan hosts and independent colonization events per harpacticoid family. Note that grand total of host genera and species is lower than the summation of numbers for each copepod family since some (in)vertebrates are utilized by more than one family (27 species serve as host for more than one harpacticoid species).

	Number of host genera	Number of host (sub)species	Number of copepod genera	Number of copepod (sub)species	Number of colonization events
Ameiridae	16	26	6	14	6
Balaenophilidae	6	10	1	2	4
Canthocamptidae	7	12	2	5	2
Canuellidae	10	29	10	17	9
Dactylopusiidae	1	1	1	1	1
Ectinosomatidae	9	12	3	4	4
Hamondiidae	1	1	1	1	1
Harpacticidae	4	4	3	3	3
Laophontidae	22	38	15	26	16
Miraciidae	10	10	3	9	8
Peltidiidae	11	13	2	3	2
Porcellidiidae	13	33	3	11	3
Pseudotachidiidae	4	11	7	15	3
Tachidiidae	1	1	1	1	1
Tegastidae	10	11	3	11	4
Tisbidae	20	39	13	25	10
Total	132	234	74	147	77

TABLE 3. Host group utilization and number of colonization events per harpacticoid family; unconfirmed records enclosed by square brackets.

	Cyanobacteria	Protozoa	Macroalgae	Grasses	Porifera	Cnidaria	Platyhelminthes	Annelida	Sipuncula	Mollusca	Bryozoa	Chaetognatha	Crustacea	Echinodermata	Tunicata	Fish hosts	Marine tetrapods	Total
Ameiridae						1	1						4					6
Balaenophilidae													[1]				3	4
Canthocamptidae													2					2
Canuellidae									1				7	2				10
Dactylopusiidae			2					1										3
Darcythompsoniidae				1														1
Ectinosomatidae								1			1	[1]			1			3
Hamondiidae					1													1
Harpacticidae			?							1			1	1				3
Laophontidae						1				1	1		11	1				15
Miraciidae	1					1		1		1			4		1			9
Peltidiidae					1	1												2
Porcellidiidae										1			1	1				3
Pseudotachidiidae													2		1			3
Tachidiidae													1					1
Tegastidae		1				3					1							5
Thalestridae			4															4
Tisbidae			?							3			4	2		1		10
Total	1	1	6	1	2	7	1	3	1	7	3	1	36	7	3	1	3	86

Symbiotic harpacticoids are typically associated with species belonging to a single host category. The only exceptions include *Microsetella norvegica* (Boeck, 1865), which infests (and/or preys on) both chaetognaths and oikopleurid appendicularians, and *Balaenophilus manatorum* (Ortíz, Lalana & Torres Fundora, 1992), which has been recorded from manatees, sea turtles and, potentially, barnacles.

Although several families of copepods have successfully colonized fresh water, only about 8% of the 5,306 valid symbiotic copepod species worldwide have entered into associations with freshwater hosts. The great majority of the 450+ freshwater species (representing nine families) that made the transition to a symbiotic mode of life almost exclusively utilize actinopterygian fishes as hosts. Copepods associated with freshwater invertebrates are remarkably rare with examples known only from sponges (*e.g.* Stanković 1960; Mazepova 1978), gastropods (*e.g.* Ho & Thatcher 1989; Gamarra-Luque *et al.* 2004; Boxshall & Strong 2006), bivalves (*e.g.* Titar & Chernogorenko 1982; Chernysheva 1988) and crustaceans (*e.g.* Fiers 1991; Huys *et al.* 2009, 2014). Their limited success can presumably be attributed to the scarcity of suitable invertebrate hosts in the freshwater realm. Most macroinvertebrate phyla have not attained the same level of radiation or diversification in freshwater habitats as their marine counterparts (*e.g.* Porifera, Cnidaria, Mollusca, Annelida) and some that serve as important host categories to marine copepods are even completely absent in low salinity environments (*e.g.* Echinodermata, Tunicata). However, the fact remains that some groups such as the freshwater sponges and bivalves have not been properly surveyed for copepod associates. The few harpacticoids known to be associated with freshwater hosts mostly represent isolated forays into a symbiotic lifestyle from an otherwise free-living lineage of copepods. Some members of the family Canthocamptidae are associated with cambarid crayfish in eastern North America (Prins 1964; Bowman *et al.* 1968) while others belonging to the family Ameiridae are known as symbionts of astacid crayfish in western Eurasia (*e.g.* Behning 1936; Defaye 1996; Huys *et al.* 2014) and land crabs from around the central Atlantic region and Papua New Guinea (*e.g.* Fiers 1990; Huys *et al.* 2009). Unidentified harpacticoid copepods have been recorded from freshwater crabs (Hobbs & Villalobos (1958) and snail hosts (El-Bahy 1998; Sullivan & Yeung 2011). The only record (a species of *Moraria* Scott & Scott, 1893a) from a freshwater sponge (Smirnov 1930) requires confirmation.

Symbiotic relationships. The term *Symbiotismus* was first introduced by Frank (1877) in his study of crustose lichens and subsequently adopted as *symbiosis* by the German mycologist Anton de Bary (1879) to designate the common phenomenon in which two or more dissimilar organisms live together for an extended period of time. From the conceptual perspective of de Bary, symbiosis (from Greek *σύν* "together" and *βίωσις* "living") is an association defined by intimacy of interaction, rather than by the consequences of that interaction. Symbiotic copepods include those species commonly labelled in the literature as "associated" (*sensu* Gooding (1957)), a term which refers to cases in which there is little definite evidence about the nature of the association. Various types of symbioses, whether beneficial or harmful, are described by the terms commensalism (van Beneden 1876), mutualism (van Beneden 1873), and parasitism, reflecting the costs and benefits experienced by the partners. They can further be characterized in terms of the degree of interdependency among the associates (facultative *vs* obligate symbiosis), host specificity (generalists *vs* specialists), and the location of the guests in or on the host (endosymbionts, ectosymbionts, mesosymbionts, cohabitants).

In a mutualistic symbiosis both partners benefit from the relationship but the extent to which each symbiont benefits may vary and generally is difficult to quantify. There probably is not an example of mutualism in which both partners benefit equally (de Bary 1879) and there is not a single copepod that has been reported living in a mutualistic relationship with its host (Ho 2001).

Few harpacticoids derive their source of energy from living host tissues, either by feeding on them or absorbing from them, and thus can be classified as genuine parasites. Most members of the subfamily Cholidyinae, a single monophyletic lineage of 13 parasitic species, representing nine genera in the family Tisbidae, utilize octopodan cephalopods as hosts. Recent evidence indicates that the entire copepodid phase is completed inside the tissues of the cephalopod while the free-swimming phase has been reduced to the naupliar and adult stages (López-González *et al.* 2000). The life cycle of cholidyinids is unique among harpacticoid copepods since it comprises alternating endoparasitic and ectoparasitic phases. *Neoscutellidium yeatmani* Zwerner, 1967 occurs on the gills of the bathydemersal Antarctic eelpout, *Lycodichthys dearborni* (DeWitt, 1962), and is the only confirmed record of a harpacticoid utilizing a fish host (Zwerner 1967). Some species of the planktonic genus *Microsetella* Brady & Robertson, 1873 have been found to parasitize chaetognaths (Øresland & Bray 2005). They were usually observed in the body coelom or inside the gut of the host and their feeding behaviour appears to cause partial castration. Two members of the laophontid genus *Microchelonia* Brady, 1918 (= *Namakosiramia* Ho & Perkins, 1977) (family Laophontidae) are known to live as ectoparasites of North Pacific holothurians (Ho & Perkins 1977; Kim 1991). Both species of *Balaenophilus* Aurivillius, 1879a occur in high numbers on various marine tetrapods, however, there has been contentious debate over the nature of their symbiotic relationship. Data on the gut contents using SEM and immunohistochemistry analysis appear to confirm an ectoparasitic life style (Badillo *et al.* 2007) despite the lack of evidence that they cause skin damage or behave as scavengers feeding on sloughed skin (Suárez-Morales *et al.* 2010). Ovigerous females and both early and late naupliar stages of *Nitocra bdellurae* (Liddell, 1912) (family Ameiridae) have been observed inside the egg cases or cocoons of two bdellourid flatworm associates of the xiphosuran *Limulus polyphemus* (Linnaeus, 1758). Based on gut contents observations Liddell (1912) inferred that *N. bdellurae* preyed on triclad embryos. Mating, reproduction and hatching of the nauplii takes place inside the egg case, making it the first documented case of hypersymbiosis in the Harpacticoida.

The precise nature of the relationship between the great majority of associated harpacticoids and their hosts has yet to be elucidated but can probably be defined as commensalistic in its broadest sense, where the benefit to the copepod may be nutritional or protective. Hard factual data on the nature of food taken and how they obtain their nourishment are limited, hampering an objective assessment of their dependence on the host. Some species were originally described as associates of invertebrates (Edwards 1891; Leigh-Sharpe 1936; Humes 1957b) or vertebrates (Leigh-Sharpe 1936; Humes 1964), but are now considered as free-living members of benthic or phytal copepod communities. Others were originally described as free-living but have subsequently been implicated as commensals of crustacean and polychaete hosts (Bowman *et al.* 1968; Moore & O'Reilly 1993). Species that inhabit the cloacal cavity of compound ascidiaceans (*e.g. Xouthous purpurocinctus* (Norman & Scott, 1905)) or the rectum of sea urchins (*e.g. Echinosunaristes bathyalis* Huys, 1995) are exposed to a constant exhalant stream of faecal material, mucus strands and small organic particles and can be classified as debris feeders. Other species depend for their food on a water current created by the host and are associated with areas through or around which substantial amounts of particulate matter must pass. These sites, among others, include the atrium and ostia of sponges (Hicks 1986a; Huys 1990a), the pallial cavities of bivalve molluscs (Humes 1954; Huys & Song 2004), the branchial chambers of tunicates (Seiwell 1928; Saito 2009), and the baleen plates of whales (Vervoort & Tranter 1961; Bannister & Grindley 1966). Copepods occupying such sites on the host can be considered as commensals (or messmates) in the original strict sense of the term as defined by van Beneden (1876) for associations in which one animal shares food caught by another. Some species of the families Laophontidae (Jakubisiak 1932; Petkovski 1964a; Raibaut 1969), Miraciidae (Humes 1953; Itô 1972; Soyer 1973) and Tisbidae (Gurney 1933; Gooding 1957) live attached to the gill filaments or mouthparts of decapod crustaceans and obtain their food from the respiratory current of the host.

Many marine invertebrates secrete large quantities of mucus which constitutes a major nutrient source for associated copepods. Humes (1985) assumed that most copepods associated with cnidarians probably feed on mucus and its associated detritus rather than live tissue. Members of the families Peltidiidae and Tegastidae that utilize scleractinian corals as hosts (*e.g.* Humes 1981b, 1984) are probably mucus feeders.

Most commensal harpacticoids are ectosymbiotic but some live as endocommensals in various cavities of plants and animals, microhabitats which provide considerable protection from predation. Five species of Dactylopusiidae and four species of Thalestridae have been reported to actively excavate the fronds of brown or red algae, and some of these algicolous species are known to induce the formation of galls (*e.g.* Fahrenbach 1954; Ho & Hong 1988; Shimono *et al.* 2004a, 2007). *Amphiascus soyeri* (Lang, 1965) (family Miraciidae) was found in galls formed by the seafan *Eunicella stricta* (Bertoloni, 1810) in southern France (Theodor 1963). One species of the family Pseudotachidiidae, *Xouthous purpurocinctus*, occurs in very large numbers in the common cloacal cavity of the compound ascidian *Aplidium yamazii* (Tokioka, 1949) in southeastern Japan (Saito 2009). The miraciid *Paramphiascella commensalis* (Seiwell, 1928), and possibly *P. pacifica* Vervoort, 1962, inhabit the branchial chamber of colonial and solitary tunicates, respectively (Seiwell 1928; Wilson 1932; Vervoort 1962). Both sexes of *Echinosunaristes bathyalis* (family Canuellidae) live exclusively in the rectum of their echinoid host, an unidentified deepwater member of the irregular sea urchin genus *Paleopneustes* Agassiz, 1873, off San Salvador Island, Bahamas (Huys 1995).

The association of harpacticoids with other organisms is not exclusively related to food provided by the host and in some cases there is no nutritional dependence at all. One successful strategy employed by several species of pelagic harpacticoids has been to develop associations with pseudobenthic, floating substrates found in the open ocean. The three most notable examples of this strategy are the association of miraciids with filamentous, diazotroph Cyanobacteria (for a review see Huys & Böttger Schnack 1994), *Microsetella* spp. with organic aggregates and marine snow, particularly larvacean housing (Alldredge 1972; Steinberg *et al.* 1994), and *Parathalestris croni* (Krøyer, 1842) with floating macroalgal clumps (Wells 1970a; Ingólfsson & Ólafsson 1997). All these harpacticoids belong to predominantly benthic families and use their respective substrates for buoyant support as well as for food in the often oligotrophic pelagic environments.

Phoresis, inquilinism and stereotropism. In some textbooks other biological interactions, such as phoresis (phoresy) and inquilinism, which are based on the transport or shelter of one of the symbionts, are recognized as distinct categories of symbiosis. In phoretic relationships one organism (the phoront) uses another (the host) as a means of mechanical transport without establishing a close association. Phoresis may be an effective distribution mechanism for copepods in semiterrestrial and continental habitats where sufficient moisture is present only intermittently, or in habitats that periodically cycle between aquatic and terrestrial phases. Defaye (1996) suggested that *Nitocra divaricata* Chappuis, 1923 uses its crayfish host as a vehicle for dispersal into more favourable habitats. Other members of the family Ameiridae (formerly placed in the Cancrincolidae) and species of the canthocamptid genus *Pholetiscus* Humes, 1947 typically inhabit the gill chambers of grapsoidean land crabs (Humes 1947; Fiers 1990; Huys *et al.* 2009) and probably use their hosts for phoretic transport to new and potentially better habitats. Similarly, the symbiotic association of *Nitocra sphaeromata* Bowman, 1988, which attaches to the pleopods of its peracarid host, *Sphaeroma peruvianum* Richardson, 1910 (Bowman 1988), probably enhances dispersal of the phoront since the wood-boring isopods do not remain in one burrow throughout their lifetime. In addition to transport, the phoretic host may incidentally provide substrate, shelter, and even some indirect defense or protection for the phoront, but the strict definition of phoresis excludes any direct physiological benefit during transit.

In inquilinism, two or more animals of different species share a dwelling place. Inquilines (Latin *inquilinus*, "lodger" or "tenant") typically live commensally in the nest, burrow, or dwelling place of an animal of another species, obtaining shelter and in some instances taking some of the host's food. In copepods the most widely distributed types of inquiline are those found in association with hermit crabs. The families Canuellidae, Porcellidiidae, Pseudotachidiidae and Tisbidae all contain species that inhabit the apical whorls of gastropod shells utilized by pagurid and diogenid hosts (*e.g.* Hesse 1867; Scott 1893; Humes & Ho 1969a, 1969b; Humes 1972, 1981c; Hicks & Webber 1983; Ho 1986a; Kim & Kim 1996). In some cases the copepod shares the apex of its host's gastropod shell with other inquilines such as sipunculids (Stachowitsch 1980), corophiid amphipods (Turquier 1965) and spionid polychaetes (Codreanu & Mack-Firă 1961). A similar case of inquilinism is displayed by some harpacticoids that reside inside the cavity of the solitary ahermatypic coral *Heteropsammia cochlea* (Spengler, 1781) and cohabit with the sipunculan *Aspidosiphon muelleri muelleri* Diesing, 1851 and a member of the montacutid bivalve genus *Jousseaumia* Bourne, 1906 (Bourne 1906; Illg 1975; Rice 1976; present study). *Scutellidium patellarum* Branch, 1974 is a facultative inquiline living in the pallial cavity of various limpet hosts in South Africa. The species appears to be a scavenger, feeding on limpet faeces as well as algal fragments and possibly mucus produced by the hosts (Branch 1975a). The laophontid *Harrietella simulans* T. Scott, 1894b and at least some members of the subfamily Donsiellinae (Pseudotachidiidae) can be considered inquilines which live in the burrows created by wood-boring isopods (*e.g.* Pinkster 1968; Coull & Lindgren 1969; Hicks 1988a, 1989; Wouters & De Grave 1992). They likely feed on wood particles, dead entombed gribbles or faecal pellets produced by the wood-borers. *Laophonte adamsiae* Raibaut, 1966 was reported as an inquiline of the cloak anemone *Adamsia palliata* (O.F. Müller, 1776), inhabiting the chitinous membranous folds at the basal disc of its host (Raibaut 1966).

The term inquiline has also been applied to aquatic invertebrates that spend all or part of their life cycles in phytotelmata (Cronk *et al.* 2001) which are water-filled structures produced by plants, including tank bromeliads and pitcher plants, or other cryptic plant-held water bodies such as tree holes, water filled coconut husks and puddles in bamboo stumps. Copepods are by far the most common Crustacea encountered in phytotelmata (Jocqué *et al.* 2013) and both cyclopoids and harpacticoids have been recorded from this habitat worldwide (Reid 2011). The group of harpacticoid families that regularly occur in phytotelms includes the Canthocamptidae, Parastenocarididae and Phyllognathopodidae. Although a proportion of the species recorded from phytotelmata are occasional presences, normally thriving in water films on vegetation or among leaf litter, phytotelmic harpacticoids display a marked predilection for this habitat, with 20 out of 28 (>70%) species exclusively known from phytotelmata (Jocqué *et al.* 2013). Most microscopic inquilines are passive dispersers and need vectors (waterfowl, large mammals, wind) to move between phytotelmata; however, observations of certain harpacticoid species living in the thin water film on the surface of vegetation suggests that they may use this pathway for dispersal and climb actively into the plants (Reid 2001). Readers interested in additional information on phytotelmic Harpacticoida should consult the excellent reviews by Reid (2001) and Jocqué *et al.* (2013).

Loeb (1906) coined the term stereotropism (or thigmotaxis) to describe the tendency of organisms to orient their bodies in a certain way toward solid objects with which they come in contact. Positive stereotropism (often also referred to as contact sensibility or tactile adhesion), in which contact especially with a solid body or a rigid surface is the orienting factor, is probably most instrumental in bringing about the accidental association of harpacticoids with many invertebrate "hosts" or substrata. Codreanu (1960) made the distinction between temporary fixation to host surfaces (stereotropism) and the virtually permanent use of crevices and shelters formed or inhabited by their hosts, for which he introduced the term cryptotropism. The canuellid *Sunaristes paguri* which inhabits the apical whorls of the gastropod shell used by the hermit crab *Diogenes pugilator* (Roux, 1828), was cited by Codreanu & Mack-Firă (1961) as a specific example of such cryptotropic behaviour. The term cryptotropism is here considered synonymous with inquilinism.

Host specificity. Although the majority of symbiotic harpacticoids are known from a single host species, some are generalist symbionts, being dispersed unequally among hosts of several different species. Harpacticoids with broad host distributions frequently occur on host groups such as anomurans, crayfish, wood-boring isopods, deepwater cephalopods, whales, and occasionally, hard corals (Appendix 1). The canuellids *Sunaristes tranteri* Hamond, 1973b, *S. japonica* Ho, 1986a and *Intersunaristes dardani* (Humes & Ho, 1969a) have been recorded from seven hermit crab species and a similar number of octopodan hosts are utilized by *Cholidya polypi* Farran, 1914. *Scutellidium patellarum* is known from eight patellid hosts, *Xanthilaophonte trispinosa* (Sewell, 1940) from nine decapod hosts and *Alteuthellopsis corallina* Humes, 1981b from ten scleractinian coral species. Two species of the porcellidiid genus *Kioloaria* Harris, 1994, *K. brevicaudata* (Thompson & Scott, 1903) and *K. tapui* (Hicks & Webber, 1983), are the jacks-of-all-trades among the symbiotic Harpacticoida, having been recorded from 11 and 13 hermit crab hosts, respectively.

One host species may support more than one species of harpacticoid and in some cases members of up to four different families can be found, such as in the common hermit crab, *Pagurus bernhardus*. The spider crabs *Maja squinado* (Herbst, 1788) and *M. brachydactyla* Balss, 1922 each serve as host to three species of Laophontidae. The grapsoidean land crab, *Sesarma huzardi* (Desmarest, 1825), can contain up to three species of congeneric ameirids in its gill chamber while the deepwater octopodan *Graneledone boreopacifica* Nesis, 1982 is host to three cholidyinid parasites, each belonging to a different genus. Several wood-boring isopod hosts (*Limnoria* spp.) have three to five species of primarily donsiellinid associates. The hosts with the highest number of harpacticoid symbionts are the hermit crabs, including *Calcinus gaimardii* (H. Milne Edwards, 1848), *Clibanarius virescens* (Krauss, 1843), *Diogenes senex* Heller, 1865 and *Dardanus scutellatus* (H. Milne Edwards, 1848) (three species each), *Calcinus latens* (Randall, 1840) and *Pagurus bernhardus* (four species each), and *Dardanus guttatus* (Olivier, 1812), *D. lagopodes* (Forskål, 1775) and *D. megistos* (Herbst, 1804) (six species each). Twenty-seven species serve as hosts for more than one associated harpacticoid.

The range of hosts currently utilized by a symbiont usually provides strong clues about the identity of the organism that served as host to its ancestor. Although host specificity reflects the symbiont's historical associations with its hosts, identification of the ancestral host taxon may be obscured by host switching in the past, sometimes across great host taxonomic distances. For example, present-day host utilization in the two known species of the Balaenophilidae, with one species occurring exclusively on baleen whales and the second species utilizing sea turtles and sirenian hosts, is indicative of host switching in this family. However, since it has been suggested that balaenophilids are nested within the predominantly free-living family Miraciidae (Willen 2000), their first shared ancestral host remains as yet indeterminable. Similarly, all but one of the 14 known species of the subfamily Cholidyinae utilize cephalopod hosts while *Neoscutellidium yeatmani* infests an actinopterygian fish. On morphological grounds, the latter is arguably the sistergroup of the cephalopod-associated clade, rendering it difficult to determine the ancestral host taxon of the Cholidyinae and which lineage switched hosts.

Abbreviations and terminology

The higher level taxonomic arrangement of decapod hosts follows De Grave's (2009) recently updated classification. Currently valid names of animal and macroalgal host taxa follow the *World Register of Marine Species* (WoRMS Editorial Board 2016). Articles and Recommendations cited in the text refer to the fourth edition of the International Code of Zoological Nomenclature (ICZN 1999), the provisions of which supersede those of the previous editions of the Code with effect from 1 January 2000. The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: P1–P6, for legs 1–6; exp, enp and benp for exopod, endopod and baseoendopod, respectively; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segments of a ramus; NI–NVI, for naupliar stages I–VI; CoI–CoV, for copepodid stages I–V; OD, for original description; AD, for additional description(s); TL, for type locality; BL, for body length (measured from anterior margin of rostrum to posterior margin of caudal rami). Armature elements on the exopod and endopodal lobe of leg 5 are numbered and counted from the innermost first. Publications referring to original descriptions of hosts are compiled in Appendix 2.

Associations with Cyanobacteria

The predominantly benthic family Miraciidae contains a single planktonic clade comprising four monotypic genera: *Miracia* Dana, 1846, *Oculosetella* Dahl, 1895, *Macrosetella* A. Scott, 1909 and *Distioculus* Huys & Böttger-Schnack, 1994. The essentially tropical and subtropical occurrence of these genera is largely paralleled by the distribution pattern of several filamentous colonial cyanophytes, collectively referred to under the genus name *Trichodesmium* Ehrenberg ex Gomont, 1892 and formerly known as the marine *Oscillatoria* species complex. The most comprehensively studied species is *Macrosetella gracilis* (Dana, 1847) but many of the biological observations pertaining to this species are likely to be confirmed in the other three planktonic miraciids. Although having evolved a pelagic life style, all life cycle stages of *M. gracilis* show limited swimming ability (Björnberg 1965). The creeping nauplii and copepodids use floating *Trichodesmium* colonies as a physical substrate in the open ocean and this association with their nursery grounds appears to be obligate (Sheridan *et al.* 2002). Adults may be less highly dependent on the cyanobacterium as a floating substrate than previously assumed (Calef & Grice 1966) since they have been recorded in waters too deep or too cold to sustain *Trichodesmium* (Huys & Böttger-Schnack 1994). Laboratory studies (Roman 1978; O'Neil & Roman 1994; O'Neil *et al.* 1996) have shown that *M. gracilis* and other planktonic miraciids can feed on *Trichodesmium* despite it being toxic to most copepods. Both *M. gracilis* and *Miracia efferata* Dana, 1849 appear to be immune to the toxicity of *Trichodesmium* bloom extracts but the mechanism these species employ to protect themselves from the effects of the diazotroph neurotoxins is unknown (Hawser *et al.* 1992). In contrast to previous grazing experiments, a recent analysis of gut contents and natural abundance of stable isotopes ($\delta^{15}N$, $\delta^{13}C$) in copepod tissue suggested that *M. gracilis* does not feed predominantly on *Trichodesmium* in the field (Eberl & Carpenter 2007). The symbiotic relationship between planktonic miraciids and the cyanobacterium may therefore have evolved primarily from the requirement of a floating habitat for reproduction and nursery of the early instars rather than for trophic dependence. Given the toxicity of the substrate it is also conceivable that association with it provides shelter from predation by hydroids and chaetognaths, both of which are known to feed on juveniles and adults of *M. gracilis* (Borstad & Brinkmann-Voss 1978; Post *et al.* 2002). Like in benthic members of the Miraciidae, ovigerous females of all four species carry paired, typically biseriate egg sacs, however, eggs can also be packed in a uniseriate arrangement when their number is low (Huys & Böttger-Schnack 1994). Freshly fertilized eggs are dark blue, but their colour changes to red, orange or black as they mature (Wilson 1932; Krishnaswamy 1951; Björnberg 1965). Huys & Böttger-Schnack (1994) reviewed various aspects of the biology of planktonic miraciids, including reproduction, postembryonic development, vertical and geographical distribution, bioluminescence and photoreception.

Key to planktonic Miraciidae

1. Paired cephalic cuticular lenses absent; P1 exp-3 with three setae/spines . . . . *Macrosetella gracilis* (Dana, 1847).
   Paired cephalic cuticular lenses present; P1 exp-3 with four setae/spines . . . . 2.
2. Cephalic cuticular lenses not touching middorsally; P1 enp-2 with two setae . . . . *Distioculus minor* (T. Scott, 1894a).
   Cephalic cuticular lenses touching middorsally; P1 enp-2 with three setae/spines . . . . 3.

3. Rostrum well developed, defined at base; antennule 7-segmented in ♀, with aesthetascs on segments 3 and 7; antennary exopod absent; P5 baseoendopod with three setae in ♀ and two setae in ♂ ....*Oculosetella gracilis* (Dana, 1849).
Rostrum minute, fused to cephalothorax; antennule 8-segmented in ♀, with aesthetascs on segments 4 and 8; antennary exopod present; P5 baseoendopod with five setae in ♀ and three setae in ♂ .... *Miracia efferata* Dana, 1849.

Macrosetella gracilis (Dana, 1847)

Morphological data indicate that *M. gracilis* occurs as a single, circumglobal species across the tropical and subtropical Atlantic and Pacific (Huys & Böttger-Schnack 1994). A recent analysis of mitochondrial DNA sequence data (COI) showed moderate to high levels of diversity and limited phylogeographic structure in *M. gracilis* (Eberl *et al.* 2007). The hypothesis of a global distribution of *M. gracilis* was supported by low genetic distances between most COI sequences across the sampling range, and by shared haplotypes between the Atlantic and the Pacific. Haplotypic diversity was highest in samples from Japan, suggesting that the Indo-West Pacific may be the center of diversity for *M. gracilis*. Phylogenetic analysis placed samples from the Atlantic and the Pacific within the same clades, suggesting some level of interoceanic exchange or retention of ancestral polymorphisms across a vast geographic area (Eberl *et al.* 2007). In the Red Sea and the western Indian Ocean, adults of both sexes are represented by two distinct size morphs which differ considerably in spatio-temporal distribution (Böttger-Schnack 1989, 1991; Böttger-Schnack & Schnack 1989), suggesting the possibility of cryptic speciation (Eberl *et al.* 2007).

Ovigerous females carry paired egg sacs, each containing 5–11 eggs depending on the size morph and the state of eclosion. Eggs do not hatch simultaneously but successively, starting at the posterior end of the ovisac, with the nauplii creeping forwards on the sac until they reach the paternal female's fourth swimming legs (Huys & Böttger-Schnack 1994). O'Neil (1998) observed females actively affixing eggs to trichomes of a *Trichodesmium thiebautii* colony. Nauplii frequently held on to the caudal rami of the paternal female while being transferred to the nursery habitat of the colonies (O'Neil 1998). Females were also observed to hold on to the colony until all nauplii hatched successively a few hours after depositing the eggs (Björnberg 1965; Huys & Böttger-Schnack 1994; O'Neil 1998). Eberl & Carpenter (2007) observed females dropping their caudal ramal setae, and nauplii using them as temporary rafts until they encountered a colony; however, this unusual parental care may be an artifact of culturing conditions in the laboratory.

Bioluminescence has been reported by Russian investigators for *M. gracilis* in the Caribbean (Artyomkin *et al.* 1966, 1969) and *Macrosetella* sp. in the Red Sea (Rudyakov & Voronina 1967), but these cursory records have to be regarded uncertain pending further confirmation (Herring 1988).

OD: Dana (1847—as *Setella gracilis*): 155 (Latin diagnosis only).

AD: Dana (1847): 154 (as *Setella tenuicornis* Dana, 1847), 155 (as *S. aciculus* Dana, 1847, *S. crassicornis* Dana, 1847 and *S. longicauda* Dana, 1847). Dana (1854–1855): 1198–1199, Plate 84 (fig. 3a–g) (as *S. gracilis*); 1200, Plate 84 (fig. 5a–g) (as *S. aciculus*); 1199, Plate 84 (fig. 4a–e) (as *S. crassicornis*); 1197, Plate 84 (fig. 2a–a^1) (as *S. longicauda*); 1196, Plate 84 (fig. 1a–l) (as *S. tenuicornis*). Lubbock (1860—as *Setella tenuis* Lubbock, 1860): 181, Plate 29 (Fig. 12). Claus (1863—as *Setella messinensis* Claus, 1863): 137; Plate XXI (Figs 15–16). Brady (1883—as *S. gracilis*): 108–109; Plate L, figs 1–10. Giesbrecht (1893—as *S. gracilis*): 559–563; Plates 1 (Fig. 12), 45 (Figs 1–15). Wheeler (1901—as *S. gracilis*): 188; Fig. 24. Breemen (1908—as *S. gracilis*): 178–179; Fig. 192. Brady (1910—as *S. gracilis*): 508; Plate LII, fig. 5; Textfig. III. Pesta (1912): 56–57; Fig. 19. Mori (1929—as *S. gracilis*): 201; Plate VIII (Figs 8–10). Wilson (1932): 281–283; Fig. 174. Rose (1933): 288; Fig. 367. Steuer (1935): 292–293; Fig. 1c. Mori (1937—as *S. gracilis*): 115; Plate 64 (figs 1–5). Dakin & Colefax (1940): 104, 106; Fig. 163a–c. Krishnaswamy (1949): 78; Plate 1. Krishnaswamy (1950): 44, 48–49; Figs 49–52. Krishnaswamy (1951): 256–270; Figs 1–75; Tables I–II. Carvalho (1952): 161–162; Plate II (Figs 76–81). Legaré (1964): 70–71; Plate 14 (Figs 5, 5a, 6, 6a). Björnberg (1965): 513–518; Figs 1–2, 4, 5a, 6–7. Zheng *et al.* (1965): 195–197; Fig. 93. Tokioka & Bieri (1966): 178–184; Text-figs 1–4; Plates V–VI. Owre & Foyo (1967): 105–106; Figs 773–774. Ramírez (1970): 98–99; Plate XX (Fig. 170). Chen *et al.* (1974): 68–69; Plate 24 (Figs 3–6). Boxshall (1979): 236–238; Fig. 16H–K. Zheng *et al.* (1984): 370–371; Fig. 186A–E. Björnberg *et al.* (1981): 677–678; Fig. 288-7. Sazhina (1985): 100; Fig. 93(5–7). Zheng *et al.* (1989): 269–270; Fig. 184A–E. Dahms (1990b): 212–213, 216; Fig. 15B. Björnberg *et al.* (1994): 9; Fig. 3-2. Campos-Hernández & Suárez Morales (1994): 257, 259; Figs 142, 260. Huys & Böttger-Schnack (1994): 231–243, 254–257, 259–260, 262–263, 266, 272; Figs 15–22, 30–38, 40(A–B); Tables 1–2. Ferrari & Dahms (1998): 299–300, 302–305; Fig. 3; Table 2. Bradford-Grieve *et al.* (1999): 886, 1081; Fig. 7.439. Al-Yamani & Prusova (2003): 114–115; Fig. 43. Conway *et al.* (2003): 211. Avancini *et al.* (2006): 130; Plate 98. Ferrari & Dahms (2007): 85; Tables XX–XXI. Mulyadi (2010): 58–59; Fig. 5. Vives & Shmeleva (2010): 111–113; Fig. 43. Al-Yamani *et al.* (2011): 122–123; Figs 272–273.

TL: Pacific Ocean; between Kermadec Islands and Tongatabu (Tonga).

BL: 1,060 µm (♀) [Dana 1847]; 1,000 µm (♀) [Claus 1863]; 1,400 µm (♀) [Brady 1883]; 1,400–1,500 µm (♀), 1,160–1,300 µm (♂) [Giesbrecht 1893; Wheeler 1901; Breemen 1908; Wilson 1932; Rose 1933]; 1,160–1,300 µm (♂) [Steuer 1935]; 1,200–1,500 µm (♀), 1,150–1,300 µm (♂) [Mori 1937]; 484 µm (CoI), 616 µm (CoII), 742 µm (CoIII), 922 µm (CoIV), 1,240 µm (CoV♀), 1,010 µm (CoV♂), 1,400 µm (♀), 1,100 µm (♂) [Krishnaswamy 1949]; 129 µm (NII), 484 µm (CoI) [Krishnaswamy 1950]; 100 µm (NI), 128 µm (NII), 163 µm (NIII), 193 µm (NIV), 234 µm (NV), 285 µm (NVI—the measurement given in the text (815 µm) is probably incorrect, *cf.* Huys & Böttger-Schnack 1994: 255), 348 µm (CoI), 410 µm (CoII), 452 µm (CoIII), 874 µm (CoIV), 1,270 µm (CoV♀), 1,100 µm (CoV♂) [Krishnaswamy 1951]; 1,420–1,500 µm (♀), 1,000–1,150 µm (♂) [Carvalho 1952]; 1,500 µm (♀), 1,100 µm (♂) [Krishnaswamy 1953]; 1,800 µm (♀), 1,250 µm (♂) [Björnberg 1963]; 120–150 µm (NI), 350 µm (NVI), 480 µm (CoI), 575 µm (CoII), 775 µm (CoIII), 910 µm (CoIV), 1,320 µm (CoV) [Björnberg 1965]; 1,100–1,400 µm (♀), 980–1,000 µm (♂) [Zheng *et al.* 1965]; 130 µm (NI), 165 µm (NII), 210 µm (NIII), 280 µm (NIV), 345 µm (NVI—labelled as NV), 450 µm (CoI) [Tokioka & Bieri 1966]; 1,450 µm (♀) [Ramírez 1970]; 1,200–1,300 µm (♀), 1,000–1,200 µm (♂) [Chen *et al.* 1974] 1,210–1,500 µm (♀), 1,130–1,160 µm (♂) [Boxshall 1979]; 1,800 µm (♀), 1,250 µm (♂) [Björnberg *et al.* 1981]; 130 µm (NI), 210 µm (NII), 250 µm (NIII), 300 µm (NVI) [Sazhina 1985]; 260 µm (NIII) [Björnberg *et al.* 1994]; 1,400–1,500 µm (♀), 1,100 µm (♂) [Campos-Hernández & Suárez Morales 1994]; 880–1,620 [1,780] µm (♀), 860–1,340 µm (♂) [Huys & Böttger-Schnack 1994]; 1,200–1,500 µm (♀), 1,150–1,300 µm (♂) [Chihara & Murano 1997]; 1,450–1,500 µm (♀), 1,130–1,160 µm (♂) [Bradford-Grieve *et al.* 1999]; 980–1,620 µm (♀), 880–1,300 µm (♂) [Conway *et al.* 2003]; 1,200–1,500 µm (♀), 1,100–1,200 µm (♂) [Avancini *et al.* 2006]; 1,200–1,450 µm (♀), 1,150–1,300 µm (♂) [Mulyadi 2010]; 880–1,620 µm (♀), 880–1,340 µm (♂) [Vives & Shmeleva 2010]; 1,220 µm (♀), 1,010 µm (♂) [Al-Yamani *et al.* 2011].

Miracia efferata **Dana, 1849**

Both sexes of *M. efferata* are a brilliant bluish purple (*e.g.* Brady 1883; Mrázek 1895) even after a considerable time of preservation (Boxshall 1979), and males are much paler than females (Wheeler 1901). Wilson (1932), based on Richard Rathbun's unpublished coloration notes, gave a vivid description of the colour pattern in live specimens. Each egg sac typically contains 4–6 eggs (Huys & Böttger-Schnack 1994).

OD: Dana (1849): 46 (Latin diagnosis only).

AD: Dana (1854–1855): 1260–1261; Plate 88, fig. 11. Brady (1883): 102–104; Plate XLIII, Figs 1–16. Claus (1891): 267–284; Plates I–III. Giesbrecht (1893): 563–565; Plate 45 (Figs 39–48). Mrázek (1895): 2; Plate XIV (Figs 1–3). Wheeler (1901): 188–189; Fig. 25. Wilson (1932): 284–286; Fig. 176. Steuer (1935): 392–393; Fig 1a. Krishnaswamy (1950): 44, 49–51; Figs 53–57. Krishnaswamy (1953): 72–73; Fig. 2. Legaré (1964): 70–71; Plate 14 (Figs 8, 8a). Björnberg (1965): 513–515, 518; Figs 3, 5b, 8. Owre & Foyo (1967): 105–106; Figs 767–768. Vives (1972): 229; Fig. 8. Boxshall (1979): 235–236; Fig. 16A–D. Björnberg *et al.* (1981): 677–678; Fig. 288-8. Sazhina (1982): 1159, 1162; Fig. 2-9. Zheng *et al.* (1982): 152–154; Fig. 98. Zheng *et al.* (1984): 370–371; Fig. 186F–K. Sazhina (1985): 99–100; Fig. 93(1–4). Zheng *et al.* (1989): 270; Fig. 184F–K. Björnberg *et al.* (1994): 9; Fig. 3-1. Campos-Hernández & Suárez Morales (1994): 256–258; Figs 140, 259. Huys & Böttger-Schnack (1994): 211–220; Figs 1–7. Bradford-Grieve *et al.* (1999): 886, 1081; Fig. 7.440. Conway *et al.* (2003): 209. Vives & Shmeleva (2010): 114–115; Fig. 44.

TL: Atlantic Ocean. Dana (1849, 1854-1855) did not specify a type locality, but mentioned that the species occurred in the Atlantic between 4–7°N and 20–21°30'W, and at 4°30', S 25°W.

BL: 1,587 µm (♀) [Dana 1849]; 2,100 µm (♀) [Brady 1883]; 1,500 µm (♂) [Giesbrecht 1893]; 1,750–2,000 µm (♀), 1,500 µm (♂) [Wheeler 1901]; 1,750–2,000 µm (♀), 1,400–1,600 µm (♂) [Wilson 1932]; 1,210–1,530 µm (♀), 1,450–1,810 µm (♂) [Steuer 1935]; 750 µm (CoI—as CoII) [Krishnaswamy 1950]; 2,100 µm (♀)

[Krishnaswamy 1953]; 1,900 µm (♀) [Björnberg 1963]; 150–190 µm (NI), 380 µm (NVI), 600 µm (CoI), 650 µm (CoII) [Björnberg 1965]; 1,450–2,000 µm (♀), 1,400–1,600 µm (♂) [Boxshall 1979]; 1,450–2,000 µm (♀), 1,400–1,600 µm (♂) [Björnberg *et al.* 1981]; 1,890–1,940 µm (♀) [Zheng *et al.* 1982]; 170 µm (NI), 210–250 (NII), 400 µm (NVI) [Sazhina 1985]; 380 µm (NVI) [Björnberg *et al.* 1994]; 1,400–2,000 µm (♀), 1,400–1,600 µm (♂) [Campos-Hernández & Suárez Morales 1994]; 1,450–2,000 µm (♀), 1,400–1,600 µm (♂) [Bradford-Grieve *et al.* 1999]; 1,550–1,850 µm (♀), 1,300–1,650 µm (♂) [Huys & Böttger-Schnack 1994]; 1,550–1,850 µm (♀), 1,300–1,650 µm (♂) [Chihara & Murano 1997]; 1.550–1,850 µm (♀), 1,300–1,650 µm (♂) [Conway *et al.* 2003]; 1,550–2,000 µm (♀), 1,400–1,600 µm (♂) [Vives & Shmeleva 2010].

Oculosetella gracilis **(Dana, 1849)**

This is a rare species and, when recorded, is usually represented by only a few specimens in plankton hauls. Huys & Böttger-Schnack (1994) compiled most pre-1995 valid records; to their list should be added the records by Kanaeva (1960), Owre (1962), Björnberg (1963), De Decker & Mombeck (1964), Wiborg (1964), Deevey (1971), Sander & Moore (1978), Vives (1982), Kovalev & Shmeleva (1982), De Decker (1984) and Campos-Hernández & Suárez Morales (1994). Post-1994 records include Dias (1995), Errhif *et al.* (1997), Hure & Kršinić (1998), Bradford-Grieve *et al.* (1999), Harvey *et al.* (1999), López-Salgado *et al.* (2000), Conway *et al.* (2003), Richardson *et al.* (2006), Khelifi-Touhami *et al.* (2007), Fernandes (2008), Dias & Bonecker (2009), Cornils *et al.* (2010), Hidalgo *et al.* (2010), Vives & Shmeleva (2010), Salah *et al.* (2012), Belmonte *et al.* (2013), Jagadeesan *et al.* (2013) and Lidvanov *et al.* (2013).

Grazing experiments showed that *O. gracilis* ingested *Trichodesmium thiebautii* at comparable rates to *M. gracilis* and *M. efferata* (O'Neil & Roman 1994), suggesting that this species can use diazotroph Cyanobacteria for nutrition. Ovigerous females carry paired egg sacs, each typically containing four eggs (Huys & Böttger-Schnack 1994).

OD: Dana (1849—as *Miracia gracilis*): 46 (Latin diagnosis only).

AD: Dana (1854–1855—as *M. gracilis*): 1261–1262; Plate 88, fig. 12a–c. Sars (1916—as *Setella oculata* Sars, 1916): 13–14; Plate VII. Steuer (1935): 292, 294; Fig. 1d. Owre & Foyo (1967): 106; Figs 775–779. Vives (1972): 228; Fig. 7. Boxshall (1979): 236–237; Fig. 16L–N. Björnberg *et al.* (1981): 677–678; Fig. 288-10. Campos-Hernández & Suárez Morales (1994): 256, 258; Fig. 141. Huys & Böttger-Schnack (1994): 221–230; Figs 8–14. Bradford-Grieve *et al.* (1999): 886, 1082; Fig. 7.442. Conway *et al.* (2003): 210. Vives & Shmeleva (2010): 115–117; Fig. 45.

TL: Pacific Ocean. Dana (1849, 1854-1855) did no specify a type locality. The species was found in two localities in the South Pacific, one off Sunday Island, the other north of New Zealand at 32°24'S, 177°E.

BL: 1,587 µm (♀) [Dana 1849]; 1,300 µm (♀) [Sars 1916]; 1,080–1,740 µm (♀), 1,000–1,420 µm (♂) [Steuer 1935]; 1,100 µm (♀) [Wiborg 1964]; 1,200–1,350 µm (♀), 1,150–1,300 µm (♂) [Boxshall 1979]; 1,200 µm (♀), 1,150 µm (♂) [Björnberg 1963; Björnberg *et al.* 1981]; 1,500 µm (♀), 1,000 µm (♂) [Campos-Hernández & Suárez Morales 1994]; 1,200–1,300 µm (♀), 820 µm (♂) [Huys & Böttger-Schnack 1994]; 1,200–1,350 µm (♀), 1,150–1,300 µm (♂) [Bradford-Grieve *et al.* 1999]; 1,200–1,300 µm (♀), 800 µm (♂) [Conway *et al.* 2003]; 1,200–1,300 µm (♀), 820 µm (♂) [Vives & Shmeleva 2010].

Distioculus minor **(T. Scott, 1894a)**

Soyer-Gobillard (1965) recorded a single ovigerous female from Banylus-sur-Mer which deviated from typical *D. minor* in the armature of legs 2 (exp-3 with one outer spine instead of two, enp-3 with two inner setae instead of one) and 4 (inner seta of enp-1 absent instead of present). The author stated that the P5 exopod bears six setae but only five can be discerned in the accompanying photograph. Conversely, the baseoendopod bears five setae instead of four but the left-right asymmetry in size and position suggests that the specimen is aberrant rather than representing an as yet undescribed species.

Each egg sac typically contains four eggs (Giesbrecht 1895) but egg number appears to be positively correlated with body size. For example, females from the Red Sea and Gulf of Aden were significantly smaller (700 µm) and usually had only two eggs per ovisac (Huys & Böttger-Schnack 1994). Unlike *M. gracilis* eclosion starts at the proximal end of the egg sac.

OD: Scott (1894a): 102–104; Plate XI, Figs 18–30.

AD: Giesbrecht (1895): 217–223; Plate 9 (Figs 1–13). Mrázek (1895—as *Miracia gracilis* Dana, 1849): 6–9; Plate XIV (Figs 4–17). Wilson (1932—as *Macrosetella oculata* (Sars, 1916)): 283–284; Fig. 175. Steuer (1935): 292–293; Fig. 1b. Krishnaswamy (1956): 458–460; Figs 14–21. Owre & Foyo (1967): 105–106; Figs 770–772. Boxshall (1979): 235–236; Fig. 16E–G. Björnberg *et al.* (1981): 677–678; Fig. 288-9. Campos-Hernández & Suárez Morales (1994): 255, 257; Figs 139, 258. Huys & Böttger-Schnack (1994): 243–253; Figs 23–29; Table 3. Bradford-Grieve *et al.* (1999): 1082; Fig. 7.441. Conway *et al.* (2003): 212. Vives & Shmeleva (2010): 110–111; Fig. 42.

TL: Gulf of Guinea; 5°58’1”S, 0°1’5”E; 235 fms (430 m).

BL: 930 µm [Scott 1894a]; 850 µm (♀), 770 µm (♂) [Giesbrecht 1895]; 950 µm (♂) [Mrázek 1895]; 1,200–1,350 µm (♀), 1,150–1,300 µm (♂) [Wilson 1932]; 930–1,740 µm (♀), 830–1,450 µm (♂) [Steuer 1935]; 900 µm (♀) [Krishnaswamy 1956]; 900–930 µm (♀), 820–930 µm (♂) [Boxshall 1979]; 850 µm (♀), 770 µm (♂) [Björnberg *et al.* 1981]; 1,300 µm (♀), 1,200 µm (♂) [Campos-Hernández & Suárez Morales 1994]; 795–915 µm (♀), 770–920 µm (♂) [Huys & Böttger-Schnack 1994]; 930 µm (♀) [Bradford-Grieve *et al.* 1999]; 790–910 µm (♀), 770–920 µm (♂) [Conway *et al.* 2003]; 790–910 µm (♀), 770–920 µm (♂) [Vives & Shmeleva 2010].

Associations with Protozoa

While harpacticoids frequently serve as hosts (basibionts) to ciliate epibionts (Fernandez-Leborans 2001, 2010; Fernandez-Leborans & Tato-Porto 2000a, b) there is only one documented case of a reverse symbiotic association between a copepod and a protozoan. Ivanenko *et al.* (2008a) recorded thousands of specimens of nauplii and copepodid stages of *Tegastes falcatus* (Norman, 1869) (Tegastidae) in washings of the bryozoan *Flustra foliacea* (Linnaeus, 1758) (Gymnolaemata, Cheilostomatida) which served as a substratum to an unidentified suctorian protist (Ciliophora). The bryozoan colonies were collected from boulders at depths of 18–20 m off the Karelian coast of the Kandalaksha Gulf in the White Sea.

Live observations of *T. falcatus* nauplii showed that they attach themselves to the shafts of the sessile suctorian ciliates which form a dense layer on the surface of the bryozoan colonies. The cell body of the ciliate and the nauplii are of comparable size. Nauplii typically hold the distal part of the attachment stalk of the suctorian with their mandibular chelae. The pointed distal endopodal segments of the antennae are used to pierce the pellicle of the ciliates, suggesting that at least some naupliar instars feed on the protists. Nauplii appear unable to swim or creep efficiently over surfaces. Ivanenko *et al.* (2008a) observed a poorly sclerotized mouth tube in some specimens of all naupliar stages except nauplius I. The first two stages lack an anus and presumably do not feed.

Ivanenko *et al.* (2008b) assumed that copepodids are also directly associated with the suctorian epibionts and only indirectly with the bryozoan basibiont. They suggested that the endopodal subchelae of their maxillipeds and the stout seta on the maxillary bases served functions during the copepodid phase similar to those of the naupliar limbs. Ivanenko & Smurov (1997) sampled *Flustra foliacea* colonies from the same locality but failed to find neither suctorians nor tegastids, probably indicating that the presence of sessile ciliates is the critical factor in the symbiotic association rather than the bryozoan substratum itself. *Tegastes falcatus* is so far the only crustacean reported as an associate of a protistan during its naupliar phase of development.

Associations with macroalgae

In phytal habitats two general associations of harpacticoids can be recognized, *i.e.* those characteristic of the sediments trapped by algae when the fronds and holdfasts are heavily loaded with silt-clay or detritus, and the genuine algae-dwelling forms (Hicks & Coull 1983). Specialized families with dorsoventrally flattened (Peltidiidae, Porcellidiidae, Tisbidae) or laterally compressed (Tegastidae) members show a universal occurrence of parallelism in phytal habitats (Hicks 1980, 1985). Increased complexity (surface area) of the algal substratum typically results in a concomitant increase in harpacticoid abundance and diversity (Hicks 1977a). While the majority of phytal copepods appear to be substratum generalists, others show a marked preference for particular algal taxa and it has been suggested that feeding requirements lie probably at the root of some of these relations (Hicks 1980). Apart from a limited number of direct observations, however, there is no critical experimental verification of their trophic dependence on the algae. Hicks (1980) observed how *Parathalestris clausii* (Norman, 1869) (Thalestridae) utilizes mucilage secreted from *Fucus serratus* Linnaeus, 1753 and gathers it together with associated bacteria, diatoms, blue-green algal and fungal cells into an aggregate bolus which is then ingested. This feeding behaviour may be a response to the specific composition of the mucilaginous exudates and *Aufwuchs* community of the macrophyte, resulting in the observed preference. A similar explanation was advanced by Hicks (1977b) for *Dilatatiocauda dilatata* (Hicks, 1971) (Porcellidiidae) which has been demonstrated in experiments to actively select the brown alga *Zonaria turneriana* J. Agardh, 1870. Hicks & Grahame (1979) described self-elaboration in the phytal species *Diarthrodes nobilis* (Baird, 1846) whereby individuals from the late nauplius through to the adult stage secrete mucus through large integumental vents which the animal quickly manipulates into an enmeshing capsule. They concluded that the copepod inhabitants of these capsules were trophically dependent on the colonized bacteria and organic matter which adhered to the mucus. In contrast to nauplii of frond-mining species (see below), only a reduced antennary gnathobase and a simple tricuspidate mandibular cutting edge are present in the nauplii of *D. nobilis*, and over prolonged periods very little frond erosion by either stage in the life cycle can be observed (Hicks & Grahame 1979). It appears that the species does not make direct nutritional use of the algae since it is capable of survival and normal development inside capsules which are unattached to the fronds. Members of the Ectinosomatidae, such as *Ectinosoma melaniceps* Boeck, 1865 and *E. californicum* Lang, 1965, can frequently be observed trailing mucous threads immediately after their removal from algae, however, whether or not these are accumulations of algal-derived mucilage or self-produced remains unknown (Hicks 1985).

Although harpacticoids are occasionally encountered on marine algae drifting in the open ocean currents (Yeatman 1962), very few species are dependent for survival on the extremely unpredictable habitat of floating seaweed. *Parathalestris croni*, a widespread pelagic species in the North Atlantic north of 42°N, is often associated with floating macroalgal clumps (Wells 1970a; Ingólfsson & Ólafsson 1997) and represents the only member of the Thalestridae that has secondarily colonized the open pelagic. The species is apparently planktonic for the greater part of the copepodid phase of its life cycle during which it shows no or little affinity for floating seaweed, however, the algal substratum proves essential for the development of the naupliar stages (Ingólfsson & Ólafsson, 1997). The high ratio of ovigerous females in the seaweed and their absence in the water column are consistent with the hypothesis that the clumps serve a nest function for these harpacticoids. The photophobic adults attach themselves to the macroalgal clumps primarily with their subchelate maxillipeds, and to a lesser extent, the first two pairs of swimming legs. Eggs are deposited on the algae individually or in loose groups and, under laboratory conditions (8–9 ºC), hatch into nauplii within five days. Nauplii cannot swim and, once dislodged from the algal substratum, are unable to reattach themselves. They crawl on the algae until they metamorphose into the first copepodid stage (CoI), 15–18 days after eclosion, leaving the naupliar exuvium attached to the algal surface. The CoI copepodids abandon the floating weed and undergo the remaining moults while dispersing in the water column. Newly found clumps are colonized, probably by adults or late copepodids (CoIV–V). Precopulatory mate guarding and mating probably take place in the water column since copepodid V stages are typically rare in the clumps while pairs in amplexus are completely absent. Ingólfsson & Ólafsson (1997) observed adults in the water column during all seasons and consequently considered it likely that the life cycle of *P. croni* lasts longer than one year. The species was found to be closely associated with seaweed originating in the intertidal zone and forming floating clumps on the surface of the seas around Iceland (Ingólfsson 1995, 2000; Ingólfsson & Ólafsson 1997). The abundance of the copepod increased with distance from the coast, suggesting an off-shore planktonic habit, and was positively correlated with macroalgal clump size. Ingólfsson & Ólafsson (1997) suggested that *P. croni* showed special affinities to the alga *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863 and its red epiphyte *Vertebrata lanosa* (Linnaeus) T.A. Christensen, 1967 but this was not supported in a more extensive study (Ingólfsson 2000).

Another, more intimate, association between harpacticoids and their algal substrata involves frond-mining and/or the production of galls, a phenomenon that has recently received considerable attention (*e.g.* Apt 1988; Ho & Hong 1988; Tsukidate 1991; Saido & Yamaguchi 2003; Neill *et al.* 2008; Park *et al.* 2008). The earliest mention of a harpacticoid copepod living in marine algae is that by Barton (1891) who observed a harpacticoid, identified by G.S. Brady as *Harpacticus chelifer* (O.F. Müller, 1776), living in the rhodophyte *Palmaria palmata* (Linnaeus) Weber & Mohr, 1805. Since then five species of Dactylopusiidae and four species of Thalestridae have been

TABLE 4. Harpacticoids infesting macroalgae. Note that *Diarthrodes nobilis* is here included for its mucus-gardening capsules although it is not frond-mining. For authorities of algal hosts see text and Table 5; valid names according to AlgaeBase (Guiry & Guiry 2015).

Symbiont	Algal host	Country	Locality	Reference
Dactylopusiidae				
Dactylopusioides fodiens	*Dictyota coriacea* [1]	Japan	Hyogo Prefecture (Honshu)	Shimono *et al.* (2004a)
	Dictyota dichotoma	Japan	Hyogo Prefecture (Honshu)	Shimono e*t al.* (2004a)
Dactylopusioides macrolabris	*Dictyota dichotoma*	England	Torquay (Devon)	Green (1958)
			near Selsey Bill (West Sussex)	Ventham (2011) [2]
	Sargassum fusiforme [3]	Korea	Jeju Island	Lee (2004)
	various [4]	Algeria	El Marsa (= Jean-Bart) (Algiers)	Monard (1937)
	various [4]	Tunisia	Dar El Hout (= Salammbô)	Monard (1935)
	unknown	Ireland	Lough Hyne, Co. Cork	Holmes (2002)
	unknown	France	Nice (Alpes-Maritimes)	Claus (1866)
	unknown	Greece	Skala (Astypalaia)	Brian (1928a, b)
Dactylopusioides malleus	*Dictyopteris undulata*	Japan	Hyogo Prefecture (Honshu)	Shimono *et al.* (2007)
	Dictyota ciliolata [5]	Japan	Hyogo Prefecture (Honshu)	Shimono *et al.* (2007)
	Dictyota dichotoma	Japan	Hyogo Prefecture (Honshu)	Shimono *et al.* (2007)
Dactylopusioides sp.	*Palmaria palmata*	Japan	Uchiura Bay (Hokkaido)	Takemori & Iwasaki (2009)
Diarthrodes cystoecus	*Callophyllis crenulata*	U.S.A.	San Juan Archipelago	Fahrenbach (1962)
	Callophyllis edentata	U.S.A.	San Juan Archipelago	Fahrenbach (1962)
	Cryptopleura lobulifera	U.S.A.	west coast	Fahrenbach (1962)
	Cryptopleura ruprechtiana	U.S.A.	San Juan Archipelago	Fahrenbach (1962)
		Canada	Queen Charlotte Strait (B.C.)	Fahrenbach (1962)
	Cryptopleura spatulata	U.S.A.	San Pedro (California)	Fahrenbach (1962)
	Cryptopleura stenoglossum	U.S.A.	west coast	Fahrenbach (1962)
	Gloiocladia fryeana [6]	U.S.A.	San Juan Archipelago	Fahrenbach (1962)
	Gloiocladia laciniata [7]	U.S.A.	San Juan Archipelago	Fahrenbach (1962)
	Halosaccion glandiforme	U.S.A.	Moss Beach (California)	Fahrenbach (1954)
	Halymenia (?) sp.	U.S.A.	San Juan Archipelago	Fahrenbach (1962)
Diarthrodes feldmanni	*Cryptopleura ramosa* [8]	France	Roscoff (Brittany)	Bocquet (1953)
	Erythroglossum laciniatum [9]	France	Roscoff (Brittany)	Bocquet (1953)

……*continued on the next page*

TABLE 4. (Continued)

Symbiont	Algal host	Country	Locality	Reference
	Haraldiophyllum bonnemaisonii [10]	France	Roscoff (Brittany)	Bocquet (1953)
	Rhodophyllis divaricata [11]	France	Roscoff (Brittany)	Bocquet (1953)
	Rhodymenia pseudopalmata [12]	France	Roscoff (Brittany)	Bocquet (1953)
	Stenogramma interruptum [13]	France	Roscoff (Brittany)	Bocquet (1953)
	unknown	Ireland	Lough Hyne, Co. Cork	Holmes (2002)
Diarthrodes nobilis	*Ceramium virgatum* [14]	England	Robin Hood's Bay (Yorkshire)	Hicks & Grahame (1979)
	Heterosiphonia plumosa	England	Robin Hood's Bay (Yorkshire)	Hicks & Grahame (1979)
Harpacticidae				
Zaus sp.	*Palmaria palmata*	Japan	Uchiura Bay (Hokkaido)	Takemori & Iwasaki (2009)
Thalestridae				
Amenophia orientalis	*Undaria pinnatifida*	Japan	Tohni & Kadonohama Bays	Saido & Yamaguchi (2003)
		Korea	Gijang (Busan)	Rho *et al.* (1993), Song *et al.* (2007)
			Soando Island (Jeollanam-do)	Ho & Hong (1988)
			Songjeong (Busan)	Park *et al.* (1990), Song *et al.* (2011)
			Wando Island (Jeollanam-do)	Park *et al.* (1990), Rho *et al.* (1993)
Parathalestris infesta	*Undaria pinnatifida*	Korea	Soando Island (Jeollanam-do)	Ho & Hong (1988)
			Wando Island (Jeollanam-do)	Rho *et al.* (1993)
			Gijang (Busan)	Rho *et al.* (1993)
	unknown	Korea	Geoje Island (Gyeongsangnam-do)	Chang & Song (1997)
			Yeongok (Gangwon-do)	Back & Lee (2011)
Parathalestris sp.	*Palmaria palmata*	Japan	Uchiura Bay (Hokkaido)	Takemori & Iwasaki (2009)
Thalestris hokkaidoensis	*Palmaria palmata*	Japan	Uchiura Bay (Hokkaido)	Takemori & Iwasaki (2009)
Thalestris rhodymeniae	*Halosaccion glandiforme*	U.S.A.	San Juan Archipelago	Fahrenbach (1962)
	Palmaria palmata [15]	Ireland	Cork Harbour (Co. Cork)	Barton (1891) [16]
		Scotland	Stonehaven (Aberdeenshire)	Barton (1891) [17], Brady (1894) [18]
		Scotland	Great Cumbrae (North Ayrshire)	Harding (1954a)
		Scotland	St. Andrews Bay (Fife)	Laverack & Blackler (1974)
Thalestris sp.	*Undaria pinnatifida*	Japan	Hakodate (Hokkaido)	Torii & Yamamoto (1975) [19]
	Palmaria palmata	Japan	Uchiura Bay (Hokkaido)	Takemori & Iwasaki (2009)
	Undaria pinnatifida	Korea	Onsan-Myeon, Ulju-Gun (Ulsan)	Kang (1981) [19]

TABLE 4. (Continued)

Symbiont	Algal host	Country	Locality	Reference
Tisbidae				
Scutellidium sp.	*Undaria pinnatifida*	Korea	Wando Island (Jeollanam-do)	Park *et al.* (1990), Rho *et al.* (1993)
			Songjeong (Busan)	Park *et al.* (1990)
			Gijang (Busan)	Rho *et al.* (1993)
Unidentified				
	Ahnfeltia plicata	Germany	unknown	Gomont (1894), Houard (1908)
	Desmarestia aculeata	Scotland	Great Cumbrae (North Ayrshire)	Barton (1892)
	Undaria pinnatifida	Korea	Songjeong (Busan)	Park *et al.* (1990)
			Wando Island (Jeollanam-do)	Park *et al.* (1990, 2008 [20])
	Undaria pinnatifida	Spain	Tragova, Ría de Arousa (Galicia)	Pérez-Cirera *et al.* (1997)
			Ría de Ares y Betanzos (Galicia)	Peteiro & Freire (2013)

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[1] as *Pachydictyon coriaceum* (Holmes) Okamura, 1899.

[2] mixed brown (*Dictyota dichotoma* (Hudson) J.V. Lamouroux, 1809) and red algae (*Calliblepharis ciliata* (Hudson) Kützing, 1843; *Plocamium cartilagineum* (Linnaeus) P.S. Dixon, 1967; *Spyridia filamentosa* (Wulfen) Harvey, 1833); no frond mining recorded.

[3] as *Hizikia fusiformis* (Harvey) Okamura, 1932.

[4] mixed algae (Ulvales; *Padina pavonica* (Linnaeus) Thivy, 1960 in W.R. Taylor (1960); *Cystoseira* C. Agardh, 1820) and seagrasses (*Posidonia* König, 1805); no frond mining recorded.

[5] as *Dictyota maxima* Zanardini, 1872.

[6] as *Fauchea fryeana* Setchell, 1912.

[7] as *Fauchea laciniata* J. Agardh, 1885.

[8] as *Cryptopleura ramosum* (Huts.) Kylin [*sic*].

[9] as *Polyneura Gmelini* (Grev.) Kylin, 1924.

[10] as *Nitophyllum Bonnemaisoni* Greville [*sic*].

[11] as *Rhodophyllis bifida* (Greville) Kützing, 1847.

[12] Bocquet (1953) listed the species as *Rhodymenia Palinetta* (Esper) Grev. [*sic*] but probably meant *R. palmetta* (Stackhouse) Greville, 1830, a junior synonym of *R. pseudopalmata* (J.V. Lamouroux) P.C. Silva, 1952.

[13] as *Stenogramme interrupta* [*sic*].

[14] as *Ceramium rubrum* C. Agardh, 1811.

[15] as *Rhodymenia palmata* (Linnaeus) Greville, 1830.

[16] based on a herbarium specimen.

[17] as *Harpacticus chelifer* (O.F. Müller, 1776), *cf.* Harding (1954a).

[18] as *Fucitrogus rhodymeniæ* Brady, 1894 (based on nauplii).

[19] this record probably refers to *Parathalestris infesta (cf.* Ho & Hwang 1988: 1635).

[20] probably *Amenophia orientalis* and/or *Parathalestris infesta*.

reported to actively excavate the fronds of brown or red algae (Table 4). Members of other families such as the Harpacticidae (*Zaus* sp.) and Tisbidae (*Scutellidium* sp.) have also been observed inside galleries (Park *et al.* 1990; Rho *et al.* 1993; Takemori & Iwasaki 2009) but the algal dependence of these anecdotal records requires confirmation. The spherical shape of the nauplius appears to be typical of most algicolous nauplii that have been described (Brady 1894; Harding 1954a; Green 1958; Fahrenbach 1962; Song *et al.* 2011) but the underlying reason (except for accommodating the capacious gut) remains obscure.

Many members of the Thalestridae and Dactylopusiidae are recorded as living among algae and it seems therefore conceivable that other species of these families will be found to have frond mining habits. Unidentified burrowing copepods have been reported from the brown alga *Undaria pinnatifida* (Harvey) Suringar, 1873 along the southwestern and southeastern coasts of Korea (Park *et al.* 1990, 2008) and in two localities in Galicia, northwestern Spain (Pérez-Cirera *et al.* 1997; Peteiro & Freire 2013). Barton (1892) reported small, solitary or gregarious swellings, comprising hypertrophied tissue of tightly interwoven elements, on the thalli and stipes of the brown alga *Desmarestia aculeata* (Linnaeus) J.V. Lamouroux, 1813. The causative organism in the original material was incomplete, largely immature and not specifically identifiable (Spooner 2009). Similar gall-like protuberances exhibiting an exterior opening have been reported on the thalli of the rhodophyte *Ahnfeltia plicata* (Hudson) E.M. Fries, 1836 (Ahnfeltiales) and are probably of copepodan origin (Gomont 1894; Houard 1908).

A compilation of all available records of frond-mining harpacticoids shows that the Rhodophyta contains the most heavily and routinely inhabited hosts (Table 5). Sixteen species in five orders of red algae are attacked by burrowing copepods while only six species in three orders of brown algae serve as hosts. The reason for this preference is unknown but Fahrenbach (1962) remarked that most red algae have deep and loosely structured medullary tissues which can easily be invaded by copepods and are spacious enough to accommodate even late copepodid stages. Algae with thinner monostromatic fronds are less suitable since the later developmental stages would be forced out onto the surface as they increase in size during moulting and are, consequently, more easily dislodged.

Family Dactylopusiidae

Frond-mining strategies have evolved twice in this family, *i.e.* in the genera *Dactylopusioides* Brian, 1928b (at least three species) and *Diarthrodes* Thomson, 1883 (two species).

Dactylopusioides Brian, 1928b

All three species of *Dactylopusioides* are obligately endophagous in dictyotalean brown algae (Table 4), spending most of their lives in their burrows, eating only host algal tissues (Shimono *et al.* 2004b). *Dactylopusioides malleus* Shimono, Iwasaki & Kawai, 2007 differs from its congeners in secreting a dome-shaped capsule on the external surface of the alga during the copepodid and adult stages, whereas *D. macrolabris* (Claus, 1863) and *D. fodiens* Shimono, Iwasaki & Kawai, 2004a spend their entire life cycle within the medullary tissues of their algal hosts (Green 1958; Shimono *et al.* 2004a; Shimono & Kawai 2005). Laboratory experiments showed that *Dactylopusioides* species preferably feed on highly acidic algae (Shimono *et al.* 2004b). Takemori & Iwasaki (2009) recorded an unidentified species of *Dactylopusioides* in the opened galleries inside *Palmaria palmata* that were made and abandoned by *Thalestris hokkaidoensis* Takemori & Iwasaki, 2009.

Key to species of *Dactylopusioides* Brian, 1928b

1. Antennule ♀ 7-segmented; P1 exp-3 with four elements; P5 endopodal lobe ♂ with three elements . . . . 2.
Antennule ♀ 8-segmented; P1 exp-3 with five elements; P5 endopodal lobe ♂ with two elements . . . . *D. fodiens* Shimono, Iwasaki & Kawai, 2004a.
2. Antennary exopod with three elements; P2–P4 exp-3 with two outer spines. . . . . *D. macrolabris* (Claus, 1866).
Antennary exopod with six elements; P2–P4 exp-3 with three outer spines . . . . *D. malleus* Shimono, Iwasaki & Kawai, 2007.

TABLE 5. Algal species utilized by frond-mining harpacticoids. Classification and nomenclature according to AlgaeBase (Guiry & Guiry 2015) [* species used as substratum but not genuinely excavated by *Diarthrodes nobilis*; *cf.* Hicks & Grahame 1979]. For references containing original descriptions of host algae see Appendix 2.

PHAEOPHYCEAE	
Desmarestiales	*Desmarestia aculeata* (Linnaeus) J.V. Lamouroux, 1813
Dictyotales	*Dictyopteris undulata* Holmes, 1896
	Dictyota ciliolata Sonder *ex* Kützing, 1859
	Dictyota coriacea (Holmes) I.K. Wang, H.-S. Kim & W.J. Lee, 2004
	Dictyota dichotoma (Hudson) J.V. Lamouroux, 1809
Fucales	*Sargassum fusiforme* (Harvey) Setchell, 1931
Laminariales	*Undaria pinnatifida* (Harvey) Suringar, 1873
RHODOPHYTA	
Ahnfeltiales	*Ahnfeltia plicata* (Hudson) E.M. Fries, 1836
Ceramiales	* *Ceramium virgatum* Roth, 1797
	Cryptopleura lobulifera (J. Agardh) Kylin, 1924
	Cryptopleura ramosa (Hudson) L. Newton, 1931
	Cryptopleura ruprechtiana (J. Agardh) Kylin, 1924
	Cryptopleura spatulata N.L. Gardner, 1927
	Cryptopleura stenoglossum (J. Agardh) Kylin, 1924
	Erythroglossum laciniatum (Lightfoot) Maggs & Hommersand, 1993
	Haraldiophyllum bonnemaisonii (Kylin) A.D. Zinova, 1981
	* *Heterosiphonia plumosa* (J. Ellis) Batters, 1902
Gigartinales	*Callophyllis crenulata* Setchell, 1923
	Callophyllis edentata Kylin, 1925
	Rhodophyllis divaricata (Stackhouse) Papenfuss, 1950
	Stenogramma interruptum (C. Agardh) Montagne, 1846a
Halymeniales	*Halymenia* (?) sp.
Palmariales	*Halosaccion glandiforme* (S.G. Gmelin) Ruprecht, 1850
	Palmaria palmata (Linnaeus) Weber & Mohr, 1805
Rhodymeniales	*Gloiocladia fryeana* (Setchell) Sánchez & Rodríguez-Prieto, 2007
	Gloiocladia laciniata (J. Agardh) Sánchez & Rodríguez-Prieto, 2007
	Rhodymenia pseudopalmata (J.V. Lamouroux) P.C. Silva, 1952

Dactylopusioides macrolabris (Claus, 1866)

Claus (1866) provided a concise description of *Dactylopus macrolabris* Claus, 1866 which included illustrations of the antennule, antennary exopod, paragnaths and leg 1. Brian (1928a) mentioned "*Dactylopusioides stampaliae* n. gen. n. sp." as a *nomen nudum* in his list of the benthic copepods of the Aegean Sea. The name became available in an appendix to a subsequent report (Brian 1928b) which presented an illustrated description of the female of *D. stampaliae* which was based on a single specimen collected between algae and seagrasses along the rocky shores of Astypalaia (Italian: Stampalia), Dodecanese, in the southeastern Aegean Sea. According to Brian (1928b) the type locality of *Dactylopusioides stampaliae* (station IV) is situated off the limestone cliffs ("scogliera calcarea") of the fishing port of Skala ("Porto Scala"). Lang (1948: 564) erroneously interpreted Brian's depiction of the *locus typicus* and stated that the species had been found between coralline (calcareous) algae, a misconception that perpetuated in later papers such as those by Shimono *et al.* (2004a: 14; 2007: 66).

The subsequently recognized synonymy between *Dactylopus macrolabris* and *Dactylopusioides stampaliae* initiated a dispute between André Monard and Karl Lang. The first account that established the conspecificity of both species was published by Monard (1935a) who obtained numerous females and males in washings of algae from the rocky shores around the quarantine station (lazaret) and Cap Carthage near Dar El Hout (Salammbô) in Tunesia. He also provided the first description of the male and confirmed the validity of the genus *Dactylopusioides*. Lang (1936a), without examining material, arrived at the same conclusion regarding the synonymy, but did not cite Monard's (1935a) publication. Monard (1937) collected *D. macrolabris* in algal washings from the Algiers region in Algeria, and claimed priority as the First Reviser for the nomenclatural act by stating "Lang (1936) en a fait de même". Lang (1948: 563) vigorously rejected Monard's (1937) assertion, claiming instead that he had stolen his thunder based on prior correspondence between both authors.

Green (1958) was the first to discover and observe the frond-mining habits of *D. macrolabris*. His examination of the fronds of the brown alga *Dictyota dichotoma* (Hudson) J.V. Lamouroux, 1809 collected in Torquay, England, revealed various naupliar stages, one copepodid and an associated adult female, all of which inhabited galleries between the two epidermal layers of the alga. Unlike the mediterranean specimens which have a yellow (Claus 1866, Monard 1935a) or tawny (Brian 1928b) appearance, all stages in the Torquay material displayed a brilliant crimson colour. The naupliar stages have powerful antennary gnathobases which are used to penetrate the algal cortex and feed on the medullary tissues. The only other record from northwestern Europe is that by Ventham (2011) who recorded the species from mixed algae (*Calliblepharis ciliata* (Hudson) Kützing, 1843; *Plocamium cartilagineum* (Linnaeus) P.S. Dixon, 1967; *Spyridia filamentosa* (Wulfen) Harvey, 1833; *Dictyota dichotoma*) near Selsey Bill on the West Sussex coast (England).

Lee (2004) reported *D. macrolabris* from the brown alga *Sargassum fusiforme* (Harvey) Setchell, 1931 (as *Hizikia fusiformis* (Harvey) Okamura 1932) (Fucales) from Jeju Island, Korea. The algal host assumes a limited distribution in East Asia, including confirmed records from Japan, Korea and China. Lee's drawings confirm that he was dealing with a member of *Dactylopusioides* but his illustrations cast doubt on the authenticity of his identification. The female antennule in the Korean specimens is described as 8-segmented, showing four, one and one spiniform elements on segments 2–4, respectively. Re-examination of Ventham's (2011) material (NHMUK reg. nos 2015.997–1000) of *D. macrolabris* confirmed the 7-segmented condition of the antennule and the presence of two and three enlarged bulbiform setae on segments 2 and 3, respectively. Lee's (2004) illustration of leg 5 corresponds well with the European descriptions in the morphology of the baseoendopod, but is radically different in the armature of the exopod. The innermost seta (I) is four times as long as seta V in the Korean specimens as opposed to both setae being equally long in the European populations; this character is not found in any other member of the genus and, provided the observation is correct, would substantiate the distinct specific status of Lee's material. Shimono *et al.* (2003) also reported *D. macrolabris* from Japanese coastal habitats but did not gave any detailed information about the locality or host algae. Although not being confirmed by the authors it is possible that this material corresponds to one of the two *Dactylopusioides* species that were subsequently discovered in Japanese waters (Shimono *et al.* 2004a, 2007).

OD: Claus (1866—as *Dactylopus macrolabris*): 29; Plate III (Figs 26–29) (♀).
AD: Brian (1928b—as *Dactylopusioides stampaliae* Brian, 1928b): 338–340; Figs 53–59. Monard (1935a): 41–45, 89–90; Figs 43–55. Green (1958): 49–52; Figs 1–13.
TL: France, Provence-Alpes-Côte d'Azur, Alpes-Maritimes Department, Nice; no other locality data given but presumably obtained from algal washings.
BL: 850 µm (♀) [Claus 1866]; 600 µm (♀) [Brian 1928b]; 700–820 µm (♀), slightly smaller (♂) [Monard 1935a]; 103–234 µm (nauplii) [Green 1958].

Dactylopusioides fodiens **Shimono, Iwasaki & Kawai, 2004a**

This species inhabits galleries mined in the thalli of two species of brown algae, *Dictyota dichotoma* and *D. coriacea* (Holmes) I.K. Wang, H.-S. Kim & W.J. Lee, 2004 (Dictyotales), in western Japan. It was not found in other Dictyotales occurring in the region, such as *Dictyopteris prolifera* (Okamura) Okamura, 1930, *Padina arborescens* Holmes, 1896, *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim, 2009, and *Zonaria diesingiana* J. Agardh, 1841. Galleries are excavated beneath the cuticle of the cortical cells, leaving the epidermal layers unaffected (Shimono & Kawai 2005: Fig. 1). Laboratory experiments showed that the copepods occupied galleries only for a few days and continuously moved to newly mined ones. Ovigerous females carry a single egg sac, containing 6–14 eggs, for 2–4 days after which it is deposited in the gallery. Nauplii emerge after a few days while the development time from nauplius I to adult takes 20–30 days under laboratory conditions at 18 °C (Shimono *et al.* 2004a). Adults display a reddish colour. Monthly sampling at the type locality showed that *D. fodiens* occurs from April to September in both intertidal and subtidal zones.

OD: Shimono *et al.* (2004a): 10–14; Figs 1–3.

TL: Japan, Honshu, Sea of Japan; Hyogo Prefecture, Mikata district; Kami, Imagoura (35°40'N, 134°37'E); inside galleries mined in thalli of *Dictyota dichotoma* (Hudson) J.V. Lamouroux, 1809 (Phaeophycaea, Dictyotales).

BL: 700 µm (♀; holotype 720 µm), 600 µm (♂).

Dactylopusioides malleus Shimono, Iwasaki & Kawai, 2007

According to Shimono *et al.* (2007) most life cycle stages can be found inside burrows excavated in the thalli of the dictyotalean brown algae *Dictyopteris undulata* Holmes, 1896, *Dictyota ciliolata* Sonder ex Kützing, 1859 and *D. dichotoma*.

Shimono *et al.* (2007) conducted laboratory experiments showing that eggs hatched in 3–4 (3.6 ± 0.5) days. The first naupliar stages penetrated the thallus with their mouthparts creating a burrow between the epidermal layers of the algal host. Nauplii underwent several moults inside the gallery, forming a gelatinous matrix within which they metamorphosed. After metamorphosis copepodids left the burrow and continued development on the surface of the algal tissue, inside a capsule made of mucus they secreted. At 18 °C, the copepodid phase was completed in 9–13 (11.2 ± 1.5) days. Both nauplii and copepodids occasionally left the burrows or capsules and formed new ones while adult females changed capsules at intervals of 2.2 ± 1.2 days. Ovigerous females produced a single egg sac, containing 7–24 (17.1 ± 4.1) eggs, at intervals of 4.3 ± 1.2 days, and retained the egg sac until the nauplii emerged. The colour of the adults ranges from greenish-brown to brownish-green.

Unlike *Diarthrodes nobilis*, which secretes mucus capsules for self-elaboration (Hicks & Grahame 1979), *D. malleus* feeds on the host algal tissue and utilizes the capsules only as a physical protection from wave action or predators.

The species is so far endemic to Honshu, Japan, where it was recorded on both northern and southern coasts of Hyogo Prefecture. Shimono *et al.* (2007) reported it from Imagoura, Kasumi (35°39'N, 134°38'E) on the Sea of Japan coast and Maiko, Kobe (34°37'N, 135°2'E) in addition to two localities on Awaji Island (Oiso, 34°33'N, 134°59'E; Yura, 34°16'N, 134°57'E) in the Seto Inland Sea. It was found from May to August in the intertidal and subtidal zones.

OD: Shimono *et al.* (2007): 60–65; Figs 1–3.

TL: Japan, Honshu, Seto Inland Sea; Hyogo Prefecture; Awaji Island, Oiso (34°33'N, 134°59'E); inside galleries mined in thalli of *Dictyota dichotoma* (Hudson) J.V. Lamouroux, 1809 (Phaeophycaea, Dictyotales).

BL: 740 µm (♀; holotype 760 µm), 620 µm (♂).

Diarthrodes Thomson, 1883

The genus *Diarthrodes* currently accommodates 41 valid species (Wells 2007; Gómez *et al.* 2008), two of which, *D. feldmanni* Bocquet, 1953 and *D. cystoecus* Fahrenbach, 1954, are known to inhabit red algae. Both species are morphologically very similar and actively feed on the algal medullary tissues, the nauplii being the particularly destructive phase in the life cycle. In *D. cystoecus* the production of encapsulating mucus domes by copepodids and adults emerging from the burrows has been attributed to the protection of the copepods and their progeny from currents and mechanical dislodgement by adjacent moving fronds (Fahrenbach 1962). Previous reports have shown that other *Diarthrodes* species such as *D. minutus* (Claus, 1863) and *D. nobilis*, in response to mechanical or chemical irritation, secrete a viscid fluid which solidifies in contact with water, forming a capsule around the animal on the surface of the algal frond (Sars 1906a: 143; Lang 1948: 126). Although little is known about the feeding biology of the nauplii of these species, a direct trophic dependence of *D. nobilis* adults on the bacteria and organic agglutinations that adhere to the mucus has been demonstrated (Hicks & Grahame 1979).

Gómez *et al.* (2008) divided the genus into seven groups based on the number of segments in the antennary exopod and the ramal segmentation of leg 1. Both *D. feldmanni* and *D. cystoecus* were placed in Group VII and can be identified using the key below. Note that the antennary exopod of *D. major* (Scott & Scott, 1895a) was incorrectly scored as 2-segmented instead of 3-segmented (*cf.* Sars (1911—as *Pseudothalestris monensis* Brady, 1902)) in Wells's (2007: 365) tabular keys; the species should therefore key out to KG4 (Wells 2007: 372) together with *D. tetrastachyus* Yeatman, 1976, *D. lilacinus* Pallares, 1977 and *D. brevipes* Wells & Rao, 1987. The taxonomy of *Diarthrodes* is in a state of disarray and extreme caution must be exercised while attempting to identify species from outside the type locality. Lang (1948, 1965) in particular has contributed to the taxonomic confusion by lumping together several species which look vaguely similar, supporting the concept of highly variable, widely distributed species within the genus. For example, despite its inadequate and fragmentary original description, *D. ponticus* Krićagin, 1877 was used as a repository to assimilate *Westwoodia saturni* Farran, 1913, *W. assimilis* var. *dubia* Brian, 1921 and *W. mediterranea* Monard, 1928. Recently, Wells & Rao (1987) sustained the concept of *D. cystoecus* being a virtually cosmopolitan species (with records from California and Washington State, Tierra del Fuego, India, the Maldives and the Andamans); however, given its supposed conspecificity with the northwest European *D. feldmanni* (*cf.* Fahrenbach 1962; Pallares 1977) its status as a highly variable species has by now probably been stretched beyond its limits. The key below attempts to take this local "variability" into account but a full revision of the group is desirable before correct identifications can be arrived at with entire confidence.

Key to species of *Diarthrodes* Thomson, 1883—Group VII only

1.	Antennary exopod 1-segmented	2.
	Antennary exopod 2-segmented	3.
	Antennary exopod 3-segmented [1]	4.
2.	P1 with 2-segmented rami	Group I [2].
	P1 with 2-segmented exopod and 3-segmented endopod	Group II [3].
3.	P1 with 1-segmented exopod and 3-segmented endopod	Group III [4].
	P1 with 2-segmented exopod and 3-segmented endopod	Group V [6].
4.	P1 with 1-segmented exopod and 3-segmented endopod	Group IV [5].
	P1 with 2-segmented rami	Group VI [7].
	P1 with 2-segmented exopod and 3-segmented endopod	Group VII...5.
5.	P4 enp-2 with two inner setae [8]	6.
	P4 enp-2 with one inner seta [8]	11.
6.	Antennule ♀ 6-segmented, with aesthetasc on segment 3; P1 enp-1 inner seta reaching well beyond distal margin of enp-3; P1 enp-3 inner claw about 1.5 times as long as outer claw	*D. brevipes* Wells & Rao, 1987.
	Antennule ♀ 6-, 7- or 8-segmented, with aesthetasc on segment 4; P1 enp-1 inner seta reaching at most to distal margin of enp-3; P1 enp-3 inner claw at least twice as long as outer claw	7.
7.	Antennule ♀ 7-segmented; P5 ♀ with four elements on both exopod and baseoendopod; P5 ♂ with four elements on exopod	*D. tetrastachyus* Yeatman, 1976.
	Antennule ♀ 6- or 8-segmented; P5 ♀ with 5–6 elements on exopod and five elements on baseoendopod; P5 ♂ with five or six elements on exopod	8.
8.	Antennule ♀ 6-segmented; P1 enp-1 inner seta originating from proximal third of segment	*D. minutus* (Claus, 1863) [8].
	Antennule ♀ 8-segmented; P1 enp-1 inner seta originating from middle third of segment	9.
9.	P1 exp-2 with inner seta; P5 ♀ with six elements on exopod	*D. septemtrionalis* **sp. nov.** [9].
	P1 exp-2 without inner seta; P5 ♀ with five elements on exopod	10.
10.	P2 enp-2 with two inner setae; P5 ♂ with five elements on exopod	*D. lilacinus* Pallares, 1977.
	P2 enp-2 with one inner seta; P5 ♂ with six elements on exopod	*D. major* (Scott & Scott, 1895a).
11.	Antennule ♀ 5-segmented with aesthetasc on segment 3; P5 exopod with six elements in both sexes	*D. assimilis* (Sars, 1906a) [10].
	These characters not combined	12.
12.	P1 enp-3 inner claw at most 1.5 times the length of outer claw	13.
	P1 enp-3 inner claw at least twice the length of outer claw	14.
13.	Antennule ♀ 8-segmented with aesthetasc on segment 4; P2 enp-2 ♀ with one inner seta; P5 exopod ♀ with six elements	*D. roscoffensis* (Monard, 1935b).
	Antennule ♀ 6-segmented with aesthetasc on segment 3; condition of P2 enp-2 ♀ and P5 exopod ♀ unconfirmed	*D. ponticus* (Krićagin, 1877) [11].
14.	P1 exp-2 with seta on inner margin, two distal and 2–3 outer elements	15.
	P1 exp-2 without inner seta; with two distal and 2–3 outer elements [12]	23.
15.	Antennule ♀ 6-segmented with aesthetasc on segment 4; inner seta on P1 enp-1 arising from proximal quarter of segment	*D. minutus* (Claus, 1863) [8].
	Antennule ♀ 6-segmented with aesthetasc on segment 3; inner seta on P1 enp-1 arising from middle third of segment	16.
16.	Caudal ramus seta V ♀ modified, forming bulbous section in proximal part	*D. ponticus orientalis* Apostolov, 1975.
	Caudal ramus seta V ♀ normally developed	17.

17. Insertion site of inner seta on P1 enp-1 located halfway down the margin (50% of length) .... 18.
Insertion site of inner seta on P1 enp-1 located more proximally, at 30–40% of margin length .... 19.

18. P1 enp-3 inner claw 2.2 times as long as outer claw; P5 ♀ endopodal setae II–V about equally long; exopodal seta I twice the length of seta III .... *D. ponticus* (Krićagin, 1877) *sensu* Apostolov (1973b).
P1 enp-3 inner claw 2.75 times as long as outer claw; P5 ♀ endopodal setae II–IV distinctly longer than seta V; exopodal setae I and III about equally long.. *D. feldmanni* Bocquet, 1953.

19. Antennulary segment 3 in ♀ 0.8 times as long as segments 4–6 combined (measured along non-setiferous posterior margin); P5 ♀ exopodal seta I distinctly shorter than seta III .... 20.
Antennulary segment 3 in ♀ as long as or longer than segments 4–6 combined (measured along non-setiferous posterior margin); P5 ♀ exopodal seta I at least as long as but typically distinctly longer than seta III .... 21.

20. P5 ♀ exopodal setae IV–V equally long; endopodal seta III much longer than seta IV................................ .... *D. cystoecus* Fahrenbach, 1954 *sensu* Wells & Rao (1987)[13].
P5 ♀ exopodal seta V distinctly shorter than seta IV; endopodal setae III–IV about equally long .... *D. cystoecus* Fahrenbach, 1954 *sensu* Sewell (1940)[14].

21. P1 enp-3 inner claw 3.7 times as long as outer claw; P5 ♀ endopodal seta II distinctly shorter than seta IV............... .... *D. cystoecus* Fahrenbach, 1954[15].
P1 enp-3 inner claw at most three times as long as outer claw; P5 ♀ endopodal setae II and IV about equally long....... 22.

22. Antennulary segment 3 in ♀ 1.3 times as long as segments 4–6 combined (measured along non-setiferous posterior margin); P5 ♀ exopodal seta V about 90% of length of seta IV, and seta I about 1.5 times as long as seta III .... *D. ponticus* (Krićagin, 1877) *sensu* Thompson & Scott, 1903[14].
Antennulary segment 3 in ♀ about as long as segments 4–6 combined (measured along non-setiferous posterior margin); P5 ♀ exopodal seta V about 60% of length of seta IV, and seta I about 3.5 times as long as seta III.......................... .... *D. cystoecus* Fahrenbach, 1954 *sensu* Pallares (1977).

23. P1 enp-3 inner claw 2.2–2.6 times as long as outer claw....... *D. ponticus* (Krićagin, 1877) *sensu* Brian (1921[16], 1928a[17]).
P1 enp-3 inner claw 3.1–3.5 times as long as outer claw .... 24.

24. Antennule ♀ 6-segmented; P5 ♀ endopodal lobe, distal edge between setae II and III smoothly curved and with short fine setules .... *D. ponticus* (Krićagin, 1877) *sensu* Farran (1913)[18].
Antennule ♀ 5-segmented; P5 ♀ endopodal lobe, distal edge between setae II and III straight and not ornamented.......... .... *D. ponticus* (Krićagin, 1877) *sensu* Monard (1928)[19].

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[1] Wells & Rao (1987) noted variability in the segmentation of the antennary exopod in their specimens of *D. cystoecus*; females of their varieties C and D in addition to all males examined show the 2-segmented condition while females of varieties A and B display a distinctly 3-segmented exopod. Given that all varieties (A–D) came from the Middle and South Andamans, the authors believed that there was insufficient evidence to place them in separate species and preferred to think that they belong to a single, highly variable species. Contemporary taxonomists would probably reject this concept in favour of a set of sibling species which does not include *D. cystoecus*. Only the specimens displaying a 3-segmented antennary exopod are included in this key.

[2] includes *D. andrewi* (T. Scott, 1894b); *D. tumidus* (Brady, 1910); *D. intermedius* (T. Scott, 1912); *D. falcipes* Marinoni, 1964; *D. dissimilis* Lang, 1965; *D. glaber* Wells, 1967; *D. hirami* Por, 1967; *D. gravellicola* Soyer, 1975; *D. tripartitus* Gómez, Chertoprud & Morales-Serna, 2008; and *D. apostolovii* Gómez, Chertoprud & Morales-Serna, 2008.

[3] includes *D. novaezealandiae* Thomson, 1883; *D. nanus* (T. Scott, 1914); *D. aegidaeus* (Brian, 1928a); *D. gurneyi* Lang, 1948; *D. unisetosus* Lang, 1965; *D. drachi* Bodiou, 1974; *D. parvulus* Pallares, 1977; *D. latisetosus* Chislenko, 1978; and *D. imitator* Gómez, Chertoprud & Morales-Serna, 2008.

[4] includes *D. purpureus* (Gurney, 1927).

[5] includes *D. nobilis* (Baird, 1846) and *D. fahrenbachi* Bodin, 1968.

[6] includes *D. imbricatus* (Brady, 1883); *D. pygmaeus* (Scott & Scott, 1895a); *D. sarsi* (A. Scott, 1909); *D. pusillus* (Brady, 1910); *D. campbelliensis* Lang, 1948; and *D. hexasetosus* Gómez, Chertoprud & Morales-Serna, 2008.

[7] includes *D. zavodniki* Apostolov & Petkovski, 1980; *D. nhatrangensis* Gómez, Chertoprud & Morales-Serna, 2008; and *D. savinkinii* Gómez, Chertoprud & Morales-Serna, 2008.

[8] since the armature formula of P2–P4 of *D. minutus* is unknown the species is included in both alternatives of this couplet. Lang (1948) suspected that the discrepancies between the mediterranean (Claus 1863; Brian 1928b; Monard 1928) and northwest European (Sars 1906a) descriptions possibly reflect the existence of a species complex. Sars (1906a) illustrates the male P2 with two instead of three outer spines on the distal exopodal segment; provided his observation is correct, this character differentiates the Norwegian *D. minutus* material from all other congeners in *Diarthrodes*. Since the brief descriptions by Claus (1863—as *Westwoodia minuta* Claus, 1863), Brian (1928b—as *W. minuta*) and Monard (1928—as *W.* (*Pseudothalestris*) *minuta*) contain conflicting evidence (*e.g.* armature of P1 exp-3) the characters used in this key are based on Sars's (1906a) redescription, admitting however that it may well have been based on a species different from Claus's *D. minutus*.

[9] Kornev & Chertoprud (2008: 192–194; Figs 5.91A–E, 5.92A–B) provided a brief redescription of a *Diarthrodes* species from an undisclosed locality in the White Sea (probably Kandalaksha Gulf) which they attributed to *D. roscoffensis*, presumably on the basis of the 8-segmented antennule and the presence of only one seta on P2 enp-2. The presence of two

setae on P4 enp-2 (although the setal formula makes mention of only one inner seta their Fig. 5.92B clearly shows two) and the proportional lengths of the two claws on P1 enp-3 indicate that the authors were dealing with a different, as yet undescribed, species. The female specimen illustrated by Kornev & Chertoprud (2008: 193) in their Fig. 5.91.A is here designated as the holotype of *D. septemtrionalis* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the key above and those mentioned and illustrated in Kornev & Chertoprud (2008) (ICZN Art. 13.1). The specific epithet refers to the northern distribution of the species.

[10] Apostolov's (1972) Black Sea specimens described as "*D. assimilis?* ♂" were recognized as a distinct species, *D. apostolovii*, by Gómez *et al.* (2008); although Apostolov attributed his drawings to the male, at least the antennule and the dorsal habitus are based on the female.

[11] Based on Krićagin's (1877) original description from material collected in shallow water off Novorossiysk in the Black Sea (Russia); although his illustration of the female antennule leaves doubt for interpretation the author does explicitly state in the text that it is 6-segmented.

[12] Pesta's (1959) specimens identified as *D. ponticus* key out here but are omitted from the remaining couplets because the size difference of the endopodal claws between the female and male leg 1, in addition to the alleged variability in the female leg 5, suggest that his material consisted of a mixture of two or more species.

[13] Varieties A and B only (Wells & Rao 1987: 45–46, Table 3, Figs 43–45).

[14] As *Pseudothalestris imbricata* Brady, 1883.

[15] Based on Fahrenbach's (1962) redescription.

[16] As *Westwoodia assimilis* var. *dubia* Brian, 1921.

[17] As *Westwoodia dubia* Brian, 1921.

[18] Originally described as *Westwoodia saturni* Farran, 1913 based on Irish material; this name was subsequently considered a junior subjective synonym of *D. ponticus* by Lang (1948).

[19] Originally described as *Westwoodia* (*Pseudothalestris*) *mediterranea* Monard, 1928 based on material from Banyuls-sur-Mer; this name was subsequently considered a junior subjective synonym of *D. ponticus* by Lang (1948).

Diarthrodes feldmanni **Bocquet, 1953**

Bocquet (1953) recorded the species from several red algae collected in the aquarium tanks of the Station Biologique de Roscoff, including three species of Ceramiales (*Cryptopleura ramosa* (Hudson) L. Newton, 1931; *Erythroglossum laciniatum* (Lightfoot) Maggs & Hommersand, 1993; *Haraldiophyllum bonnemaisonii* (Kylin) A.D. Zinova, 1981), two species of Gigartinales (*Rhodophyllis divaricata* (Stackhouse) Papenfuss, 1950; *Stenogramma interruptum* (C. Agardh) Montagne, 1846a) and one member of the Rhodymeniales (*Rhodymenia pseudopalmata* (J.V. Lamouroux) P.C. Silva, 1952).

According to Bocquet (1953) nauplius I is the infective stage which penetrates the host by active feeding. During most of their life cycle the copepods continue to feed on the medullary tissues of the thallus, leaving only the cuticle intact. All stages of *D. feldmanni*, from nauplius I to copepodid V are found in the burrows. The naupliar stages form a subrectilinear gallery which is gradually widened out with every moult to a semicircular terminal chamber. Copepodids moult several times inside the chamber, depositing their exuvia. The copepod leaves the algal host at copepodid V stage but stays in close contact on the external surface of the thallus, being embedded in a gelatinous matrix within which the final moult is completed. Mating takes place outside the host. The adults are dark red, displaying bluish-brown spots. Except for Holmes' (2002) records from Lough Hyne in Ireland the species has not been recorded again since its original description.

OD: Bocquet (1953): 101–104; Figs 1–2; unnumbered plate.
TL: France, Brittany, Roscoff; aquarium of Station Biologique de Roscoff; inside galleries excavated in the thalli of Rhodophyta. Bocquet (1953) listed six species of red algae (Table 4) but did not specify which one the type material originated from.
BL: ≈ 900 μm (♀), 700–750 μm (♂).

Diarthrodes cystoecus **Fahrenbach, 1954**

Fahrenbach (1954) observed large numbers of ovigerous females in the organic and silty sediment inside the water-filled bladder-like thalli of the intertidal red alga *Halosaccion glandiforme* (S.G. Gmelin) Ruprecht, 1850. About 70–80% of the algae at the type locality in California were infected by *D. cystoecus*. In a subsequent study of subtidal red algae in the San Juan Archipelago, Washington, Fahrenbach (1962) found *D. cystoecus* consistently in *Gloiocladia fryeana* (Setchell) Sánchez & Rodríguez-Prieto, 2007, *G. laciniata* (J. Agardh) Sánchez & Rodríguez-Prieto, 2007 and *Cryptopleura ruprechtiana* (J. Agardh) Kylin, 1924, and occasionally in *Callophyllis edentata* Kylin, 1925, *C. crenulata* Setchell, 1923 and *Halymenia* (?) sp. Within the geographical range delimited by Queen Charlotte Sound, British Columbia in the north and San Pedro, California in the south herbarium specimens of other algae also showed signs of infestation, *i.e. Cryptopleura lobulifera* (J. Agardh) Kylin, 1924, *C. spatulata* N.L. Gardner, 1927 and *C. stenoglossum* (J. Agardh) Kylin, 1924 (Table 4) (Fahrenbach 1962). Although the type host alga, *H. glandiforme*, assumes a north Pacific distribution from the Kamchatka Peninsula in Asia to Point Conception, California in North America (Guiry & Guiry 2015), it is unlikely that the geoegraphical range of *D. cystoecus* mirrors that of its host. Fahrenbach (1962) examined *Halosaccion* in the San Juan Archipelago but only found infestations by *Thalestris rhodymeniae* (Brady, 1894).

Early naupliar stages burrow into the inside wall of the *Halosaccion* thallus and, as they moult into successive stages, produce a gall (up to 1.5 mm in diameter) which projects about 1 mm above the external surface (Fahrenbach 1954). On the inner side of the bladder similar protuberances develop as the copepods grow, each showing eventually a perforation through which the animals (often tightly packed ovigerous females) escape. Most bladders have small ruptures opening to the exterior, enabling the copepods to leave the host and (probably after nauplii have hatched) infect neighbouring algae. Some fronds can be heavily infected showing up to 33 galls per 10 cm^2, leading to extensive perforation of the algae. In contrast to the condition in the type host, *H. glandiforme*, no such galls appear in any other algae (Fahrenbach 1962). Instead, the nauplii either excavate sharply delimited tunnels with wide terminal chambers (in *Callophyllis*, *Cryptopleura* and *Halymenia*) or feed on the medullary tissues in a more irregular, circular fashion (in *Gloiocladia*). Fahrenbach (1962) observed that naupliar burrows radiated from a common starting point, presumably coinciding with the region in which the adult female had abraded the cortical layer of the algal frond. In monostromatic algae such as *Cryptopleura* spp. nauplii and early copepodids eat the cells in their entirety leaving only the superficial cell walls and pectin layer intact. Population densities of *D. cystoecus* in the San Juan Archipelago and California appear to peak around late July-early August after which the species becomes relatively rare and eventually disappears. It is unknown in which stage and in which alga the population maintains itself during winter. Fahrenbach (1962) described the complete life cycle, comprising six naupliar and five subadult copepodid stages.

In algae other than *H. glandiforme* adult females typically form protective dome-shaped capsules on the surface of the frond within which the eggs are laid and develop. Capsule formation takes place in 10–15 minutes by secreting a mucoid substance that hardens on contact with water. The cement which forms the capsules is contained in large paired reservoirs that fill the cavity of the cephalothorax and first two pedigerous somites almost entirely between gut and body wall. Prior to mating, the free-swimming male invades a cement capsule housing a mature female, usually within 24 hours of the female's final moult. During precopulatory mate guarding, which can take hours to days, males firmly clasp a single caudal ramus seta with both antennules. When mating is attempted, the male turns ventrally under the female's abdomen, maintaining its grip on the caudal seta which becomes bent at a 90° angle. The male modified leg 2 engages the setae of the female leg 5, resulting in its eventual raising and the consequent exposure of the genital field. Spermatophore transfer lasts about 10–15 seconds after which the male returns to its original clasping posture. Spermatophore discharge takes place immediately upon successful insertion of its neck into the copulatory pore. Oviposition starts about 24 hours later and is completed in less than five hours. Eggs at the time of oviposition have an average diameter of 75 µm. Rather than being enclosed by a common egg sac membrane, adjacent envelopes of eggs are fused to form a three-dimensional honeycomb throughout the egg sac which on average contains 18 eggs. The almost spherical first naupliar stage is incapable of swimming or crawling and depends on the cement dome for protection and initial survival. Upon eclosion (after eight days at 12 °C), it starts to feed at once on the algal medulla, which has previously been made accessible by the maternal female's gradual abrading of the cortical layer. When successful, the first nauplius becomes completely embedded inside the algal tissue in 24–32 hours. The second or third copepodid emerges from the burrow to feed on the algal surface and completes the remaining moults inside a secreted capsule. The copepodid phase prior to the final moult lasts for 13–16 days at 13 °C. The adult female frequently abandons the enclosure after the terminal moult in favour of a newly secreted one elsewhere on the frond (Fahrenbach 1962). Adults are a ruby-red colour and have a deep-red nauplius eye in life.

During feeding adults adpress the oral cone tightly to the algal substratum. Tearing of the algal cells is accomplished by the maxillules, particularly the arthrites which convey the torn off food material into the mouth which subsequently is guided into the oesophagus by the mandibular gnathobases. In the nauplii only the antennae are used for feeding. During this process the oral area is pressed against the cell wall by the action of the mandibles. Cell walls are eaten away with the cell contents. Nauplii are constant and voracious feeders, ingesting between 10 and 40 "stomach-fulls" per day or a maximum of one stomach-full every 36 minutes. During moulting extreme adduction of the antennary bases and gnathobases results in the withdrawal of the gnathobasal setae from the mouth. According to Fahrenbach (1962) this allows moulting of the cuticular stomodeum without causing the topological difficulties that would arise if two interlocking cuticular parts were to moult simultaneously. The feeding activity of the copepodids is less vigorous, showing long quiescent intervals alternating with short active periods. Attempts to raise the nauplii and maintain the adults on artificial substrata such as agar or agar combined with algal extracts were unsuccessful (Fahrenbach 1962).

Although Fahrenbach (1954) stated that the presence of males could not be ascertained, his illustration of leg 5 clearly depicts the male condition. Unfortunately, his supplementary description of both sexes (Fahrenbach 1962) is deficient in several aspects, making it difficult to decide whether any of the subsequent records can be attributed to this species. Pallares (1977) claims to have rediscovered *D. cystoecus* off Isla de los Estados, Tierra del Fuego (Argentina) where she collected it in plankon samples taken at low tide, washings of *Macrocystis* clumps and from sediments covered with red algae (Delesseriaceae). She argued that the species may be conspecific with *D. feldmanni* but, in the absence of available specimens from the two type localities, refrained from synonymizing them. Lang (1965) believed that Sewell's (1940) female of *Pseudothalestris imbricata* Brady, 1883 from the Maldives in reality may be identical with *D. cystoecus* rather than representing the previously unknown female of *Diarthrodes imbricatus* (Brady, 1883). Wells & Rao (1987) considered it reasonable to assume that the distribution range of *D. cystoecus* extends to the Indian Ocean and included Krishnaswamy's (1957) Indian specimens of *P. imbricata* from the Chennai coast as another probable record of *D. cystoecus*. Wells & Rao (1987) themselves described four female varieties (based on 15 specimens!) from the Andaman Islands which may be referable to this species. However, the considerable differences between the various descriptions throw doubts on the conspecificity of all these populations and whether any of them can be assigned to *D. cystoecus* is unclear. It is conceivable that authors have described real variation, but whether this is due to the species being morphologically plastic or *Diarthrodes* containing suites of very similar, closely related species remains unconfirmed (Wells 2007). None of the post-Fahrenbach records made mention of frond-mining activities or other symbiotic relationships with an algal host.

Fahrenbach (1962) employed histological methods to elucidate the details of the internal anatomy, including the integument, the digestive, reproductive, excretory and nervous systems, sense organs and glands.

OD: Fahrenbach (1954—as *D. cystœcus*): 326–328; Figs 1–9.

AD: Sewell (1940—as *Pseudothalestris imbricata* Brady, 1883): 237–239; Text-Fig. 47. Fahrenbach (1962—as *D. cystœcus*): 306–374; Table I; Figures 1–3; Plates I–IX. Pallares (1977): 10–11; Plate III. Wells & Rao (1987): 42–46, 215, 267–269; Table 3; Figs 43–45.

TL: U.S.A., California, San Mateo County, Moss Beach; inside the water-filled bladder-like thalli of *Halosaccion glandiforme* (S.G. Gmelin) Ruprecht, 1850 (Rhodophyta, Palmariales).

BL: 740 µm (♀) [Sewell 1940]; 500–800 µm (♀) [Fahrenbach 1954]; 88–92 µm (Nauplius I), 100–120 µm (Nauplius II), 141–148 µm (Nauplius III), 180–185 µm (Nauplius IV), 201–225 µm (Nauplius V), 207–280 µm (Nauplius VI), 290–323 µm (CoI), 383–445 µm (CoII), 540–660 µm (CoIII), 540–782 µm (CoIV), 630–860 µm (CoV), 720–880 µm (♀), 720–880 µm (♂) [Fahrenbach 1962]; 690–850 µm (♀), 600–758 µm (♂) [Pallares 1977]; 710–725 µm (♀), 404–410 µm (♂) [Wells & Rao 1987].

Family Thalestridae

Three thalestrid genera are known to contain representatives that exhibit frond-mining activities, *i.e. Thalestris* Claus, 1862, *Amenophia* Boeck, 1865 and *Parathalestris* Brady & Robertson, 1873.

Amenophia Boeck, 1865

The genus currently accommodates four species, *A. peltata* Boeck, 1865, *A. pulchella* Sars, 1906a, *A. ovalis* Brady, 1910 and *A. orientalis* Ho & Hong, 1988, of which only the latter is known to excavate seaweed in the Far East. Although *A. orientalis* can readily be distinguished from its congeners, identification of the remaining species is notoriously difficult. Wells (2007) remarked that caution needs to be exercised when using traditional characters such as body size, relative length of the rami of leg 1 and colour patterns as these may not be viable due to the degree of compression in mounted specimens, incorrect alignment, and pigment loss in preserved material, respectively.

Except for Roe's (1958) record of a single aberrant female from a rock crevice on Dalkey Island, Co. Dublin, no other illustrations of *A. pulchella* have been published since its original description from Kristiansund in western Norway (Sars 1906a) and the male has remained unknown. Although additional records have been noted from Bergen, Norway (Drzycimski 1969) and the Svaberget banks off the Swedish west coast (Berggren 2012; Karlsson *et al.* 2014), the species appears to be rare. *Amenophia ovalis* is known only from the type locality in Observatory Bay in the Kerguelen, southern Indian Ocean. Unfortunately Brady's (1910) poorly rendered illustrations make reliable identification virtually impossible. The position of the inner endopodal seta on leg 1 and the spacing of the setae on the endopodal lobe of the female leg 5 cast doubt on the generic assignment of this species. The exopod of the latter leg also appears to be foreshortened in Brady's Text-fig. XXIV–7. Pending re-examination of the types, *A. ovalis* is here considered a *species inquirenda* and excluded from the key below.

The European species, *A. peltata* and *A. pulchella*, have traditionally been differentiated by body size (750 *vs* 500 µm in ♀) and the relative length of the endopod of leg 1 (shorter *vs* slightly longer than exopod) (Sars 1906a; Lang 1948; Wells 2007). However, these comparisons did not take into account that Scott & Scott (1895c) had previously recorded much smaller specimens (600 µm) of *A. peltata* from the Firth of Forth. The subsequent discovery of populations of *A. peltata* from the White Sea (Chislenko 1967; Kornev & Chertoprud 2008) and Franz Josef Land (Chislenko 1977) casted doubt on the validity of these discriminants and, consequently, the status of *A. pulchella*. Females from the former region ranged 580–750 µm in length while the single specimen from Franz Josef Land measured only 625 µm. The morphometrics of leg 1 similarly fail to produce a clearcut difference between both species. For example, the length ratio of enp-1:exp-2 (measured along the outer margin of the segments) is variable, amounting to 1.65 in *A. pulchella* (Sars 1906a) and 1.36 (Sars 1906a), 1.55 (Chislenko 1977) and 1.60 (Kornev & Chertoprud 2008) in *A. peltata*. Apart from the possible significance of colour patterns (which have not been confirmed in every population examined) the only potentially reliable difference between both species is expressed in the shape of the endopodal lobe of the female leg 5 (see key below).

Based on the morphology of legs 1 and 5 and the slightly more robust body form, the single female (but originally recognized as a probable male) specimen of *A. peltata* collected from the Isles of Scilly by Brady (1880: 138–140; Plate LIII, figs 11–19) is more reminiscent of *A. pulchella*. Chislenko (1967) rightly questioned the validity of Thompson's (1893: 203–204; Plate XXIII, Fig. 3c–d) record of *A. peltata* from the Isle of Man but his claim that this material is conspecific with *A. pulchella* should be refuted. Assuming Thompson's illustrations are adequate, the morphology of leg 5 suggests that his specimens do not belong to *Amenophia*.

Key to species of *Amenophia* Boeck, 1865

1. Antennary endopod with three strong serrated claws at distal inner margin; endopodal claw of maxilliped acutely curved, hook-like and shorter than half the basal length; P5 exopod ♀ oval and about 1.5 times as long as maximum width, all endopodal setae short and at most half the length of exopod . . . .*A. orientalis* Ho & Hong, 1988.
Antennary endopod with three normally developed spines at distal inner margin; endopodal claw of maxilliped slightly bent, slender and about 3/4 the basal length; P5 exopod ♀ elongate and about 2.5 times as long as maximum width, longest endopodal setae at least as long as exopod . . . . 2.
2. P5 endopodal lobe ♀ with rounded margin bearing five setae . . . . *A. peltata* Boeck, 1865.
P5 endopodal lobe ♀ with distal part forming broad conical protuberance bearing four setae, fifth seta positioned about halfway inner margin. . . . . *A. pulchella* Sars, 1906a.

Amenophia orientalis Ho & Hong, 1988

This species exclusively utilizes the phaeophycaean *Undaria pinnatifida* as host and is regarded as the major causative agent of pinhole disease in the Far East (Rho *et al.* 1993; Park *et al.* 1990, 2008). It was originally described from Soando Island (Ho & Hong 1988) but has been recorded since from other localities along the southern (Park *et al.* 1990; Rho *et al.* 1993) and southeastern coasts (Park *et al.* 1990; Rho *et al.* 1993; Song *et al.* 2007, 2011) of the Korean peninsula. Recently, Saido & Yamaguchi (2003) collected the species from the Tohni and Kadonohama Bays (Iwate Prefecture) in northeastern Honshu, Japan.

The phaeophyte *U. pinnatifida* (locally known as Wakame in Japan, or Miyeok in Korea), is the most widely cultivated and consumed seaweed in Korea and Japan. According to FAO (2015) the combined harvest production in these countries is, overall, between 450,000 and 500,000 wet tons annually, being lower than in China (a few hundred tonnes) where this species is not as popular as *Laminaria*. The need to increase production to meet demand for this seaweed has led to a substantial expansion in the surface area being used for *U. pinnatifida* farming in Korea. In the last 30 years pinhole disease has been a major problem afflicting the *Undaria* industry. Algae affected by the disease typically show galls with pinholes (0.5 to 1.5 mm in diameter) produced by copepods on the fronds, midribs, and sporophylls (Ho & Hong 1988; Song *et al.* 2011). Algal cells on the periphery of the excavated pinholes contain considerably more brown pigments than the normal cells in the uninfested parts of the thallus and the tissues surrounding the pinholes are often swollen and raised (Ho & Hong 1988; Rho *et al.* 1993; Park *et al.* 2008; Song *et al.* 2011). These abnormalities are attributable to the host plant's reaction to the frond-mining activity of burrowing copepods. Affected thalli are considered unsuitable for human consumption, cannot command a good market price and are instead used as feed for abalone (Ho & Hong 1988; Park *et al.* 2008). Partial control methods, using freshwater to remove the copepods, have been developed but practical and effective preventive and control measures are yet to be designed (Anonymous 1991). Traditionally, the cultivation period for *U. pinnatifida* spanned from October to April, with thalli being harvested between December and April. In recent years, the harvest season has been shortened to December–February, in order to avoid the period of most severe infestation by copepods and the resulting outbreak of pinhole disease. Growth trials indicate that maximum sporophyte growth, in terms of increase in biomass, occurs during March–April. Shortening the harvest season to avoid the impact of pinhole disease therefore results in an estimated 30% biomass loss to the *Undaria* industry (*ca.* 5–8 tons wet weight per hectare) (Park *et al.* 2008). Surprisingly, there are no published records of copepods frond-mining the second Korean *Undaria* species, *U. peterseniana* (Kjellmann) Okamura 1915, which is restricted to Cheju Island and its vicinity (Kang 1990).

Ho & Hong (1988) based their description of *A. orientalis* on adult specimens but did not specify whether they were obtained by dissecting the galls or by washing of the fronds. They found that the nauplii are active excavators which feed on the medullary tissues of the algal host. According to Song *et al.* (2007) pinholes are caused only by the nauplii and copepodid stages but not by the adults. However, Rho *et al.* (1993) studied the development under culture conditions and showed that copepodids abandoned the pinholes immediately after metamorphosis and grazed the surface of the algal fronds without excavating them. According to Saido & Yamaguchi (2003) nauplii colonize only existing galls which had previously been excavated by adult females. Conversely, Park *et al.* (2008) claimed that the galls were occupied by the adults during mating and subsequent eclosion of the eggs. Generation time from egg to egg under laboratory conditions at 10–18 ºC takes 31–37 days (Rho *et al.* 1993). Nauplius I (60–76 µm) moults into the next stage after 2–3 days and naupliar development is completed within 4–6 days, resulting in an average body size increase from 80 µm (NI) to 240 µm (NVI). Copepodid development takes about seven days during which the gall undergoes a 7-fold increase in size. Copepodid body size increases from 268 to 660 µm during this phase after which it takes 9–13 days for the adult females (860–1200 µm) to become ovigerous. According to Ho & Hong (1988) neither copepodids nor adults of *A. orientalis* produce encapsulating mucus domes or other mucilaginous exudates.

The naupliar and copepodid stages were described by Song *et al.* (2011). Saido & Yamaguchi (2003) showed that *A. orientalis* can survive in culture when offered other algae. Most likely their results reflect laboratory adaptability rather than feeding generalism since survival rates were generally low (33–60%) compared to when the copepods were fed *U. pinnatifida* (90%). Saido & Yamaguchi (2003) also reported oil (lipid) droplets contained within the cephalothorax of adult *A. orientalis*. The precise function of these oil reserves is unknown but it is probable that they are utilized for basal metabolic needs during the summer when sporophyte degeneration occurs and only the microscopic gametophyte stage is evident, causing normal feeding to cease. Laboratory experiments showed that adult *A. orientalis* can survive for up to three months under extreme starving conditions.

Nauplii of harpacticoid copepods burrowing in kelp stipes may have to be reared to adult stages in order to correctly identify them as the real pathogens. Most references describe pinhole disease by the symptoms expressed in the host, but fall short of demonstrating causality, implying that more obvious secondary invaders could be mistakenly attributed as the primary cause of the disease. Park *et al.* (1990) recorded an unidentified species of *Scutellidium* Claus, 1866 which occurred consistently with *A. orientalis* in washings of *U. pinnatifida* fronds in Korea. Collectively, these two species comprised over 87% of the total number of harpacticoids found in samples from Wando Island (southwestern coast) and Songjeong (southeastern coast) and both were represented by numerous ovigerous females. A similar situation was observed by Rho *et al.* (1993). However, culture experiments (Park *et al.* 1990; Rho *et al.* 1993) using infested frond samples containing pinholes showed that all frond-mining nauplii developed in 15 days at 15 °C into copepodids and adults that exclusively belonged to *A. orientalis*, confirming the latter as the causative agent for the pinhole disease of cultivated Miyeok in southern Korea. Conversely, Park *et al.* (2008) suggested that the more regular and larger pinholes observed exclusively on the pinnate sections of older algae may be attributed to infection by another species of copepod. A possible candidate inhabitant for these pinholes is *Parathalestris infesta* Ho & Hong, 1988 which has a larger body size (♀: 1,490–1,810 µm; ♂: 1,160–1,540 µm) and is known to cohabit with *A. orientalis* in *Undaria* fronds (Ho & Hong 1988). The latter outnumbered *P. infesta* in all of the observed incidences. Other harpacticoids have been obtained in washings of cultivated Miyeok, such as *Amonardia coreana* Song, Rho & Kim, 2007 (Miraciidae) from algal beds in Gijang (southeastern Korea), but this species does not appear to show any mining activities (Song *et al.* 2007).

Undaria pinnatifida is an opportunistic seaweed which has spread mainly by fouling ship hulls or via farming of Japanese oysters (*Crassostrea gigas* (Thunberg, 1793)). In 1983, it was deliberately introduced into the North Atlantic in the coastal areas of Brittany by the French Institute for the Exploitation of the Sea (IFREMER) for commercial exploitation. It forms dense underwater forests, resulting in competition for light and space which may lead to the exclusion or displacement of native plant and animal species. *Undaria pinnatifida* has been nominated as among the world's 100 worst invasive species according to the Global Invasive Species Database (2015). Native to cold temperate coastal areas of Japan, Korea, northern China and the Kamchatka Peninsula of Russia, it has extended its range to include four continents since the 1980s (James *et al.* 2015). It is conceivable that al least some of these alien populations were introduced with their native symbionts such as *A. orientalis*. Spanish reports (Pérez-Cirera *et al.* 1997; Peteiro & Freire 2013) of burrowing copepods in Galician populations of *Undaria* await further identification but may well refer to *A. orientalis*.

OD: Ho & Hong (1988): 1624–1629; Figs 2–5.
AD: Song *et al.* (2011): 343–354; Figs 1–9; Table 1 [naupliar and copepodid stages]. Lee *et al.* (2012): 214–218; Figs 149–151 [reproduced from Ho & Hong (1988)].
TL: Korea, Jeollanam-do, Soando Island; collected from cultivated *Undaria pinnatifida* (Harvey) Suringar, 1873 (Phaeophycaea, Laminariales).
BL: 930–1,160 µm (♀), 710–830 µm (♂).

Parathalestris **Brady & Robertson, 1873**

The genus currently includes 26 valid species and three species of uncertain status (Wells 2007). Virtually all species are typically associated with the surface of macrophytes but only *P. infesta* Ho & Hong, 1988 has been reported to mine algal fronds (Ho & Hong 1988). Takemori & Iwasaki (2009) recorded *Parathalestris* sp. in abandoned galls excavated in the thalli of *Palmaria palmata* by *Thalestris hokkaidoensis* Takemori & Iwasaki, 2009. It is not known, however, whether this unidentified species itself displays any mining activities. *Parathalestris infesta* belongs to a group of eight species which share a leg 1 endopod that is significantly shorter than the corresponding exopod. Note that Wells (2007: codon KG 3/3, p. 743) mistakenly scored the number of exopodal setae on the male P5 as five for this species whereas it should have been six.

Partial key to species of *Parathalestris* Brady & Robertson, 1873

1. P1 exopod and endopod approximately the same length . . . . Group I [1].
P1 exopod significantly shorter than endopod . . . . Group II [2].
P1 exopod significantly longer than endopod . . . . 2.
2. Palmar margin of maxillipedal basis distinctly concave . . . . 3.
Palmar margin of maxillipedal basis straight or slightly convex . . . . 7.
3. Caudal ramus about 1.3 times as long as wide; setae I–II of ♀ P5 baseoendopod spiniform and of equal length; P5 exopod ♂ with seven elements . . . . *P. ganio* Brehm, 1938.
Caudal ramus of different proportions; setae I–II of ♀ P5 baseoendopod setiform, seta I at most half the length of seta II; P5 exopod ♂ with six elements . . . . 4.
4. Caudal ramus about 1.5 times as long as wide; posterior margin of pedigerous somites with corniform protuberances . . . . *P. verrucosa* Itô, 1970.
Caudal ramus about as long as wide; posterior margin of pedigerous somites smooth . . . . 5.
5. Dorsal posterior margin of cephalic shield with three prominent processes in ♀; antennary exopod with one seta on proximal segment; maxilla with one seta on praecoxal endite . . . . *P. infesta* Ho & Hong, 1988 [3].
Dorsal posterior margin of cephalic shield without processes in ♀; antennary exopod with two setae on proximal segment; maxilla with two setae on preacoxal endite . . . . 6.
6. Caudal ramus seta II bulbous in proximal part; exopod of maxillule enlarged, with three setae; inner claw of P1 enp-3 about twice as long as outer one; inner endopodal seta of ♂ P5 distinctly shorter than middle one; body length 1,600 µm (♀), 1,250 µm (♂) . . . . *P. pacifica* Chislenko, 1971 [4].
Caudal ramus seta II normal; exopod of maxillule not enlarged, with two setae; inner claw of P1 enp-3 about three times as long as outer one; inner endopodal seta of ♂ P5 longer than middle one; body length 1,000 µm (♀), 700 µm (♂) . . . . *P. californica* Lang, 1965.
7. Caudal ramus setae IV–V spiniform in ♀, only as long as last two urosomites combined (condition in ♂ unknown); outer spines of P1 exp-1 and -2 and proximal outer spine of exp-3 elongate, being all longer than length of exp-1; P1 endopod extending beyond distal margin of exp-2; seta I of P5 exopod ♀ longer than, and positioned immediately adjacent to, seta II . . . . *P. coatsi* T. Scott, 1912.
Caudal ramus setae IV–V setiform in both sexes, much longer than last two urosomites combined; outer spines of P1 exp-1 and -2 and proximal outer spine of exp-3 not elongate, being clearly shorter than length of exp-1; P1 endopod not reaching distal margin of exp-2; seta I of P5 exopod ♀ shorter than, and separated by distinct gap from, seta II . . . . 8.
8. Antennule ♂ with strong and densely plumose seta on segment 1 and distinct setular tuft on segment 3; outer spine of P1 exp-2 originating halfway down the segment; outer claw of P1 enp-3 less than half the size of inner one; P5 exopod ♀ not reaching beyond distal margin of endopodal lobe, all setae (I–VI) arranged around extreme distal end of exopod . . . . *P. mourei* Masunari, 1988.
Antennule ♂ unconfirmed; outer spine of P1 exp-2 originating in distal third of segment; both claws on P1 enp-3 equally long; P5 exopod ♀ reaching far beyond distal margin of endopodal lobe, setae II–VI originating from outer margin of exopod . . . . *P. affinis* T. Scott, 1912.

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[1] includes *P. croni* (Krøyer, 1842); *P. harpactoides* (Claus, 1863); *P. jacksoni* (T. Scott, 1899); *P. similis* Lang, 1936a; *P. irelandica* Roe, 1958; *P. cambriensis* Wells, 1964; *P. bulbiseta* Lang, 1965; *P. dovi* Marcus, 1966; *P. areolata* Itô, 1972; *P. vinosa* Pallares, 1975a; *P. parviseta* Chang & Song, 1997.

[2] includes *P. clausii* (Norman, 1869); *P. hibernica* (Brady & Robertson, 1873); *P. intermedia* Gurney, 1930a; *P. incerta* Lang, 1936a; *P. paraharpactoides* Lang, 1936a; *P. aurantiaca* Pallares, 1975a; *P. patagonica* Pallares, 1975a.

[3] The original incorrect spelling *infestus* is here amended to *infesta* in accordance with ICZN Art. 31.2.

[4] The original incorrect spelling *pacificus* is here amended to *pacifica* in accordance with ICZN Art. 31.2.

Parathalestris infesta Ho & Hong, 1988

This species was originally recorded from the cultivated brown seaweed, *U. pinnatifida*, at Soando Island and identified as a causative agent of pinhole disease (Ho & Hong 1988). Its association with the alga appears to be less specific than for the co-occurring *A. orientalis* since it has also been recorded in light trap samples (Chang & Song 1997) and unspecified macro-algal washings (Back & Lee 2011). *Parathalestris infesta* belongs to a group of eight species that display a P1 exopod which is significantly longer than the endopod. Females of this species can readily be identified by the presence of three prominent processes on the dorsal posterior margin of the cephalic shield. Chang & Song (1997) recorded *P. infesta* from two localities (Myongsa and Chisepo) on Geoje (Koje) Island along the south coast of the Korean peninsula. They noted a slight variation in the female leg 5, *i.e.* the exopod being larger and extending to the distal margin of the endopodal lobe, and the endopodal setae II–IV being considerably longer. Ho & Hong (1988) observed their specimens using the hanging drop method (Humes & Gooding 1964) which may have resulted in a slightly foreshortened view of leg 5. Back & Lee (2011) redescribed both sexes from algal washings obtained at Yeongok beach (37°51'43"N, 128°51'04"E) near Gangneung, East Sea coast. It should be noted that their Figure 10 (supposed to illustrate P1–P2) is an inadvertent duplication of Figure 9; for a correct reproduction see Fig. 167 in Lee *et al.* (2012).

Infestation of *U. pinnatifida* by thalestrid copepods was first reported by Torii & Yamamoto (1975) from the Japanese Wakame farms in Hakodate, Hokkaido. According to Kang (1981) Miyeok beds in Onsan-Myeon, Ulju-Gun (Ulsan) along the southeast coast of Korea had similarly been inflicted by pinhole disease since 1974. In both reports the causative agent was identified as *Thalestris* sp., however, Torii & Yamamoto's (1975) illustrations suggest that they had been dealing with a species of *Parathalestris* (Ho & Hong 1988). It is equally conceivable that the '*Thalestris* sp.' reported by Kang (1981) is in reality *Parathalestris infesta*. While Torii & Yamamoto (1975) claimed that only one species caused the infestations in Japan, Ho & Hong (1988) consistently observed the coexistence of *Amenophia orientalis* and *P. infesta* in Korea, with the latter being outnumbered by the former. Based on the number of eggs per egg sac they concluded that the potential fecundity of *P. infesta* (120 ± 20) was twice that of *A. orientalis* (60 ± 6), however, no information was available on how many clutches of eggs were produced by individual females. The rate of production of egg sacs is determined by the time taken for embryos to develop to hatching and by the time between hatching of one clutch and the appearance of the next. While some of this information is available for laboratory populations of *A. orientalis* (Rho *et al.* 1993) no data exist on generation turnover, egg sac production or interclutch period for *P. infesta*. Both Torii & Yamamoto (1975) and Kang (1981) claimed that the midrib, stipe, and holdfast were not invaded by '*Thalestris* sp.' but this was contradicted by Ho & Hong's (1988) observations. Although *A. orientalis* has been identified as the primary causative agent of pinhole disease, nauplii of *P. infesta* are also active excavators and seem to consume the medullary tissue of the thalli (Ho & Hong 1988); this observation, however, has not been confirmed in subsequent studies.

OD: Ho & Hong (1988): 1630–1634; Figs 6–8.
AD: Chang & Song (1997): 228–229; Fig. 4H. Back & Lee (2011): 91–97; Figs 8–13 [reproduced in Lee *et al.* (2012): 235–242; Figs 165–170].
TL: Korea, Jeollanam-do, Soando Island; collected from cultivated *Undaria pinnatifida* (Harvey) Suringar, 1873 (Phaeophycaea, Laminariales).
BL: 1,490–1,810 µm (♀), 1,160–1,540 µm (♂) [Ho & Hong 1988]; 1,500 µm (♀), 1,080 µm (♂) [Back & Lee 2011].

Thalestris Claus, 1862

Two species are known to infest red macroalgae, *T. rhodymeniae* and *T. hokkaidoensis* Takemori & Iwasaki, 2009. Although both species are very closely related and utilize the same alga, their ecological relationships with the host are different; the former induces galls in the British Isles while the latter exhibts frond-mining habits in northern Japan. Torii & Yamamoto (1975) and Kang (1981) noted copepod infestations in cultivated Wakame beds in Hokkaido, Japan and southeastern Korea, respectively. In both reports the causative agent was identified as *Thalestris* sp. but Ho & Hong (1988) suspected that they were dealing with a species of *Parathalestris*, possibly *P. infesta* (see above). An unidentified species of *Thalestris* was found inside the opened galleries that were abandoned by *T. hokkaidoensis* (Takemori & Iwasaki 2009). The genus currently accommodates ten valid species (Wells 2007; Takemori & Iwasaki, 2009) which can be differentiated by the key below.

Key to species of *Thalestris* Claus, 1862

1. P1 exopod and endopod approximately the same length . . . . 2.
P1 exopod distinctly longer than endopod . . . . 4.
P1 exopod distinctly shorter than endopod . . . . *T. normani* T. Scott, 1903a.
2. Caudal ramus about three times as long as wide; P5 ♀ (excluding the setae) short, extending only to about halfway along the genital double-somite . . . . *T. gibba* (Krøyer, 1842).
Caudal ramus approximately as long as wide; P5 ♀ (excluding the setae) long, extending far beyond the distal margin of the

genital double-somite . . . . 3.

3. Palmar margin of maxillipedal basis convex; P1 enp-1 about 7.5 times as long (measured along midline of anterior surface) as maximum width; P5 exopod ♂ about 1.4 times as long as maximum width . . . . *T. frigida* T. Scott, 1899.
Palmar margin of maxillipedal basis concave; P1 enp-1 about 5.0 times as long (measured along midline of anterior surface) as maximum width; P5 exopod ♂ about 2.75 times as long as maximum width . . . . *T. longimana* Claus, 1863.

4. Palmar margin of maxillipedal basis concave. . . . . 5.
Palmar margin of maxillipedal basis straight or convex . . . . 6.

5. Caudal ramus about twice longer than wide; outermost endopodal seta of P5 ♂ less than half the length of other endopodal setae; body length ♀ around 2 mm . . . . *T. gigas* Chislenko, 1980.
Caudal ramus about as long as wide; all three endopodal setae of P5 ♂ about equally long; body length ♀ around 900 µm. . . . . *T. rufoviolascens* Claus, 1866.

6. P5 ♀ endopodal lobe almost reaching to distal margin of exopod, the latter being longer than wide . . . . 7.
P5 ♀ endopodal lobe distinctly shorter than exopod, the latter being as long as wide. . . . . 8.

7. Palmar margin of maxillipedal basis straight; apical two setae of P5 ♀ endopodal lobe about as long as exopod; pseudoperculum forming a single triangular extension with irregular posterior margin . . . . *T. brunnea* Sars, 1905a.
Palmar margin of maxillipedal basis convex; apical two setae of P5 ♀ endopodal lobe distinctly shorter than exopod; posterior margin of pseudoperculum with 4–5 rounded lobes. . . . . *T. purpurea* Sars, 1905a.

8. P1 endopod reaching to distal third of exp-2; P5 ♀ inner two exopodal setae longer than segment; P5 endopodal lobe of ♂ obsolete . . . . *T. rhodymeniae* (Brady, 1894).
P1 endopod reaching to distal margin of exp-2; P5 ♀ inner two exopodal setae distinctly shorter than segment; P5 endopodal lobe of ♂ almost reaching to distal margin of exopod . . . . *T. hokkaidoensis* Takemori & Iwasaki, 2009.

Thalestris rhodymeniae Brady (1894)

The occurrence of galls in the marine red alga *Palmaria palmata* was first reported by Barton (1891), based on dulse material from Stonehaven, Scotland. The galls, in the form of minute papillae on the surface of the affected frond, were found to contain harpacticoid copepods which were later examined by G.S. Brady who considered them to represent adults of two different species. The first was identified as *Harpacticus chelifer*, a common and free-living species which he regarded as of accidental occurrence in the gall cavities (Brady 1894). The second species remained unnamed at first but was subsequently described as a new genus and species, *Fucitrogus rhodymeniae*, and identified as the causative agent of the galls (Brady 1894). He considered but rejected the possibility of it representing a naupliar stage, interpreting the unusual morphology of the cephalic limbs instead as a retrogression arising from its parasitic life style. Brady (1894), having previously adopted Thorell's (1859) division of the Copepoda according to the structure of their oral appendages and mouths, failed to place the genus in any of the three sections recognised at that time (Gnathostomata, Poecilostomata, Siphonostomata) and proposed a fourth one, Choneostomata, to accommodate it. Brady's (1894) paper remained largely unnoticed until Harding (1954a, 1954b; in Varley (1954)) showed that the morphology of the specimens examined by Brady (1894) had been almost completely misinterpreted in the original description. He proved instead that they did not represent adults but a nauplius stage of a well known genus of harpacticoids, *Thalestris*. Lang (1948: 774) had previously classified the species as a juvenile stage of a copepod but rejected the notion that it belonged to the Harpacticoida. According to Harding (1954a, 1954b; in Varley 1954) the skin of the six spherical naupliar stages is soft and extensible, capable of a certain amount of stretching during each instar. At each of the naupliar moults a doubling of the volume of the limbs takes place but with remarkably little increase in their complexity. The volume of Nauplius VI is similar to that of the adult female and larger than that of the male. The naupliar antennae have a biting gnathobase, resembling the mandibular gnathobase present in the copepodid stages and adults; being misled by this similarity, Brady (1894) erroneously identified the antenna as the mandible. Harding (1954a) found no evidence for more than two copepodid stages and believed the copepodid phase of *T. rhodymeniae* to be abbreviated. The first copepodid is advanced with regard to the number of appendages, but these are underdeveloped in structure and appear not to be functional. The animal at this stage probably lives on internal reserves laid in during the voracious nauplius phase and a reduction in volume takes place as it matures. The last copepodid has normal appendages and appears to be able to feed. The gall is by now open to the exterior and the adult male and female are probably free-living, feeding on plant and animal matter which comes in from the outside. The number of copepodid stages needs confirmation since six appears to be the rule in other species of *Thalestris* (Dahms 1990a). Adult males are outnumbered by females in the open galls and pairs *in amplexus* were never observed, suggesting that mating probably occurs outside. However, ovigerous females with eggs close to eclosion were observed inside the galls. Newly hatched nauplii may burrow a serpentine track internally, away from the parental gall, and subsequently occupy their own new galls. Adults are pink in colour (Harding 1954a).

Harding (1954a) found that infections mostly occurred in the older proximal parts of the fronds during the autumn and winter. Galls which were completely closed usually contained a nauplius or copepodid while older ones had an opening to the exterior or into nearby galls and harboured adults of *T. rhodymeniae*, or occasionally other copepods. Harding (1954a) suspected that the specimens identified by Brady as *Harpacticus chelifer* in reality represented adults of *T. rhodymeniae*. Galls caused by the latter, although not commonly reported, are probably frequent, at least locally (Spooner 1994). Laverack & Blackler (1974) reported that all developmental stages of the galls can be found, especially in autumn and winter, in the eulittoral and sublittoral zones of St. Andrews Bay. Barton (1891) observed similar proliferations on a herbarium specimen of *P. palmata* collected at Cork Harbour (Ireland). It is conceivable that *T. rhodymeniae*, like its host, is widely distributed around the British Isles, especially on rocky shores. The species is morphologically similar to *Thalestris purpurea* Sars, 1905a and some of the records attributed to the latter may in reality refer to *T. rhodymeniae* (Harding 1954a). A remarkable distributional outlier from the San Juan Archipelago, U.S.A., was reported by Fahrenbach (1962) who allegedly observed the species inside the red alga *Halosaccion glandiforme*, the type host of *Diarthrodes cystoecus* in California.

OD: Brady (1894—as *Fucitrogus Rhodymeniæ*): 168–169; Plate V (nauplius).
AD: Harding (1954a): 154–159; Figs 1–24; unnumbered plate (Figs 1–5); Table I.
TL: Scotland, Aberdeenshire, Stonehaven; inside galls on fronds of *Palmaria palmata* (Linnaeus) Weber & Mohr, 1805 (Rhodophyta, Palmariales).
BL: 500 µm (nauplius) [Brady 1894]; 90–400 µm (nauplii), 850 µm (♀), 650 µm (♂) [Harding 1954a].

Thalestris hokkaidoensis Takemori & Iwasaki, 2009

This species was found in the thalli of the red alga *Palmaria palmata* (Linnaeus) Weber & Mohr, 1805 and is so far known only from its intertidal type locality in southwestern Hokkaido (Uchiura Bay). Takemori & Iwasaki (2009) examined other algal species in the surveyed area, representing 13 families of red and brown algae, but failed to find any *T. hokkaidoensis*, suggesting that the species is highly alga specific. Females were described as being semitransparent while males show a purplish colour on the first three pedigerous somites.

Copepods were found in the thalli during most months (January–July) when *P. palmata* occurred (December–July). They typically make galleries between the two epidermal layers of the thallus, but do not induce gall-like swellings like in *T. rhodymeniae*. As a rule galleries are occupied by a single individual of *T. hokkaidoensis*, usually a nauplius or copepodid. Percentages of different life cycle stages observed in the galleries by Takemori & Iwasaki (2009) were 68.3% for nauplii, 28.2% for copepodids, and 3.5% for adults (n = 2988). More than one copepod was found living in a gallery in only seven instances. Ovigerous females or pairs *in amplexus* were not observed. Other harpacticoid copepods such as *Dactylopusioides* sp., *Parathalestris* spp., *Thalestris* sp., and *Zaus* sp. were occasionally found inside abandoned galleries.

OD: Takemori & Iwasaki (2009): 286–294; Figs 1–6; Tables 1–3.
TL: Japan, Hokkaido, Uchiura Bay; Muroran, intertidal zone at Charatsunai beach (42°30'N, 140°98'E); in thalli of *Palmaria palmata* (Linnaeus) Weber & Mohr, 1805 (Rhodophyta, Palmariales).
BL: 860–930 µm (♀), 640–700 µm (♂).

Associations with grasses

Rutledge & Fleeger (1993) studied the abundance and species composition of stem-dwelling meiofauna associated with the saltmarsh cordgrass *Spartina alterniflora* Loiseleur-Deslongchamps, 1807 (Poaceae) in a Louisianian estuary. Most harpacticoid copepods were associated with epiphytic algae found relatively high on standing stems; however, one species, *Leptocaris brevicornis* (Douwe, 1905) (Darcythompsoniidae), was almost exclusively associated with the vascular tissue of *S. alterniflora*. Being the most abundant species, comprising 47% of all harpacticoids sampled, it predominated the stem-dwelling harpacticoid community from December till May, reaching maximum densities of 426 ± 127 ind.100 cm^{-2} in September. Although *L. brevicornis* was occasionally encountered in the epiphytic algae or the intertidal sediment, most frequently it was found burrowed in the soft outer sheath of the cordgrass. The copepods typically excavate sharply delimited tunnels which follow the longitudinal axis of the stems. Various studies in fringe mangrove forests in Florida (Hopper *et al.* 1973), lagoonal mangal habitats in Brazil (Por 1983a, 1984a) and mangrove forests in peninsular Malaysia (Gee & Somerfield 1997; Somerfield *et al.* 1998) have suggested that darcythompsoniids are the most typical harpacticoids of mangrove litter systems and play an important role in their degradation. The adoption of a cylindrical or vermiform body shape by all members of this group is an ancestral trait of the family Darcythompsoniidae and obviously related to their colonization of the soft flat surfaces of decaying mangrove leaves (and other organically enriched microhabitats). The secondary colonization of the specialized *S. alterniflora* micro-niche by the phylogenetically advanced *L. brevicornis* can therefore be seen as a behavioural example of exaptation. Its extreme vermiformicity made the species particularly well pre-adapted for life in the vascular tissues of cordgrass stems. Gregg & Fleeger (1998) suggested that copepods living within the stem sheath and vascular tissue of *S. alterniflora* were not susceptible to predation by the grass shrimp *Palaemonetes pugio* Holthuis, 1949b. Analysis of the vertical profile of the various harpacticoid species associated with *S. alterniflora* indicated that *L. brevicornis* occurs very high in the stems, usually above the high-tide line (Rutledge & Fleeger 1993). Gee & Somerfield (1997) assumed that the copepod effectively feeds on the vascular tissues of the cordgrass.

Invertebrate hosts

Porifera

The number of metazoan associates inhabiting individual sponges may reach very high levels, leading Pearse (1934b: 119) to claim that large poriferans with good-sized internal canals may serve as “veritable living hotels”. Copepods in particular can sometimes populate the outer surfaces and water passages of sponges in considerable numbers. Although their trophic relationships with the host sponges have rarely been studied, it is likely that most copepod symbionts use their hosts only for space and protection, seeking shelter in the microhabitat consisting of the numerous choanocyte chambers and internal canals. Even if copepods are metabolically independent of their hosts they may still rely on the host’s water current for a supply of suspended food particles. The number of individuals, as well as the number of species inhabiting sponges may vary with host species, sponge volume, niche structure, water depth and other macro- and microecological factors. Sponges are among the most popular invertebrate host groups for members of the Siphonostomatoida, and the majority of these symbionts appear to exhibit a high level of host specificity. Many harpacticoid species have been recorded from sponge washings, but whether these are specific associates of sponges must await confirmation while in several cases these records are merely to be treated as accidental (see below). Genuine records of spongicolous harpacticoids are rare and all of them were found in association with eastern Pacific sponges, *i.e.* the type species of *Hamondia* Huys, 1990a (Hamondiidae) and the two known species of *Alteuthoides* Hicks, 1986a (Peltidiidae).

Family Hamondiidae

Hamondia Huys, 1990a

Hamondia superba Huys, 1990a

Huys (1990a) based his description on material obtained from washings of unidentified sponges collected at the entrance of Port Phillip, Victoria (Australia). Only very few individuals were found, including adults of both sexes, an ovigerous female and a copepodid V male. The ovoid, shield-shaped, dorsoventrally flattened body morphology, the strongly prehensile leg 1 endopod and the presence of appendages playing an auxiliary role in attachment (antenna, maxilliped) suggest an intimate association with its host. Nothing is known about the biology of the copepod or the attachment site on the host. Huys (1990a) observed variability in the setation of the maxillipedal coxa, the shape of the middle endopodal segment of the male leg 2, the armature of the same segment of the male leg 3, and the length of the median spinular row on the male baseoendopods of leg 5. The species has not been recorded again since its original description. There is no relationship with other harpacticoid lineages displaying a similar dorsoventrally depressed body (*e.g.* Porcellidiidae, Peltidiidae, …).

OD: Huys (1990a): 55–77; Figs 1–16.
TL: Australia, Victoria, entrance to Port Phillip; washings from unidentified sponges taken at a depth of 15–18 m on a vertical rock face at Pope's Eye.
BL: 790–805 µm (♀), 745–755 µm (♂).

Family Peltidiidae

Alteuthoides Hicks, 1986a

Hicks (1986a) proposed a new genus *Alteuthoides* to accommodate a single new species, *A. kootare*, collected in New Zealand waters. Kim & Kim (1998) added a second species, *A. affinis*, from Jeju (Cheju) Island, Korea. Both species are associated with sponges and can be differentiated using the key below.

Key to species of *Alteuthoides* Hicks, 1986a

1. Distal segment of P1 exopod with strong apical claw, a reduced accessory nail and a setule; exopodal segments of leg 2 with pinnate outer spines; caudal ramus seta IV twice as long as seta VI, outer distal element (seta II?) stout, naked and spiniform . . . . *A. kootare* Hicks, 1986a.

\- Distal segment of P1 exopod with strong apical claw and two setules; exopodal segments of leg 2 with plumose outer setae; caudal ramus setae IV and VI equally long, outer distal element (seta II?) relatively slender, bipinnate and setiform . . . . *A. affinis* Kim & Kim, 1998.

Other characters employed by Kim & Kim (1998) to differentiate both species such as rostrum shape, size of the posterior extensions of the genital double-somite, and number of setae on the maxillipedal basis are not reliable discriminants.

Alteuthoides kootare Hicks, 1986a

Hicks (1986a) obtained 44 females and 50 males from atrial washings of the hexactinellid sponge *Symplectella rowi* Dendy, 1924 (family Euplectellidae) collected in the Bay of Plenty of the North Island (New Zealand). In a postscript he reported the discovery of additional specimens from an unidentified hexactinellid (*Symplectella* sp.) from Conway Rise, south-east of Kaikoura on the South Island. Hicks (1986a) reported substantial variability in the setal positions on the antennary exopod and the armature formula of the swimming legs.

OD: Hicks (1986a): 350–355; Figs 1–3.
TL: New Zealand, North Island, Bay of Plenty, off East Coromandel Coast (36º49.2'S, 176º05.4'E), 120 m depth; atrial washings of *Symplectella rowi* Dendy, 1924 (Euplectellidae).
BL: 680–740 µm (♀), 670–710 µm (♂).

Alteuthoides affinis Kim & Kim, 1998

Kim & Kim (1998) obtained 42 females and 13 males from washings of three specimens of the demosponge

Callyspongia elegans (Thiele, 1899) (family Callyspongiidae) collected off the south coast of Jeju Island, Korea, and suspected *A. affinis* to be found throughout the range of its host. Although *C. elegans* has it centre of distribution in Indonesia, populations are sustained in more northerly regions which are under the influence of the Kuroshio Current which transports warm, tropical water northward. The host is common in the shallow waters of the Korean peninsula.

OD: Kim & Kim (1998): 203–208; Figs 1–4 [reproduced in Lee *et al.* (2012): 162–167; Figs 112–115]. Note that Fig. 4D in Kim & Kim (1998) refers to the distal segments of the male antennule and not leg 5 as indicated in the legend; coincidently, the same structure was erroneously labelled as the "second metasomite" in Lee *et al.* (2012: Fig. 112D).

TL: Korea, Jeju Island, Mun Island (Munsum or Mosquito Island) off Seogwipo; depth about 30 m; washings of *Callyspongia elegans* (Thiele, 1899) (Callyspongiidae).

BL: 760–520 µm (♀), 580–650 µm (♂).

Cnidaria

The Cnidaria has more copepod associates than any other group of marine macro-invertebrates. Copepods are associated with all three classes of Cnidaria. They have developed associations especially with the Anthozoa, both octocorallians and hexacorallians, and within the latter, Scleractinia serve as hosts to many more copepods than other groups. While the Cyclopoida contains by far the greatest number of species associated with cnidarians, members of the Siphonostomatoida are much less frequent, and the Harpacticoida and Calanoida are represented by relatively small numbers (Humes 1985). Currently, 12 species of harpacticoids, belonging to six genera and five families, are known to utilize cnidarians as hosts, including hydrozoans, scyphozoans and anthozoans. This low number is likely to be a gross underestimate due to neglect. In particular, associations of peltidiid and tegastid copepods with cnidarians may be more common than previously believed (Humes 1981b).

Family Ameiridae

Nitocra Boeck, 1865

Nitocra medusaea Humes, 1953

Approximately 1,030 individuals of this species were discovered on the exumbrellar surface of a living medusa of an unidentified species of the moon jellyfish genus *Aurelia* Lamarck, 1816a (family Ulmaridae) collected in Portsmouth harbour, New Hampshire (Humes 1953). Copepods exclusively occupied the more than thirty flask-shaped pits in the convex outer surface of the umbrella, the largest pit being about 11.5 mm deep and 1 mm in diameter. Each pit contained 10–30 or more individuals. Since the copepods, massed together in their pits, were opaque or slightly cream-coloured, the medusa appeared to the unaided eye as though there were sand grains in the jelly. When examined under intense illumination or when disturbed with a needle, the copepods become active and crawl in and out of the pits and over the exumbrellar surface, clinging tenaciously to debris and jelly fragments. Whether or not *N. medusaea* excavates the pits on the exumbrella is unknown but their position on the host appears to be unique. Other copepods (Macrochironidae, *Pseudolubbockia dilatata* Sars, 1909b) utilizing scyphozoan hosts were either found on the oral arms and gastric cirri (Browne & Kingsford 2005) and within the subumbrellar cavity (Gasca *et al.* 2007) of the medusoid stages, or inside the gastrovascular cavity of the benthic scyphistomae (polyps) (Tang *et al.* 2012).

In life the body is transparent, without distinct colour, while the median nauplius eye is bright red. The dorsoventrally flattened egg sac reaches well beyond the caudal rami and contains 28–30 eggs arranged in two layers, each egg about 51 µm in diameter.

Lang (1965) suggested that *N. medusae* [*sic*] may be conspecific with *N. spinipes* Boeck, 1865 but did not formally synonymize it. Bodin (1997 and previous versions) consistently listed it as a potential junior synonym of

N. spinipes. Coull (1977) formally accepted the synonymy and this course of action was adopted by Humes (1981b); Wells (2007) excluded it from his tabular keys. However, various authors (Gotto 1979; Ohtsuka *et al.* 2009; Tang *et al.* 2012) have accepted the species under its original name and this position is adopted here pending a thorough revision of the variable *N. spinipes*. Boxshall & Halsey (2004: 8) erroneously stated that it "… lives on *freshwater* medusae", a misconception repeated in Boxshall & Strong (2006). Humes' (1985: 317) Table III appears to suggest that there are two harpacticoid species known to be associated with scyphozoans but it is unclear where the second record originated from. *Nitocra medusaea* has not been recorded again since its original description.

OD: Humes (1953): 360–366; Figs 1–28.
TL: U.S.A., New Hampshire, Portsmouth harbour, off Fort Stark; in pits on exumbrellar surface of a living medusa (*Aurelia* sp.) (Ulmaridae), about 7.5 cm in diameter.
BL: 750–820 µm (♀); 600–640 µm (♂).

Family Laophontidae

Laophonte Philippi, 1840

Laophonte adamsiae Raibaut, 1966

Raibaut (1966) collected *Laophonte adamsiae* from the cloak anemone *Adamsia palliata* (O.F. Müller, 1776) (family Hormathiidae) [Note that the original host name used by Raibaut, *Adamsia palliata* (Bohadsch, 1761), was suppressed under the plenary powers for all nomenclatural purposes in Opinion 185 (ICZN 1944); Cornelius & Ates 2003]. The host anemone is usually found growing on a gastropod shell inhabited by the pagurid hermit crab, *Pagurus prideaux* Leach, 1815. When it becomes too large for the shell, the anemone secretes paired chitinous membranous folds at its basal disc, thereby increasing the volume of the shell available to the hermit crab and relieving the anomuran of the necessity of having to find a larger shell. Examination of the furrows formed by the inner wall of these folds revealed a variable number of nauplii, copepodids and up to 20 adults of *L. adamsiae* per host. The dorsoventrally flattened body assists the copepods in maintaining an intimate contact in this microhabitat. Temporary attachment to the cnidarian substratum is secured by means of their maxillipeds and prehensile leg 1 endopods. The host niche preference appears very specific since no *L. adamsiae* were found anywhere inside the gastropod shell or on the pagurid. Raibaut (1966) placed the species in the *Laophonte setosa* group. Although *A. palliata* assumes a wide distribution, being found at shallow depths in the north-eastern Atlantic Ocean south to the Azores, in the North Sea and the Mediterranean Sea (basically occurring wherever its hermit crab host is found), *L. adamsiae* has not been recorded again since its original description.

OD: Raibaut (1966): 123–126; Figs 1–2; Plate II.
TL: France, Languedoc-Roussillon, Hérault, Sète; in *Adamsia palliata* (O.F. Müller, 1776) (Hormathiidae) attached to gastropod (*Natica* sp.) shell inhabited by *Pagurus prideaux* Leach, 1815; inner wall of membranous extensions of basal disc.
BL: 500 µm (♀); 370 µm (♂).

Family Miraciidae

Amphiascus Sars, 1905c

Huys (2009b) remarked that *Amphiascus* Sars, 1905c is a senior objective synonym of *Paramphiascopsis* Lang, 1944 and consequently restricted it to the species previously included in the latter. His Table 3 listed all currently valid species in *Amphiascus* but inadvertently combined three of them with the genus-group name *Amphiascopsis* Gurney, 1927, *i.e.* *Amphiascopsis paromolae* (Soyer, 1973), *Amphiascopsis triarticulatus* (Moore, 1976b) and

Amphiascopsis waihonu (Hicks, 1986b); this error is rectified here and all three species are formally placed in *Amphiascus*. The genus comprises several species that have been taken in association with other invertebrates (Soyer 1973), including *A. soyeri* (Lang, 1965) which has an apparently close association with a gorgoniid octocorallian.

Key to species of *Amphiascus* Sars, 1905c (modified after Hicks (1986b))

FEMALES

1. Caudal ramus seta V modified, basal part swollen . . . . . 2.
Caudal ramus seta V not modified, basal part normal . . . . . 3.
2. Caudal ramus seta V with a conspicuous outer bag-like swelling near base; P1 enp-1 not extending to distal end of exopod . . . . . *A. giesbrechti* Sars, 1906b.
Caudal ramus seta V with an outer evenly arched (not bag-like) swelling near base; P1 enp-1 extending slightly beyond distal end of exopod; caudal ramus seta VII situated in proximal half; mandibular exopod with three terminal setae; P5 baseoendopod with large hyaline field near insertion of exopod. . . . . *A. longirostris* (Claus, 1863).
Caudal ramus seta V swollen along both outer and inner sides of base; P1 enp-1 extending well beyond distal end of exopod; other characters not combined. . . . . *A. paromolae* (Soyer, 1973).
3. Posterior ventral edge of abdominal somites densely spinulose. . . . . *A. pallidus* Sars, 1906b.
Posterior ventral edge of abdominal somites not densely spinulose. . . . . 4.
4. Antennule with aesthetasc on segment 4 only; P1 enp-1 extending beyond distal end of exopod. . . . . 5.
Antennule with aesthetascs on segments 3 and 4; P1 enp-1 not extending beyond distal end of exopod . . . . . *A. waihonu* (Hicks, 1986b).
5. P5 endopodal setae I–II bifid at tip . . . . . 6.
P5 endopodal setae I–II not bifid at tip. . . . . *A. triarticulatus* (Moore, 1976b).
6. First segment of antennule with three short spinule rows on anterior margin; caudal ramus about 1.5 times as broad as long; P5 exopod rounded oval in shape. . . . . *A. ekmani* (Lang, 1965).
First segment of antennule without conspicuous spinular ornamentation along anterior margin; caudal ramus slightly broader than long; P5 exopod longish oval in shape . . . . . *A. soyeri* (Lang, 1965).

MALES

1. Inner margin of P1 basis with three spiniform chitinous projections (Nebendornen) . . . . . 2.
Inner margin of P1 basis with two spiniform chitinous projections (Nebendornen) . . . . . 3.
2. P1 enp-1 not reaching beyond distal end of exopod; outer spine of P2 exp-2 modified and enlarged, reaching beyond distal margin of exp-3; P5 endopodal setae and setae I–II of exopod bifid at tip. . . . . *A. waihonu* (Hicks, 1986b).
P1 enp-1 reaching beyond distal end of exopod; outer spine of P2 exp-2 not modified or enlarged, not reaching beyond distal margin of exp-3; P5 endopodal setae and setae I–II of exopod not bifid at tip. . . . . *A. longirostris* (Claus, 1863).
3. P5 exopod spatulate, elongate with concave inner edge; P5 endopodal lobe extending almost to distal margin of exopod . . . . . *A. giesbrechti* Sars, 1906b.
P5 exopod of different shape, endopodal lobe distinctly shorter . . . . . 4.
4. P1 enp-1 extending slightly beyond end of exopod; P2 enp-2 with apical serrate spine; P5 endopodal setae not bifid at tip . . . . . *A. soyeri* (Lang, 1965).
P1 enp-1 not extending to distal end of exopod; P2 enp-2 with apical plumose seta; P5 endopodal setae not bifid at tip . . . . . *A. pallidus* Sars, 1906b.
P5 endopodal setae bi-, tri-, or quadrifid at tip . . . . . 5.
5. Nebendornen of P1 basis blunt; P2 enp-2 terminating in a slightly curved spine . . . . . *A. paromolae* (Soyer, 1973).
Nebendornen of P1 basis pointed; P2 enp-2 terminating in a sparsely plumose seta. . . . . 6.
6. P2 exp-2 outer spine as long as outer spine of exp-1 and not extending beyond distal margin of exp-3; P5 exopod about 1.7 times as long as maximum width; both setae of P5 endopodal lobe equally long; posterior margin of pseudoperculum medially indented. . . . . *P. ekmani* (Lang, 1965).
P2 exp-2 outer spine twice as long as outer spine of exp-1 and extending beyond distal margin of exp-3; P5 exopod about 1.3 times as long as maximum width; inner seta of P5 endopodal lobe distinctly longer than outer one; posterior margin of pseudoperculum broadly curved, continuous. . . . . *P. triarticulatus* (Moore, 1976b).

Amphiascus soyeri (Lang, 1965)

Theodor (1963) studied the organisms enclosed in the excrescences formed by the seafan *Eunicella stricta* (Bertoloni, 1810) (often considered a junior synonym of *Eunicella singularis* (Esper, 1791)) (family Gorgoniidae) in the vicinity of Banyuls-sur-Mer. Among the fauna and flora contained in these gall-like formations he recorded cyanobacteria, pennate diatoms, chlorophytes, red algae and foraminiferans. Five out of 45 of these "pocket-like" structures also contained juveniles and adults of an unidentified species of *Paramphiascopsis* Lang, 1944. Soyer (1963) identified the copepod as *P. pallidus* (Sars, 1906b) and provided a brief illustrated redescription. Lang (1965) noted several differences between Soyer's material and Sars' (1906b) Norwegian types, including the morphology of the female antennule, legs 1 and 5 of both sexes, and the male leg 2. Based on these discrepancies he attributed distinct specific status to the Mediterranean population and renamed it *P. soyeri* Lang, 1965. Huys (2009b) remarked that the correct binomen for this species is *Amphiascus soyeri* (Lang, 1965) since *Paramphiascopsis* loses in priority to the senior synonym *Amphiascus*.

Theodor (1963) noted that excrescences can be found anywhere along the axis of the gorgonian, from the base up to the extremities of the longest branches, varying considerably in form and size. The galls were most frequently observed on the upper branches of the coral. Carnivorous caenogastropods, in particular the false cowry *Simnia spelta* (Linnaeus, 1758), regularly prey on the polyps and tissue of *Eunicella stricta* and create lesions along the branches. Predation appears to elicit a rapid host response during which newly produced gorgonin is deposited on the feeding scars (Theodor 1963). During this process of forming a physical barrier between the host and possible intruders, patches of exposed skeleton are often colonized by a variety of epibionts, including sponges, hydroids, tunicates, sedentary polychaetes and bryozoans. However, smaller motile organisms such as copepods can become imprisoned in the deposited gorgonin, forming thin-walled, hollow protrusions originating from the surface of the seafan. According to Theodor (1963) around 90% of the galls are completely closed when fully developed, suggesting there is no respiratory current inside. It is unknown whether the copepods were found in semi-closed or completely closed galls. Soyer (1973) found 11 females, three males and many nauplii and copepodids from five occupied galls, indicating that some of these were shared by several specimens or even both sexes. Presumably the gall must rupture at some point to release nauplii or early copepodids, or alternatively, the copepods leave the gall through a newly bored small aperture.

The occurrence of copepods in galls formed by scleractinian corals (Dojiri 1988; Dojiri & Grygier 1990; Kim & Yamashiro 2007; Ivanenko *et al.* 2014) and alcyonaceans (Gravier 1914; Grygier 1980; Buhl-Mortensen & Mortensen 2004; Ivanenko *et al.* 2016) is probably widespread but whether *A. soyeri* is a truly gallicolous copepod or has any control over gall formation, by chemical dissolution or mechanical means, remains unknown. The species has not been recorded again since Soyer's (1963) description. Lang (1965) suspected that Grandori's (1912) record of *Amphiascus pallidus* Sars, 1906b from the Venice Lagoon referred to *A. soyeri*, however, in the absence of any descriptive evidence this claim is to be considered unsubstantiated.

OD: Soyer (1963—as *Paramphiascopsis pallidus* (Sars, 1906b)): 572–578; Figs 1–3.
TL: France, Roussillon-Languedoc region, Pyrénées-Orientales, Banyuls-sur-Mer; in galls formed by the gorgoniid *Eunicella stricta* (Bertoloni, 1810) (Gorgoniidae). Seafan hosts were collected at 10–15 m depth off the jetty in Banyuls-sur-Mer and at 20–25 m depth in front off the Plage du Troc.
BL: 630–722 µm (♀), 596–690 µm (♂).

Family Peltidiidae

Alteuthellopsis Lang, 1948

The genus includes two species of which *Alteuthellopsis corallina* Humes, 1981b is known to be associated with scleractinian corals in the Indo-Pacific. The type species, *A. oblivia* (A. Scott, 1909), was found in washings of material dredged at 32 m depth between Maluku and West Papua in the Seram Sea (Scott 1909). Given the close morphological resemblance between both species and the possibility that dislodged coral fragments could easily have been gathered by the dredge while it was towed along the bottom, it is probable that *A. oblivia* is also associated with a scleractinian host. Humes (1981b) pointed out several differences between *A. oblivia* and *A. corallina*, including the length:width ratio of the body, the plumosity of the antennulary setae, the armature of the antennary endopod and the morphology of the caudal ramus (presence of a toothlike process near outer distal spine). These differences may not be reliable since they depend on the interpretation of Scott's (1909) relatively inadequate descriptions and illustrations. Wells (2007) also pointed out that legs 2–3 of *A. oblivia* have not been described but as it was originally established in the genus *Eupelte* Claus, 1860 it is most likely that P2–P3 exp-3 have 7 and 8 spines/setae, respectively (as opposed to 6 and 7 in *A. corallina*). Rather than using this as the only discriminating character it is recommended to use the combination of characters below.

Key to species of *Alteuthellopsis* Lang, 1948

1. Antennule ♀ 7-segmented; antennary exopod with four setae; outer spine of P4 exp-3 enlarged, much longer than outer spine of exp-2; P4 enp-2 with two inner setae; P5 endopodal lobe with two setae in both sexes . . . . *A. oblivia* (A. Scott, 1909).
   Antennule ♀ 6-segmented; antennary exopod with three setae; outer spine of P4 exp-3 small, much shorter than outer spine of exp-2; P4 enp-2 with one inner seta; P5 endopodal lobe with one seta in both sexes . . . .*A. corallina* Humes, 1981b.

Alteuthellopsis corallina Humes, 1981b

This species was originally described from washings of the hermatypic coral *Merulina ampliata* (Ellis & Solander, 1786) (family Merulinidae) collected in Nosy Bé, north-western Madagascar, but was also found on other hosts in the Nosy Bé area, New Caledonia and the Maluku Islands (Moluccas) (Humes 1981b). It was subsequently recorded from the Great Barrier Reef (Humes 1984, 1991, 1992), including a record from its type host *M. ampliata*. *Alteuthellopsis corallina* is a widespread associate of various hard corals, occurring on species in nine genera and four families: *Acropora* Oken, 1815, *Astreopora* Blainville, 1830, *Gardineroseris* Scheer & Pillai, 1974, *Goniastrea* Milne Edwards & Haime, 1848c, *Merulina* Ehrenberg, 1834, *Montipora* Blainville, 1830, *Platygyra* Ehrenberg, 1834, *Pocillopora* Lamarck, 1816a and *Stylophora* Schweigger, 1820 (Table 6). The number of copepods on a single coral colony may be very large and copepodid stages often make up a significant proportion of the population. For example, a total of 1,125 specimens (267 copepodids) of *A. corallina* were recovered from one mass of *Pocillopora damicornis* (Linnaeus, 1758) (as *P. d.* var. *caespitosa* Dana, 1846) in Madagascar (Humes 1981b). Heavy infestations in confined environments have raised serious concerns among aquarists and the reefkeeping community and have started the debate on the development of methods for its control (*e.g.* Reef'd Up Aquatics 2013). The geographical range of *A. corallina* currently extends from Madagascar to New Caledonia, including north-eastern Australia and the Maluku Islands. It is conceivable that the copepod is to be found throughout the ranges of its coral hosts. Ovigerous females carry a flattened egg sac containing 7–14 eggs, ranging from 62–96 µm in diameter. The colour of live specimens is slightly opaque grey and that of the egg sacs dark brownish grey.

OD: Humes (1981b): 227–234; Figs 1–29.
AD: Ivanenko *et al.* (2008b): 221; Fig. 24B.
TL: Madagascar, Nosy Bé, Pointe de Tafondro; depth 2 m; washings of scleractinian *Merulina ampliata* (Ellis & Solander, 1786) (Merulinidae).
BL: 550–630 µm (♀), 530–570 µm (♂).

Family Tegastidae

Tegastids are cosmopolitan in shallow water phytal communities, being predominantly associated with rhodophytes and phaeophytes that offer morphological complexity and spatial heterogeneity (see McAlice & Coffin (1990) for a review of algal substrates). Some species have secondarily colonized the interstitial environment (Cottarelli & Baldari 1987) while others inhabit cold seeps (Plum & Martínez Arbizu 2009) and hydrothermal vent environments (Ivanenko & Defaye 2004; Gollner *et al.* 2008; Back *et al.* 2010). Members of three genera have entered into symbiotic relationships with cnidarian hosts in the warm waters of the Indo-Pacific, from the African east coast to Hawaii. No symbiotic records are known from the Atlantic except for an unidentified tegastid associated with an octocorallian host in Cuba (Varela 2010).

TABLE 6. Scleractinian coral hosts and locality records of *Alteuthellopsis corallina* Humes, 1981b (family Peltidiidae) [*: *nomen dubium*; **: type host].

Family	Species	Country	Locality	Reference
Acroporidae	*Acropora exigua* (Dana, 1846)*	New Caledonia	Isle Ndié, Baie de la Dumbéa	Humes (1981b)
	Astreopora sp.	Madagascar	west of Pte. Mahatsinjo, Nosy Bé	Humes (1981b)
	Montipora verrilli Vaughan, 1907	Australia	Mermaid Cove, Lizard Island	Humes (1984)
Agariciidae	*Gardineroseris planulata* (Dana, 1846)	Australia	Big Broadhurst Reef, Great Barrier Reef	Humes (1992)
Merulinidae	*Goniastrea retiformis* (Lamarck, 1816a)	Indonesia	Poelau Parang, eastern Seram (Ceram)	Humes (1981b)
	Merulina ampliata (Ellis & Solander, 1786)**	Madagascar	Pte. de Tafondro, Nosy Bé	Humes (1981b)
		Australia	Big Broadhurst Reef, Great Barrier Reef	Humes (1991)
	Platygyra daedalea (Ellis & Solander, 1786)	Madagascar	Ambariobé, near Nosy Bé	Humes (1981b)
	Platygyra sp.	Madagascar	Ambariobé, near Nosy Bé	Humes (1981b)
Pocilloporidae	*Pocillopora damicornis* (Linnaeus, 1758)	New Caledonia	Rocher à la Voile, Nouméa	Humes (1981b)
	Stylophora pistillata Esper, 1797	Australia	Big Broadhurst Reef, Great Barrier Reef	Humes (1991)

Key to genera of Tegastidae Sars, 1904b

1.	Caudal rami three times longer than wide	*Smacigastes* Ivanenko & Defaye, 2004.
	Caudal rami at most twice as long as wide	2.
2.	P2–P3 exopods 2-segmented	3.
	P2–P3 exopods 3-segmented	5.
3.	P4 endopod 2-segmented	4.
	P4 endopod 3-segmented	*Parategastes* Sars, 1904b.
4.	P2–P3 endopods 2-segmented; P4 enp-1 forming a broad lamellar structure; P5 ♀ with distinct exopod and baseoendopod, endopodal lobe obsolete	*Arawella* Cottarelli & Baldari, 1987.
	P2–P3 endopods 3-segmented; P4 enp-1 normally developed; P5 ♀ with exopod and baseoendopod completely fused, forming massive foliaceous plate	*Syngastes* Monard, 1924.
5.	P4 endopod 2-segmented	*Feregastes* Fiers, 1986a.
	P4 endopod 3-segmented	6.
6.	P5-bearing, genital and first abdominal somite fused, forming genital triple-somite complex with conspicuous ventral expansion in both sexes; last three urosomites typically small and largely telescoped into triple-somite; P5 ♀ baseoendopods large and foliaceous, forming ventral brood pouch	*Tegastes* Norman, 1903.
	Both sexes with discrete P5-bearing somite, and fused genital and first abdominal somites forming genital double-somite (the latter with conspicuous ventral expansion in ♂ only); last three urosomites of normal development; P5 ♀ baseoendopods not expanded, semi-enclosed subthoracic brood pouch formed by P1–P4	***Aglaogastes* gen. nov.**

Tegastes Norman, 1903

The genus currently contains 32 valid species (Wells 2007; Back *et al.* 2010), however, many descriptions are inadequate in modern terms and identification at species level is fraught with difficulty. Six species are known to utilize scleractinian coral hosts (Marcus & Masry 1971; Marcus 1977; Humes 1981a, 1984). A seventh, as yet undescribed, species was collected in washings of an alcyonacean host (Varela 2010). *Tegastes cnidicus* Humes, 1981b utilizes hydroids and displays a morphology which is radically different from that of its congeners. It is here fixed as the type species of a separate genus, ***Aglaogastes* gen. nov.**

Key to species of *Tegastes* Norman, 1903 associated with scleractinian hosts

1.	P2 enp-3 with four setae/spines	2.
	P2 enp-3 with five setae/spines	3.
2.	P4 exp-3 with six setae/spines	*T. gemmeus* Humes, 1984 [1].
	P4 exp-3 with five setae/spines	*T. georgei* Marcus & Masry, 1971 [1].
3.	P4 exp-3 with seven setae/spines; P4 enp-3 with five setae/spines; P5 baseoendopod ♀ with five endopodal setae	4.
	P4 exp-3 with six setae/spines; P4 enp-3 with four setae/spines; P5 baseoendopod ♀ with two endopodal setae	5.
4.	Antennule ♀ 7-segmented; P2–P3 exp-1 with inner seta	*T. pygmaeus* Marcus, 1977.
	Antennule ♀ 6-segmented; P2–P3 exp-1 without inner seta	*T. paulipes* Humes, 1984.
5.	Distal antennary segment with inner apical claw only half the size of outer one; proximal endite of maxillary syncoxa with one short and one very long seta	*T. singularisaetus* Marcus, 1977 [2].
	Distal antennary segment with inner apical claw about 3/4 the size of outer one; proximal endite of maxillary syncoxa with two short setae	*T. acroporanus* Humes, 1981a [2].

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[1] These species are very similar but comparison is hampered by the poor quality of Marcus & Masry's (1971) description. Their illustrations are very inadequate and contain obvious errors such as the reduced armature on the exopods of legs 1 and 5 in both sexes. Humes (1984) separated the species on the basis of the shape of the modified inner seta of P4 exp-3 but this character is likely to be unreliable. I have tentatively followed Wells (2007) in using the number of elements on P4 exp-3 as a discriminating character but redescription of *T. georgei* may prove it to be equally inadequate since no other species lacks the outer distal seta on this segment.

[2] Humes (1981a) discussed differences between *T. acroporanus* and 25 congeners, but being unaware of Marcus' (1977) paper, did not compare it with its closest relative, *T. singularisaetus*, which utilizes the same coral genus as host. Both species are morphologically extremely similar and possibly conspecific despite their widely separated type localities. Wells (2007) separated them on the basis of small setal differences in the antenna (enp-1 with or without seta), mandible (endopod with three *vs* two setae) and maxilla (distal coxal endite with three *vs* two setae) but the fact that *T. singularisaetus* consistently displays the lowest number of armature elements for these appendages more than likely reflects the generally poor standard of Marcus' (1977) description.

Tegastes georgei Marcus & Masry, 1971

Marcus & Masry (1971) observed about 80 specimens of *Tegastes georgei* on a small coral head of an unidentified species of the pocilloporid genus *Stylophora* collected in the Gulf of Aqaba. Live specimens kept in an aquarium containing the original coral head left the host after six weeks only to reappear on an adjacent coral head of *Pocillopora* sp. where they had not been observed before. The copepods are distinctly black when alive and appear to avoid the tentacles of the polyps.

OD: Marcus & Masry (1971): 170–173; Fig. 1; Plates I–II.
TL: Egypt, Sinai, northern coast of Gulf of Aqaba, Marsa Murakh (near Taba); 1 m depth; from a small coral head of *Stylophora* sp. (Pocilloporidae).
BL: 420 µm (♀), 400 µm (♂).

Tegastes pygmaeus Marcus, 1977

This species is known from two specimens only, one of which was allegedly found in association with the elkhorn coral, *Acropora palmata* (Lamarck, 1816a) (family Acroporidae). The accuracy of the host identification is problematic since *A. palmata* is known to be endemic to the Caribbean, where it is considered to be one of the most important reef-building corals. Its range stretches as far north as Biscayne National Park, Florida, and as far south as Curaçao and Venezuela (Veron 2000).

OD: Marcus (1977): 77–79; Figs 3, 9–11.
TL: Tanzania, Mbudya Island (east of Kunduchi). Marcus (1977) reported one specimen from *Acropora palmata* (Lamarck, 1816a) (Acroporidae) at 2 m depth and another one from sandy sediment at 1.5 m depth. It is not clear which substratum the holotype originated from.
BL: 240 µm (♀), 200 µm (♂).

Tegastes singularisaetus Marcus, 1977

Marcus (1977) reported 86 specimens from *Acropora palmata* at 2 m depth off the coast of Dar es Salaam (Tanzania). The host record is based on an erroneous identification (see *T. pygmaeus*). Her record of a single specimen of *T. singularisaetus* on a coarse shell gravel at 100 m depth off Gonubie, about 21 km north-east of East London (South Africa) is remarkable but, if proven correct, indicates the wide niche utilization of the species. It has not been recorded again since its original description.

OD: Marcus (1977): 73–77; Figs 1–2, 6–8.
TL: Tanzania, Mbudya Island (east of Kunduchi); 2 m depth; on *Acropora palmata* (Lamarck, 1816a) (Acroporidae).
BL: 480 µm (♀), 440 µm (♂).

Tegastes acroporanus Humes, 1981a

Humes (1981a) extracted 109 females and 85 males from washings of the acroporid coral *Acropora florida* (Dana, 1846) collected in the Marshall Islands. The host is widespread, being found in the south-west and northern Indian Ocean, the central Indo-Pacific, Australia, south-east Asia, Japan and the East China Sea, Cook Island, and the oceanic west Pacific (Veron 2000).

Live specimens are opaque grey and have a red nauplius eye. The egg sac usually contains three (sometimes two) large grey eggs (approx. 167 × 120 µm) and is held between the large scoop-like fifth legs and the anterior concave surface of the genital triple-somite complex.

The species is known among aquarists and reefkeepers as the "red bug", causing serious problems to *Acropora* corals (but not *Montipora* or *Pocillopora*) in aquarium environments (Riddle 2010). Temperature, nutrients, and a number of other factors may contribute to unnatural populations or outbreaks of *T. acroporanus*. Poor polyp extension, loss of coloration and overall coral decline may be signs of a red bug infection. When latched onto a coral, red bugs are extremely hard to remove and they have an ability to lodge themselves inside the gastrovascular cavities of the polyps without being consumed. Although red bugs do tend to prefer certain *Acropora* (especially *A. valida*, the "tricolor"), they have been found on almost every species of the genus kept by reefkeeping hobbyists. A number of treatments for red bugs have become available, including quarantine, chemical control or eradication, biological controls including deliberate manipulation of physical and chemical parameters, as well as selective control by natural predators (Riddle 2010; Reef'd Up Aquatics 2013).

OD: Humes (1981a): 254–260; Figs 1–26.
TL: Marshall Islands, Enewatok (Eniwetok) Atoll, western end of Bogon Island; 2 m depth; on *Acropora florida* (Dana, 1846) (Acroporidae).
BL: 500–570 µm (♀), 460–480 µm (♂).

Tegastes gemmeus Humes, 1984

Humes (1984) recorded 24 females, 55 males and 10 copepodids in washings of the scleractinian coral, *Cyphastrea ocellina* (Dana, 1846) (family Merulinidae) collected in Hawaii, the easternmost limit of the host's range. A few individuals were also recorded from a second host at the type locality, *Montipora verrucosa* (Lamarck, 1816a) (family Acroporidae). *Tegastes gemmeus* is likely to have a much wider distribution since both coral hosts display a range that extends to at least the eastern Indian Ocean (*C. ocellina*) or beyond (*M. verrucosa*) (Veron 2000). Live specimens have a grey colour. Ovigerous females carry an egg sac containing two large eggs. According to Ivanenko *et al.* (2008b) the male genital aperture and leg 6 have undergone a 45-degree counterclockwise rotation.

OD: Humes (1984): 209–213; Figs 1–3.
AD: Ivanenko *et al.* (2008b): 219; Fig. 22.
TL: U.S.A., Hawaii, Oahu, Kaneohe Bay, Coconut Island; 1 m depth; washings of *Cyphastrea ocellina* (Dana, 1846) (Merulinidae).
BL: 410–430 µm (♀), 390–410 µm (♂).

Tegastes paulipes Humes, 1984

Humes (1984) obtained 53 females, 25 males and 4 copepodids in washings of the rasp coral, *Pocillopora verrucosa* (Ellis & Solander, 1786) (family Pocilloporidae), collected in Moorea. The species has not been recorded again but probably has a much wider range. The host coral has a widespread distribution within the Indo-West Pacific and Eastern Tropical Pacific regions from the Red Sea and the Gulf of Aden to the Pacific seaboard of Latin America. Live individuals have a grey colour with darker amber areas (nauplius eye red). The grey egg sac contains four eggs, each about 88 µm in diameter.

OD: Humes (1984): 213–217; Figs 4–6.
TL: French Polynesia, Society Islands, north-western Moorea, between Ilot Tiahura and Ilot Irioa; 12 cm depth; washings of *Pocillopora verrucosa* (Ellis & Solander, 1786) (Pocilloporidae).
BL: 410–420 µm (♀), 400–430 µm (♂).

Tegastes sp.

Varela (2010) recorded a single female of an unidentified species of *Tegastes* Norman, 1903 from washings of the alcyonacean *Plexaurella grisea* Kunze, 1916 (family Plexauridae). The octocorallian was collected at 20 m depth in Miramar, city of Havana, Cuba. No illustrations or text description were provided.

Parategastes Sars, 1904b

The genus currently contains seven valid species (Wells 2007; Saetang & Maiphae 2015) and one species of uncertain status (*P. haphe* Leigh-Sharpe, 1936—see below). The description of *P. herteli* Jakobi, 1953b is grossly inadequate and contains dubious characters such as the setation of P4 enp-2 which is not only asymmetrical in the female but also sexually dimorphic (setae absent in the male); the species is excluded from the key below. Wells (2007) pointed out that *Tegastes chalmersi* Thompson & Scott, 1903 should be transferred to *Parategastes* on the basis of the 2-segmented condition of P2–P3, inferred by Thompson & Scott's (1903) comparison with their *Tegastes imthurni*. In recent keys (Wells 2007; Saetang & Maiphae 2015) the species has been differentiated from its congeners by the unusual armature formula displayed on the rami of leg 1 (exopod and endopod with four and five elements, respectively *vs* five and six) and the distal endopod segment of leg 4 (with six elements *vs* three or five). However, these characters are doubtful, the first one probably being the result of accidentally reversing the exopod and a damaged endopod (with two elements missing), the second one clearly being an observational error since no other tegastid possesses an outer distal spine, in addition to an outer spine (which in reality represents the displaced outer distal spine), on P4 enp-3. One species, *P. conexus* Humes, 1984, has been reported as an associate of an alcyonacean host in southeast Asia.

Key to species of *Parategastes* Sars, 1904b

1. Both rami of P1 distinctly shorter than its basis; P4 enp-3 with five setae/spines . . . . 2.

Both rami of P1 at least as long as its basis; P4 enp-3 with three setae/spines. . . . . 3.

2. Maxilliped with robust endopodal claw, about 1/3 length of basis; P4 enp-3 distal inner seta about as long as other two inner setae; P5 endopodal lobe ♀ sub-triangular; genital triple-somite complex ♀ with two midventral processes. . . . . *P. conexus* Humes, 1984.

Maxilliped with elongate endopodal claw, about 1/2 length of basis; P4 enp-3 distal inner seta about as long as proximal inner seta but distinctly shorter than middle one; P5 endopodal lobe ♀ sub-oval; genital triple-somite complex ♀ with three midventral processes . . . . *P. chalmersi* (Thompson & Scott, 1903).

3. Antennule ♀ 6-segmented; P1 exopod about as long as its basis, endopod distinctly longer; P4 enp-2 with two inner setae. . . . . *P. coetzeei* Kunz, 1980.

These characters not combined . . . . 4.

4. Antennary exopod with two setae; both rami of P1 about as long as its basis; distal outer element of P1 exopod vestigial, much shorter than inner distal element . . . . *P. sphaericus* (Claus, 1863) [1].

Antennary exopod with three setae; both rami of P1 distinctly longer than its basis; distal outer element of P1 exopod well developed, longer than inner distal element . . . . 5.

5. Antennule ♀ 6-segmented; P5 exopod ♀ with four elements; found in freshwater . *P. pholpunthini* Saetang & Maiphae, 2015.

Antennule ♀ 7-segmented; P5 exopod ♀ with five elements; found in brackish—saline water (31.6 ‰ salinity) . . . . *P. caprinus* Wellershaus, 1970.

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[1] after Huys *et al.* (1996): Fig. 115, 116A–B, 119.

Parategastes conexus Humes, 1984

Both adults and copepodids were obtained in washings of the alcyonacean *Stereonephthya ulicoides* Thomas & Dean, 1931 (family Nephthyidae), collected in the Maluku Islands (Humes 1984). Live specimens have an opaque pale greyish tan, a red nauplius eye and a bright red genital triple-somite complex. The grey egg sac contains four eggs. According to Ivanenko *et al.* (2008b) the male genital aperture and leg 6 have undergone a 45-degree counterclockwise rotation. *Parategastes conexus* is most closely related to *P. chalmersi* which was described from two females obtained in pearl oyster washings in Sri Lanka (Thompson & Scott 1903). Both share the presence of two inner setae on P4 enp-2 and five elements on P4 enp-3, and have both rami of leg 1 being distinctly shorter than its basis.

OD: Humes (1984): 217–220; Figs 7–9.
AD: Ivanenko *et al.* (2008b): 218; Fig. 21B–D.
TL: Indonesia, Maluku Islands (Moluccas), Obi Islands; Gomumu (south of Obi Island), Poelau Gomumu (1º50’00”S, 127º30’45”E); 10 m depth; washings of *Stereonephthya ulicoides* Thomas & Dean, 1931 (Nephthyidae).
BL: 390–410 µm (♀), 350–430 µm (♂).

Aglaogastes gen. nov.

Both Humes (1981b) and Wells (2007) had previously noted that *Tegastes cnidicus* differed from its congeners in the absence of a ventral expansion on the female genital somite. In all other members of *Tegastes* the P5-bearing, genital and first abdominal somites are fused, forming a genital triple-somite complex with a conspicuous ventral expansion in both sexes. The last three urosomites are typically small and largely telescoped into the triple-somite. The baseoendopods of the female leg 5 are large and foliaceous, forming a ventral brood pouch shielding the developing eggs. Conversely, in both sexes of *T. cnidicus* the P5-bearing somite is discrete, and the genital and first abdominal somites form a genital double-somite which has a conspicuous ventral expansion in the male only. The last three urosomites are of normal development. The female baseoendopods of leg 5 are not expanded or involved in the formation of an incubatory pouch. Instead, a semi-enclosed subthoracic brood pouch is formed by legs 1–4, possibly because the eggs are too large for them to be embraced by the fifth legs. The former suite of characters displayed by *T. cnidicus* is surprisingly also found in members of *Smacigastes*, which is considered as the most primitive genus of the family Tegastidae (Ivanenko & Defaye 2004; Gollner *et al.* 2008). Specialized brooding in enclosed or semi-enclosed incubatory chambers has evolved independently many times in copepods but subthoracic brooding is extremely rare (Grygier & Ohtsuka 2008; Huys 2014). Members of the monstrilloid genus *Maemonstrilla* Grygier & Ohtsuka, 2008 are the only planktonic copepods that practise subthoracic brooding (Grygier & Ohtsuka 2008; Suárez-Morales & McKinnon 2014) while some Chordeumiidae (Cyclopoida) maintain their loose egg masses in a subthoracic cage that is formed from modified and ventrally downturned cephalic appendages and thoracic outgrowths (Stephensen 1935; Goudey-Perrière 1979).

Tegastes cnidicus differs from members of *Smacigastes* in the numerous reductions displayed by the antennule, antenna, mandible, maxillule, maxilla and P2–P3 exopods. It lacks the elongate caudal rami which are considered apomorphic for *Smacigastes* (Ivanenko & Defaye 2004; Gollner *et al.* 2008) and differs in the torsion of the male genital somite. According to Ivanenko *et al.* (2008b) the genital aperture and leg 6 have undergone a 45-degree clockwise rotation in *T. cnidicus* instead of 45-degree anticlockwise rotation in *Smacigastes* and various other tegastids. Based on its unique morphology *T. cnidicus* is here fixed as the type species of a new genus.

Diagnosis. Tegastidae. Urosome consisting of free P5-bearing somite, genital double-somite and three well developed postgenital somites in both sexes. Genital double-somite without ventral expansion in ♀; produced ventrally in ♂, forming large expansion with three spinous processes. Caudal ramus short, length less than twice the width; with seven setae. Antennule 7-segmented in ♀ with aesthetasc on segments 4 and 7; 8-segmented in ♂ with geniculation between segments 6 and 7 and aesthetasc on segments 3, 4 and 8. Antenna with bisetose, 1-segmented exopod; proximal endopodal segment unarmed. Mandibular palp reduced, 2-segmented, with two apical setae on endopod. Maxilla with three endites on syncoxa. Maxilliped with elongate syncoxa and robust basis and endopod; proximal part of palmar margin convex and spinulose, abruptly demarcated from the concave distal part; endopodal claw stout and curved, with four accessory setae.

Leg 1 with 1-segmented rami; exopod with three outer and two apical elements; endopod with one outer, two apical and three inner elements. Legs 2–4 with 3-segmented rami and armature formula as follows:

	Exopod	Endopod
Leg 2	0.1.222	1.2.221
Leg 3	0.1.322	1.2.321
Leg 4	0.1.322	1.2.221

Third segment of exopod of leg 4 with middle of three inner setae slightly modified, longer than adjacent setae. Leg 5 ♀ baseoendopod not enlarged or foliaceous; endopodal lobe not extending beyond exopod, with three inner and two apical setae; exopod with three outer and two apical setae. Leg 5 ♂ 2-segmented; endopodal lobe lacking; exopod with two outer and two apical setae. Male genital aperture and leg 6 showing 45-degree clockwise rotation.

Associated with Hydrozoa.

Type and only species. *Tegastes cnidicus* (Humes, 1981b) (by original designation).

Etymology. The generic name is an arbitrary contraction of the host genus name *Aglaophenia* Lamouroux, 1812 and *Tegastes*, the type genus of the family. Gender: masculine.

Aglaogastes cnidicus (Humes, 1981b) comb. nov.

Tegastes cnidicus (Humes, 1981b)

This species occurs in vast numbers on the stinging hydroid *Aglaophenia cupressina* Lamouroux, 1816 (family Aglaopheniidae) which is the only host known so far. Humes (1981b) collected 1,549 females, 251 males and 167 copepodids from several featherlike stems of the hydroid. The egg sac contains three or four black eggs (maximum diameter 62 µm). Live specimens are opaque grey (except for the red nauplius eye). Although the species has not been recorded again since its original description, the distribution range of its host suggests that *T. cnidicus* may be common in tropical reefs throughout the Indian Ocean and south-western Pacific.

OD: Humes (1981b—as *Tegastes cnidicus*): 234–239; Figs 30–53.
AD: Ivanenko *et al.* (2008b—as *T. cnidicus*): 220; Fig. 23.
TL: Indonesia, Maluku Island (Moluccas), east central Halmahera, Karang Mie (00º20’07”N, 128º25’00”E); 3 m depth; from the stems of *Aglaophenia cupressina* Lamouroux, 1816 (Aglaopheniidae).
BL: 280–300 µm (♀), 280–310 µm (♂).

Platyhelminthes

Despite their ubiquity and high diversity turbellarian flatworms do not appear to be popular hosts for copepods, presumably because the great majority are either scavengers or predators. Two species of the cyclopoid genus *Pseudanthessius* Claus, 1889 utilize polycladids as hosts (Illg 1950; Humes 1997). The only other copepod known to be associated with a platyhelminth host is a member of the primarily free-living Ameiridae.

Family Ameiridae

Nitocra Boeck, 1865

Nitocra bdellurae (Liddell, 1912)

Members of the triclad family Bdellouridae (“*Limulus* leeches”) live exclusively on the undersurface of horseshoe crabs (Xiphosura), mainly residing between the book gill lamellae of the opisthosoma but also on the legs and the ventral side of the carapace. They are ectocommensal, capable of feeding on the host’s food supply, however acid phosphatase activity observed in the ventral body wall of the triclads suggests that they may obtain some of their nutrition from haemolymph of the chelicerate host (Lauer & Fried 1977). Bdellourids episodically deposit stalked egg cases or cocoons onto the book gill lamellae of their hosts (*e.g.* Huggins & Waite 1993). Liddell (1912) examined the cocoons of three bdellourid associates of *Limulus polyphemus* (Linnaeus, 1758) and found several developmental stages of a new harpacticoid copepod, *Nitocrameira bdellurae*, in two of the species, *i.e.*, *Bdelloura candida* (Girard, 1850) and *B. propinqua* Wheeler, 1894. Occupied cocoons of *B. propinqua* measured about 1.25 mm in size, were far more common, and typically located in the basal inner section of the gill leafs. Those of *B. candida* were distinctly larger (2.5–4 mm), usually deposited not far from the outer apical margin of the gill leaf, and rarely contained copepods. These are the first cases of hypersymbiosis in the Harpacticoida. The much smaller cocoons of *Syncoelidium pellucidum* Wheeler, 1894, which were always deposited in a small area along the apical outer margin of the gill leaf, never contained any copepods.

Copepods were only found in empty egg cases which were comparatively fresh, containing a certain amount of organic debris or remains of triclad embryos. Older cocoons which contained particles of sand or inorganic debris were never occupied. The number of copepods per egg case varied from one to 29 but 3–6 individuals was the typical condition. Cocoons contained ovigerous females and both early and late naupliar stages of *N. bdellurae* but no copepodids. The egg sac contained 7–12 eggs arranged in a double row (Liddell 1912); Gurney (1930b) observed eight large eggs. Given the small size of the aperture in the capsule the copepods probably leave either prior or during the metamorphosis from nauplius VI to copepodid I. Mating, reproduction and hatching of the nauplii takes place inside the egg case. Liddell (1912) surmised that *N. bdellurae* preyed on triclad embryos since in all individuals the gut was completely filled and in one case the half-digested remains of an embryo were still discernible. Cocoons of *B. candida* can contain up to nine young flatworms (Sluys 1989), suggesting there is sufficient food supply to sustain a small batch of developing *N. bdellurae* nauplii.

Both Liddell (1912) and Gurney (1930b) obtained the copepods from preserved *Limulus* specimens deposited in the then Department of Comparative Anatomy in Oxford. The precise origin of the host material is unknown except that it was collected in North America. With the exception of rare extralimital reports, the known range of *L. polyphemus* broadly encompasses the Atlantic seaboard of the North America from Nova Scotia (Canada) in the north, extending around the Florida peninsula into the Gulf of Mexico to the Yucatan Peninsula (Mexico). It is likely that the distribution of *N. bdellurae* approximates that of its host.

Liddell (1912) believed that *N. bdellurae* held an intermediate position between *Ameira* Boeck, 1865 and *Nitocra* Boeck, 1865, and, consequently, assigned the species to its own genus, *Nitocrameira* Liddell, 1912, in the Canthocamptidae. His comparative analysis was primarily based on mouthpart characters. Monard (1927) transferred the genus to the Ameiridae, noting that it hardly differed from *Ameira*. Gurney (1927) remarked that *N. bdellurae* appeared to be identical with *Nitocra divaricata* Chappuis, 1923, but upon re-examination of material of both species withdrew this statement in a later paper (Gurney 1930b), confirming their distinctiveness and different generic assignment. Lang (1948) eventually subsumed *Nitocrameira* under *Nitocra*. Note that the species name "*bdellurae*" is based on Liddell's (1912) incorrect spelling of the host genus, *i.e. Bdellura* instead of *Bdelloura*. Boxshall & Halsey (2004: 8) erroneously included it in their category of symbiotic copepods from freshwater habitats.

OD: Liddell (1912—as *Nitocrameira bdellurœ*): 88–90, 93–94; Figs 1–2; Plates 10–11.
AD: Gurney (1930b– as *Nitocrameira bdellurae*): 107–109; Figs 9–16.
TL: North America, probably U.S.A., Atlantic coast; in empty egg capsules of *Bdelloura propinqua* Wheeler, 1894, and less frequently, *B. candida* (Girard, 1850) (Platyhelminthes, Tricladida).
BL: 890 µm (sex not specified) [Liddell 1912]; 800–970 µm (♀) [Gurney 1930b].

Annelida

Despite their diversity and broad host utilization symbiotic copepods from polychaete hosts are relatively rarely encountered and usually exist at very low prevalence rates. Conradi *et al.* (2015) listed 168 species belonging to 74 genera and 22 families but only two reports of harpacticoids were mentioned (Moore & O'Reilly 1993; O'Reilly 1995). O'Reilly (1995), referring to the work by Guérin & Cubizolles (1987), stated that one of the two tisbid species cited by Gotto (1979) as occasional commensals of holothurians had also been implicated as an associate of larval polychaetes. This statement is misleading since Guérin & Cubizolles' (1987) rearing experiments did not provide any evidence for such an association. Larval stages of the spionid *Pseudopolydora antennata* (Claparède, 1870) showed a higher survival rate and a faster growth when *Tisbe holothuriae* females were added to the culture tank. The copepods gathered food into small aggregates which facilitated nutrition of the polychaete larvae. However, this was only the case in stagnant water conditions and when the population density of *T. holothuriae* was sufficiently low. When densities were high, larvae only survived for a few days, possibly because the copepods produced a toxic metabolite (Fava 1972).

Family Dactylopusiidae

Sand gobies of the *Pomatoschistus minutus* complex are the most abundant demersal fish in the coastal waters of the continental shore of the North Sea, the Wadden Sea and the inshore waters of England and Wales (Hamerlynck 1993). While *P. lozanoi* (Buen, 1923) has a somewhat specialized diet feeding mainly on a few pelagic and hyperbenthic species (Hamerlynck *et al.* 1990), its sympatric congener, *P. minutus* (Pallas, 1770), assumes a more benthos-oriented feeding strategy, preying primarily on caridean shrimp and sedentary polychaetes, including the sand mason worm, *Lanice conchilega* (Pallas, 1766) (Hamerlynck *et al.* 1986). Stomach contents analysis revealed that *P. minutus* also consumed large numbers of *Dactylopusia vulgaris* Sars, 1905b while other harpacticoids were rare (Hamerlynck 1993). It is, however, unlikely that the numerical importance of this prey item is due to selective predation by the gobioid. Inspection of the stomachs showed that the copepods mainly occurred between the radiole crowns of *L. conchilega*, lending support to the hypothesis that they were ingested together with the radioli. Subsequent examination of *L. conchilega* samples collected off the Belgian coast revealed the virtually consistent presence of *D. vulgaris*, suggesting there is a (facultative) symbiotic relationship with its terebellid host, the preferred niche on the host being the radiole crowns (R. Huys, unpubl. data).

Family Ectinosomatidae

An as yet undescribed ectinosomatid, associated with the serpulid *Hydroides norvegica* Gunnerus, 1768, was discovered by O'Reilly (1995) when preserved worms were extracted from their calcareous tubes. A total of 48 small-sized copepods (including eight ovigerous females) were recorded from 12 infested worms collected from nine stations between 39–112 m depth in the southern Irish Sea. Although up to 20 copepods were noted on a single worm, 1–3 per individual was the more usual infestation level. Copepods were typically found embedded in the congealed epithelial mucus coat that surrounds the host. O'Reilly (1995) also encountered several detached egg sacs which had been squashed between the serpulid bodies and their tube walls in such a manner that the contained eggs occurred in a single plane. Preliminary observations (R. Huys, unpubl. data) revealed that the copepods represent a new genus, most closely related to *Sigmatidium* Giesbrecht, 1881 and *Pseudectinosoma* Kunz, 1935.

Family Miraciidae

Amphiascus Sars, 1905c

See p. 486 for a key to species.

Amphiascus giesbrechti Sars, 1906b

This species, formerly known as *Paramphiascopsis giesbrechti* (Sars, 1906b), appears to have a predilection for polychaete associated substrata. Klie (1927) found it in sediment dominated by *Alitta virens* (Sars, 1835) [as *Nereis virens* Sars, 1835] and terebellid polychaetes (*Amphitrite* spp.) on the east coast of Helgoland. Unlike other miraciid species (placed in *Amphiascus* at that time) that occurred in the sampling area, *A. giesbrechti* was never found to be associated with phytal substrata. Klie (1929) subsequently recorded *A. giesbrechti* in washings of spionid polychaetes attached to mussels in Kiel Bay.

OD: Sars (1906b—as *Amphiascus Giesbrechti*): 157–159; Plate XCVIII (♀ only).
AD: Giesbrecht (1882—as *Stenhelia ima* Brady (1872)): 119–122; Plates II (Figs 5–6), III (Fig. 5), IV (Figs 4, 9, 21), V (Fig. 11), VII (Fig. 11), VIII (Figs 16–17), IX (Fig. 8), X (Fig. 12, 27), XI (Fig. 18, 27), XII (Figs 21, 31). Klie (1927): 12–13; Figs 8–9. Klie (1929): 348. Pesta (1932): 59; Fig. 62. Hamond (1972—as *Paramphiascopsis giesbrechti* (Sars, 1906b)): 240.
TL: Norway, west coast; locality unknown.
BL: 950 µm—excluding rostrum (♀) [Giesbrecht 1882]; 1,160 µm (♀) [Sars 1906b; Pesta 1932]. Unknown for ♂.

Sipuncula

Only few copepods are known to use sipunculan worms as hosts. Members of the Ventriculinidae and two genera of the Catiniidae are external cyclopoid associates of peanut worms and have been found in both Atlantic and Indo-Pacific Oceans. The four monotypic genera of the *Akessonia*-group (Cyclopoida *incertae sedis*) (*Siphonobius* Augener, 1903; *Akessonia* Bresciani & Lützen, 1962; *Coelotrophus* Ho, Katsumi & Honma, 1981; *Golfingicola* Schwabe & Maiorova, 2015) are endoparasites inhabiting the coelomic cavity of sipunculan worms and cause sterility in the host. The use of sipunculans as hosts by copepods was surveyed by Illg (1975) who cited M.E. Rice's unpublished observations of a harpacticoid copepod utilizing a species of *Aspidosiphon* Diesing, 1851 as host. In a review of peanut worms associated with corals, Rice (1976) mentioned the presence of two copepod species, a poecilostomatoid and a harpacticoid, residing inside the cavities of Maldivian specimens of the solitary ahermatypic coral *Heteropsammia cochlea* (Spengler, 1781) (as *H. michelinii* Milne Edwards & Haime, 1848b) which are typically occupied by the sipunculan *Aspidosiphon muelleri muelleri* Diesing, 1851 (as *A. jukesii* Baird, 1873) and a member of the montacutid bivalve genus *Jousseaumia* Bourne, 1906.

The mutualistic association between the sipunculan *A. muelleri muelleri* and two genera of ahermatypic corals, *Heterocyathus* Milne Edwards & Haime, 1848a (Caryophyliidae) and *Heteropsammia* Milne Edwards & Haime, 1848b (Dendrophyliidae) is a textbook example of commensalism (*e.g.* Goreau & Yonge 1968; Yonge 1975). The juvenile *Aspidosiphon*, when 1 mm or less in size, enters an empty gastropod shell, usually a small *Cerithium*. A coral planula settles on the occupied shell, overgrowing and eventually completely enclosing it. Only those planulae settling on shells inhabited by sipunculans have any chance of survival. Subsequent growth of both coral and sipunculan are synchronized with the latter actively enlarging its cavity as a spiral tube in the base of the expanding coral while maintaining an opening of the tube on the underside of the coral (Bouvier 1895; Feustel 1965). The sipunculan extends its introvert into the surrounding substratum pulling the coral about as it probes and feeds in the sand. Through this association, the worm is provided with a protective habitat and, by movements of the sipunculan, the coral is maintained in an upright position on the surface and transported to different feeding areas.

Examination of *Heteropsammia cochlea* from New Caledonia revealed the presence of the sipunculan *A. muelleri muelleri*, a small bivalve *Jousseaumia heteropsammiae* Bourne, 1906 and a member of the cyclopoid family Catiniidae. The same copepod was observed in registered material of *H. cochlea* (KBIN/IRSNB, Brussels; reg. no. IG 27.026/171) collected at Durangit Reef, Hansa Bay, Papua New Guinea. The dorsoventrally copepods were found in the burrow made by the sipunculan in the base of the coral. However, in the Indian Ocean, *A. muelleri muelleri* appears to cohabit with harpacticoids rather than cyclopoids. In his report on the bivalve *Jousseaumia* from Sri Lanka Bourne (1906) stated "in almost every specimen I examined, whether of *Heterocyathus* or *Heteropsammia*, I found in the *Aspidosiphon* chamber one or two specimens of a small copepod belonging to the family Harpacticidae". Examination of specimens of *H. cochlea* collected off Mayotte, Comoro Islands, SW Indian Ocean, revealeded an as yet undescribed genus and species of Canuellidae living in association with *A. muelleri muelleri*. Interestingly, the new genus belongs to the *Sunaristes*-lineage which contains various other symbiotic members living in association with crustacean and echinoderm hosts (see below). The laterally compressed copepods occupy the space between the body wall of the sipunculan and the wall of the crypt it inhabits in the basis of the coral. Infection by the nauplii or early copepodids probably takes place via the opening on the underside of the corallum, or alternatively, via the series of pores which penetrate the lateral walls and open into the canal of the sipunculan. Since fossil evidence suggests that some sipunculans have lived in association with corals since mid-Paleozoic times and throughout the Mesozoic and Cenozoic (Cutler 1994), the symbiotic relationship between copepods and peanut worms is probably ancient.

There is considerable confusion about the proper name of the sipunculan host. Originally described from the Mediterranean (Diesing 1851) *A. muelleri muelleri* is now considered as the most widespread, eurytopic member of the genus, having an extraordinary number of junior synonyms and a morphology difficult to define with precision, and living in a wide variety of temperatures and depths (Cutler & Cutler 1989). Morphotypes associated with *Heteropsammia* have variously been cited as *A. jukesii*, *A. corallicola* Sluiter, 1902 and *A. muelleri muelleri*, all of which are now regarded as morphotypes of a highly polymorphic species. It is, however, questionable whether the populations associated with corals in the Indo-Pacific are identical to the ones (traditionally identified as *A. muelleri*) from Europe where, in the absence of solitary corals, they frequently inhabit empty gastropod shells or polychaete tubes (H. Zibrowius, pers. commn).

Populations of the canuellid *Sunaristes paguri* Hesse, 1867 are known to share the apical whorls of gastropod shells (usually *Aporrhais pespelecani* (Linnaeus, 1758)) used by hermit crabs with *A. muelleri* (Stachowitsch 1980) but nothing is known about the nature of the relationship between the three cohabiting organisms.

Mollusca

Harpacticoids have entered into symbiotic relationships with representatives of four of the eight extant molluscan classes. While species associated with polyplacophoran, bivalve and gastropod hosts are rare, recent work has revealed a particularly diverse lineage of harpacticoids that parasitize cephalopods.

(i) Polyplacophoran hosts

Family Harpacticidae

Harpacticus sp. *sensu* Glynn (1968)

In his ecological study on the associations of chitons in Puerto Rico, Glynn (1968) often found an unidentified species of *Harpacticus* Milne-Edwards, 1840 (Harpacticidae) clinging to the girdle of *Acanthopleura granulata* (Gmelin, 1791) (family Chitonidae), especially in proximity to sandy areas and on semiprotected shores. Sometimes *Harpacticus* sp. and a second unidentified species belonging to the family Laophontidae (see below) were found together under the same chiton. Glynn (1968) made no attempt to count the numbers present on individual chitons but casual observations showed these to be in the range of three to about 50 harpacticoids per host animal. On occasion, the West Indian green chiton (*Chiton tuberculatus* Linnaeus, 1758) was also observed to harbour this copepod in Puerto Rico.

Family Laophontidae

Heterolaophonte lalanai Varela & Ortíz, 2008

Varela & Ortíz (2008) obtained three individuals of *H. lalanai* from washings of five specimens of the West Indian fuzzy chiton (*Acanthopleura granulata*), collected from a rocky shore outside Havana, Cuba. Although no information was given about the attachment site of the copepods, the authors' extraction technique (immersion in a 5% ethanol/seawater solution) suggests this is likely to be the pallial grooves lying along the sides of the foot, or the girdle. The polyplacophoran host is widely distributed in the Caribbean, occurring from southern Florida to Mexico, south to Panama, and in the West Indies.

Glynn (1968) observed two harpacticoids clinging to the girdle of *A. granulata* in Puerto Rico, one of which he tentatively assigned to the genus *Heterolaophonte* Lang, 1948. It was also recorded from *Chiton tuberculatus* and is conceivably conspecific with *H. lalanai*.

OD: Varela & Ortíz (2008): 2–6; Figs 1–3.
TL: Cuba, City of Havana, Miramar beach; rocky supralittoral zone; washings of *Acanthopleura granulata* (Gmelin, 1791) (Chitonidae).
BL: 400 (excluding caudal rami) (♀), not given for ♂.

(ii) Cephalopod hosts

A single monophyletic lineage of 13 parasitic species, representing nine genera in the family Tisbidae, utilizes octopodan cephalopods as hosts. Unlike many other harpacticoids which live as symbionts on invertebrate hosts but do not differ significantly from their free-living relatives, the species associated with cephalopods often are modified and clearly adapted to a parasitic life style. Hochberg's (1983, 1990) reviews of the cyclopoids, harpacticoids and siphonostomatoids associated with cephalopods suggested that most of the species do not cause serious lesions to their hosts. However, the reported highly aggregated distribution of endoparasitic stages in *Vulcanoctopus hydrothermalis* González & Guerra in González, Guerra, Pascual & Briand, 1998 indicates that hosts can encounter swarms of infective stages, possibly the offspring of a single female, released *en masse* (López-González *et al.* 2000).

Family Tisbidae

Copepods parasitic on deepwater octopuses were first mentioned by Massy (1909) in her report on the cephalopodan subclass Coleoidea (Dibranchiata) in Irish waters. She noted a high prevalence of parasitic copepods on *Bathypolypus ergasticus* (Fischer & Fischer, 1892) [as *Polypus ergasticus*] collected off the south-west coast of Ireland and found specimens to be invariably attached on the inside of the web (umbrella). Massy's (1909) material formed the basis of the first description of a copepod associated with deepwater octopodans (Farran 1914). The recent work by Avdeev (1982a, 1982b, 1983, 1986, 2010) has contributed extensively to our knowledge of harpacticoid copepods associated with this host group while López-González *et al.* (2000) provided new insights into their life cycle.

Farran (1914) provisionally placed his new genus and species, *Cholidya polypi*, in the family Tisbidae (as Idyidae) and this course of action was followed by Lang (1948) who assigned it to the subfamily Tisbinae. Monod & Dollfus (1932) placed the genus in the Lichomolgidae. Boxshall (1979) discussed the phylogenetic relationships between the tisbid genera and proposed a new subfamily Cholidyinae for *Cholidyia* Farran, 1914. Avdeev (1982a, 1983, 1986) subsequently described five new genera associated with deepwater octopodans but created taxonomic confusion by placing three of them in the subfamily Cholidyinae (*Cholidyella* Avdeev, 1982a; *Brescianiana* Avdeev, 1982a; *Tripartisoma* Avdeev, 1983) and the remaining two in the subfamily Tisbinae (*Yunona* Avdeev, 1983; *Octopinella* Avdeev, 1986). This subfamilial assignment was uncritically adopted by most authors (Bresciani & Lützen 1994; Humes & Voight 1997; López-González *et al.* 2000; Wells 2007), effectively implying a dual colonization of cephalopod molluscs by two sister lineages. Both Bodin (1997) and Seifried (2003) listed all genera in the Cholidyinae without comment, reflecting the more parsimonious alternative involving a single colonization event. The latter, more plausible scenario is adopted here. Cholidyinids are known to infest at least six families of octopodan hosts (Table 7). With the exception of *Cholidyella intermedia* (Bresciani, 1970), which was found on an unidentified member of the family Cirroteuthidae, and *C. breviseta* Avdeev, 1986 which utilizes an opisthoteuthid, all other known species parasitize species of the suborder Incirrata as hosts.

Most cholidyinids that parasitize bottom-associated octopodans are known from the gills, which are located inside the mantle cavity. Only three species, *C. polypi*, *Tripartisoma trapezoidale* Avdeev, 1983 and *Genesis vulcanoctopusi* López-González, Bresciani & Huys, 2000, occur on the external surface, including the arms, web and mantle wall of their hosts. Data on host attachment in this group of copepods are scarce. Humes & Voight (1997) reported specimens of *Cholidya polypi* which were partly embedded in the skin of the arms at or near the base of the suckers but stated that the copepods were more frequently found attached by their heads, with the bodies extending free. López-González *et al.* (2000) pointed out that although infection rates can be considerable, copepodid stages had until then not been observed, not even in heavily infected hosts, suggesting that part of the life cycle is completed either in the water column, the benthic environment or elsewhere on the host (previous descriptions of cholidyinids were primarily based on specimens recovered from the gills and other external sites). Evidence in support of this supposition was provided by the discovery of juveniles of *G. vulcanoctopusi* living inside the connective tissue of the octopodan integument. At least three different copepodid stages (III–V) were discovered in a single host individual, indicating that the entire copepodid phase is completed inside the tissues of the cephalopod. López-González *et al.* (2000) suggested that the life cycle of cholidyinids is unique among harpacticoid copepods since the free-swimming phase has been reduced to the naupliar and adult stages. No other harpacticoids display alternating endoparasitic and ectoparasitic phases in their life history. Host location and subsequent infection are probably accomplished by the first copepodid (or nauplius VI) which is the primary dispersal stage. Alternatively, the ovigerous female, which retains a full suite of well developed swimming legs, may be involved in long-range host location. Upon penetration of the host's integument the first copepodid remains entirely embedded and undergoes subsequent moulting inside the host, probably completing the normal cycle of six postnaupliar moults. Within the subcutaneous cavity, the exuviae of successive moults accumulate at the posterior end of the urosome, forming darkish-brown globular bodies that contain the chitinous remains of the antennae, maxillae and other appendages of previous instars. The later copepodid stages remain in contact with the exterior via a transverse slit in the host's integument, located around the frontal end of the cephalothorax. This slit is used by the adult copepods to leave the host upon reaching sexual maturity and subsequently closes as a result of epithelial proliferation. The exuvial bodies remain inside the host for a substantial amount of time, marking previous infection sites. The life cycles of both sexes are probably essentially similar, possibly differing in the onset of the final moult and sexual maturity. Mating presumably takes place on the host in places where adult Cholidyinae have previously been reported from, such as the gills, arms and mantle. Both females and males are capable to maintain at least semipermanent contact with the host using their prehensile maxillae and maxillipeds, which are often found hooked into the host's tissue. Presumably the adults continue to feed on the superficial tissues of the octopod for the remainder of the life cycle.

TABLE 7. Cephalopod host genera (order Octopoda) used by cholidyinid harpacticoids [# = number of cholidyinid species recorded].

Suborder	Family	Genus	#
Incirrata	Bathypolypodidae	*Bathypolypus* Grimpe, 1921	2
	Enteroctopodidae	*Enteroctopus* Rochebrune & Mabille, 1889	1
		Muusoctopus Gleadall, 2004	5
		Sasakiopus Jorgensen, Strugnell & Allcock, 2010	1
		Vulcanoctopus González & Guerra, 1998	1
	Megaleledonidae	*Megaleledone* Taki, 1961	1
	Octopodidae	*Graneledone* Joubin, 1918	5
		Octopus Cuvier, 1798	2
		Pareledone Robson, 1932	4
		Tetracheledone Voss, 1955	1
Cirrata	Cirroteuthidae	Unidentified	1
	Opisthoteuthidae	*Opisthoteuthis* Verrill, 1883	1

The work by Avdeev (1982a, 1982b, 1983, 1986, 2010) indicates that octopodans host a diverse fauna of parasitic harpacticoids, particularly at and beyond the continental shelf down to over 2,600 m at mid- to high latitudes (Table 8). Most species have been recorded from the Northern Hemisphere, however, a few records are also known from the Antarctic (Avdeev 1983; Bresciani & Lützen 1994). Except for *Genesis vulcanoctopusi*, which was collected from the East Pacific Rise, cholidyinids appear so far to be absent from shallow-water hosts or octopodans at any depth in tropical regions. They appear to be restricted to benthic or benthopelagic hosts occurring on soft substrata (especially sand and fine mud) and have not been recorded yet from mesopelagic or epipelagic species. Humes & Voight (1997) examined 17 bottom-associated hosts for ectoparasitic copepods but failed to find them in 12 of these, including *Bathypolypus sponsalis* (Fischer & Fischer, 1892), *Eledone caparti* Adam, 1950, *E. gaucha* Haimovici, 1988, *E. massyae* Voss, 1964, *Graneledone antarctica* Voss, 1976, *Muusoctopus januarii* (Hoyle, 1885), *Octopus californicus* (Berry, 1911), *Pteroctopus tetracirrhus* (Delle Chiaje, 1830), *Scaeurgus unicirrhus* (Delle Chiaje [in de Férussac & Orbigny], 1841) and *Velodona togata* Chun, 1915. Seven of the 13 currently known cephalopod-associated cholidyinids have been recorded from more than one host, suggesting that host specificity is generally low in this subfamily (Table 8). Octopodans themselves may be infested by more than one parasite. For example, both *Graneledone boreopacifica* Nesis, 1982 and *Pareledone harrissoni* (Berry, 1917) serve as hosts to three cholidyinid species.

The names of various species of Cholidyinae have often been misspelled. Humes & Voight (1997) explained the confusion surrounding the spelling of the generic names *Cholidya* and *Cholidyella* (see below). Avdeev (1983) proposed the new genus *Tripartisoma* for two new species *T. ovalis* and *T. trapezoidalis*. According to ICZN Art. 30.1.2, names ending in *-soma* are neuter; hence, the specific epithets *ovalis* and *trapezoidalis* should agree in gender, and be cited as *ovale* and *trapezoidale*, respectively. Similarly, Avdeev (1986) established the genus *Octopinella* for its type and only species, *O. tenacis*. A species-group name, if it is or ends in a Latin or latinized adjective or participle in the nominative singular, must agree in gender with the generic name with which it is at any time combined (ICZN Art. 31.2). The correct nominative singular (as corrected by Huys 2009b) is *tenax* instead of *tenacis*. Finally, *Amplipedicola pectinatus* Avdeev, 2010 is also an incorrect original spelling which should be amended to *A. pectinata*.

Recent keys used to identify cholidyinid genera and species are unsound. Boxshall & Halsey (2004: 410) inadvertently omitted *Octopinella* and *Yunona* from their key to tisbid genera. Wells (2007: 748) erroneously scored the number of elements on P2–P4 exp-3 in *B. rotundata* as 6:6:6 (instead of 5:5:5) and used two endopodal characters (presence of inner seta on P1 enp-2; segmentation of P4 endopod) in his codon KG5 (p. 765) which in reality should have referred to the exopod of these limbs. The 13 cholidyinid species that use cephalopod hosts can be differentiated by the newly constructed key below. The related *Neoscutellidium yeatmani* Zwerner, 1967, which is associated with a teleost fish, is also included. Note that both sexes have been described for only six species (*C. polypi*, *C. incisa*, *C. breviseta*, *C. nesisi*, *O. tenax*, *A. pectinata*) and some males are known to display considerable sexual dimorphism in the armature of legs 2–4.

Key to species of subfamily Cholidyinae

1. Antennary exopod absent; leg 1 uniramous (exopod absent), extremely elongate (reaching beyond caudal rami when flexed backwards) and extending sideways in dorsal aspect; legs 2–4 absent. . . . . *Amplipedicola pectinata* Avdeev, 2010.

Antennary exopod present; leg 1 biramous (exopod at least indistinctly 3-segmented) and much shorter than above; leg 2 present, legs 3–4 present or (rarely) absent . . . . 2.

2. Body ♀ irregularly bean-shaped, unsegmented, not tapering posteriorly; legs 3–5 and caudal rami absent in ♀; ♂ unknown . . . . *Avdeevia antarctica* Bresciani & Lützen, 1994.

Body of both sexes either cyclopiform or inflated but always tapering posteriorly towards caudal rami, segmentation sometimes only expressed in urosome or lacking altogether; legs 3–5 present; caudal rami defined at base . . . . 3.

3. P2–P4 endopods 3-segmented. . . . . 4.

P2–P4 endopods 2-segmented. . . . . 6.

4. Antennule ♀ 9-segmented; P1 exp-3 with five elements; P3–P4 enp-2 with one inner seta; P3 enp-3 with five elements. . . . . *Neoscutellidium yeatmani* Zwerner, 1967.

Antennule ♀ 8-segmented; P1 exp-3 with six elements; P3–P4 enp-2 with two inner setae; P3 enp-3 with six elements . . . . 5.

5. Prosome gradually tapering posteriorly towards P5-bearing somite; antennary exopod with five setae; maxilliped with short, straight, pectinate claw; P4 exp-3 with eight elements; P5 exopod ♀ oval, about twice as long as wide . . . . *Octopinella tenax* Avdeev, 1986.

Cephalothorax bilaterally expanded and about 1.7 times as wide as P2-bearing somite; antennary exopod with three setae; maxilliped with strongly curved, naked claw; P4 exp-3 with seven elements; P5 exopod ♀ elongate, about four times as long as wide. . . . . *Yunona marginata* Avdeev, 1983.

6. P1 exp-3 with five elements . . . . 7.

P1 exp-3 with six elements . . . . 12.

7. P2 exopod 2-segmented with three elements on distal segment in ♀, 3-segmented in ♂; P3–P4 exopods ♀ vestigial, represented by minute segments bearing three and one seta(e), respectively; P5 ♀ a strongly chitinized plate with series of conspicuous blunt teeth along its distal margin; P5 ♂ with three setae . . . . *Cholidya polypi* Farran, 1914.

P2 exopod 3-segmented in both sexes, exp-3 with 5–6 elements; P3–P4 exopods ♀ 3-segmented; P5 ♀ without marginal teeth, exopodal lobe with two setae, endopod represented by 2–3 long setae; P5 ♂ with two setae . . . . 8.

8. P2–P4 exp-3 (exp-2 in males of some species) with six elements; P2–P4 enp-2 with four elements . . . . 9.

P2–P4 exp-3 with five elements; P2–P4 enp-2 with four elements . . . . *Brescianiana rotundata* Avdeev, 1982a.

9. P1 enp-3 with two short claws and one unipinnate seta; P2 enp-2 with two setae and two spines; P2–P3 enp-1 transversally expanded, ratio of maximum length to maximum width about 1.5; P4 exopod ♂ 2-segmented . . . . *Cholidyella breviseta* Avdeev, 1986.

P1 enp-3 with three short claws; P2 enp-2 with three setae and one spine; P2–P3 enp-1 not particularly expanded, ratio of maximum length to maximum width about 2.0; P4 exopod ♂ 3-segmented (unknown in *C. intermedia*). . . . . 10.

10. P1 exp-2 with inner seta . . . . *Cholidyella incisa* Avdeev, 1982a.

P1 exp-2 without inner seta. . . . . 11.

11. Antennule ♀ 6-segmented; P5 ♀ endopodal setae at most 1.3 times the length of the supporting segment . . . . *Cholidyella intermedia* (Bresciani, 1970).

Antennule ♀ 7-segmented; P5 ♀ endopodal setae at least twice as long as the supporting segment. . . . . *Cholidyella nesisi* Avdeev, 1986.

12. Antennule ♀ indistinctly 4-segmented; P2–P4 exp-3 with six, seven and seven elements, respectively; P2 endopod ♀ 3-segmented with armature formula 1.1.221. . . . . *Genesis vulcanoctopusi* López-González, Bresciani & Huys, 2000.

Antennule ♀ distinctly 7-segmented; P2–P4 exp-3 with five, five and six elements, respectively; P2 endopod ♀ 2-segmented with armature formula 1.221. . . . . 13.

13. Cephalic shield oval in dorsal aspect; pedigerous complex (fused somites bearing P2–P4) widest at about halfway down its length, posterolateral angles not produced; intercoxal sclerites of legs 2–3 absent . . . . *Tripartisoma ovale* Avdeev, 1983.

Cephalic shield trapezoidal-shaped in dorsal aspect; pedigerous complex (fused somites bearing P2–P4) widest near posterior margin, posterolateral corners forming lobate extensions which partly embrace P5-bearing somite; intercoxal sclerites of legs 2–3 present . . . . *Tripartisoma trapezoidale* Avdeev, 1983.

Cholidya Farran, 1914

Cholidya polypi Farran, 1914

Farran (1914) obtained numerous, mostly ovigerous, females of *Cholidya polypi* (occasionally misspelled *Cholydia*; *e.g.* Soyer 1968; Bresciani 1970) from the inner surface of the arm web of *Bathypolypus ergasticus* [as *Polypus ergasticus*]. The single host specimen was captured in deep water off the south-west coast of Ireland. Humes & Voight (1997) expressed some doubts as to the identity of the octopus on which Farran's (1914) specimens were found. Their reanalysis (no details were given) of Massy's (1909) illustrations and morphological data apparently suggested that her specimens represented at least three species, none of which was conspecific with *B. ergasticus*. The reported geographic range and depth distribution known at that time (Voss 1988) also appeared to reinforce their argument that Massy's (1909) record was based on a misidentification. However, the presence of *B. ergasticus* has now been confirmed in Scottish and Irish waters (*e.g.* Barratt *et al.* 2007; Boyle *et al.* 1998; Collins *et al.* 2001) and Muus (2002: 206) formally accepted Massy's (1909) record as valid.

Additional records of *C. polypi* were not published until Humes & Voight's (1997) extensive survey increased the number of octopodid hosts from which this copepod is known from one to six, and extended the known geographic range from the north-eastern Atlantic to the north Atlantic and into the north-eastern Pacific Ocean where it was found off the coast of Oregon on the Cascadia Abyssal Plain (Table 8). Humes & Voight (1997) provided a detailed redescription of the female and the first description of the male. Copepods found on members of *Graneledone* Joubin, 1918 from the north-eastern Pacific were partly buried in the skin of the arms, frequently at the base of the suckers, with only the caudal setae protruding outside; they were never observed on the interbrachial web. Conversely, *C. polypi* observed on *Bathypolypus arcticus* (Prosch, 1849) and *Tetracheledone spinicirrhus* Voss, 1955 from the north-western Atlantic were not enveloped by the skin of the host but usually attached themselves to the oral surface of the web by means of their maxillae and maxillipeds (as noted in Farran's (1914) original report) with their bodies hanging free. Occasionally, females were found attached between the suckers of the oral surface of the arms or, rarely, to the ventral or dorsal surfaces of the mantle. Pairs in amplexus were not observed and males occurred only on octopodid hosts from the north-eastern Pacific. Ovigerous females carry a flask-shaped, flattened egg sac which contains 11–12 eggs, each about 110 µm in diameter (Humes & Voight 1997).

OD: Farran (1914): 473–475; Plate XXI (♀ only).
AD: Humes & Voight (1997): 67–73; Figs 1–4.
TL: Ireland, off south-west coast; depth 1,116–1,244 m; on inner surface of arm web of *Bathypolypus ergasticus* (Fischer & Fischer, 1892) (Bathypolypodidae).
BL: 780–800 µm (♀) [Farran 1914]; 740–830 µm (♀), 570–620 µm (♂) [Humes & Voight 1997—material from north-western Atlantic and north-eastern Pacific]; 693–759 µm [Humes & Voight 1997—slide material in National Museum of Ireland].

Cholidyella Avdeev, 1982a

Inadvertently adopting Bresciani's (1970) incorrect subsequent spelling of the generic name *Cholidya*, Avdeev (1982a) subsequently established the new genus *Cholydiella*, the spelling of which he later changed to *Cholidyella* (Avdeev 1983: footnote on p. 1775) and was adopted in most reference works (Bodin 1988, 1997; Boxshall & Halsey 2004; Huys 2009b; Seifried 2003; Wells 2007). Unfortunately the incorrect spelling *Cholydia* persisted in the literature (*e.g.* Gotto 1979, 1993). The four species of the genus utilize octopodans belonging to four different families. The genus is so far restricted to high latitudes in the northern Pacific and Atlantic.

TABLE 8. Cholidyinae and their cephalopod hosts.

Species	Host	Locality	Depth (m)	Reference
Amplipedicola pectinata	*Muusoctopus* cf. *profundorum* (Robson, 1932)	Bering Sea	500	Avdeev (2010)
	Enteroctopus dofleini (Wülker, 1910)	Bering Sea	129	Avdeev (2010)
Avdeevia antarctica	*Megaleledone setebos* (Robson, 1932)	Antarctica, Prydz Bay	385–388	Bresciani & Lützen (1994)
Brescianiana rotundata	*Graneledone boreopacifica* Nesis, 1982	Russia, north Kurile region	1,350	Avdeev (1982a)
		Russia, south Kurile region	1,300	Avdeev (1982a)
		Japan, Honshu	1,480	Avdeev (1982a)
Cholidya polypi	*Bathypolypus ergasticus* (Fischer & Fischer, 1892)	SW of Ireland	1,116–1,244	Farran (1914), Leigh-Sharpe (1935)[1]
	unknown octopodid	west coast of Ireland	unknown	Humes & Voight (1997)[2]
	Graneledone boreopacifica Nesis, 1982	Cascadia Abyssal Plain	2,265–2,500	Humes & Voight (1997)
	Tetracheledone spinicirrhus Voss, 1955	off Florida	357	Humes & Voight (1997)
		off North Carolina	356	Humes & Voight (1997)
	Bathypolypus arcticus (Prosch, 1849)	E of North Carolina	356	Humes & Voight (1997)
		E of New Jersey	356–366	Humes & Voight (1997)
	Graneledone sp. A	Juan de Fuca Ridge	2,500	Humes & Voight (1997)
	Graneledone sp. B	California, Monterey Bay	1,336–1,347	Humes & Voight (1997)
Cholidyella intermedia	unidentified Cirroteuthidae	Faroe-Shetlands Channel	382–403	Bresciani (1970)
Cholidyella nesisi	*Muusoctopus profundorum* (Robson, 1932)	Japan, Honshu	985–1,500	Avdeev (1986)
	Muusoctopus fuscus (Taki, 1964)	Japan, Honshu	1,240	Avdeev (1986)
Cholidyella incisa	*Graneledone boreopacifica* Nesis, 1982	Russia, south Kurile region	1,300	Avdeev (1982a)
		Japan, Honshu	1,240–1,500	Avdeev (1982a)
Cholidyella breviseta	*Opisthoteuthis californiana* Berry, 1949	Japan, Hokkaido	470	Avdeev (1986)
		Japan, Honshu	800–1,340	Avdeev (1986)
		Russia, north Kurile region	660–1,285	Avdeev (1986)
		Russia, south Kurile region	825	Avdeev (1986)
Genesis vulcanoctopusi	*Vulcanoctopus hydrothermalis* González & Guerra, 1998	East Pacific Rise	2,631–2,647	López-González *et al.* (2000)
Octopinella tenax	*Muusoctopus hokkaidensis* (Berry, 1921)	Russia, Kamchatka	550	Avdeev (1986)
	Muusoctopus profundorum (Robson, 1932)	Russia, north Kurile region	500–650	Avdeev (1986)
		Japan, Honshu	600–985	Avdeev (1986)
	Octopus longispadiceus (Sasaki, 1917)	Japan, Honshu	690–950	Avdeev (1986)
	Octopus sp.	Japan, Hokkaido	115	Avdeev (1986)
	Sasakiopus salebrosus (Sasaki, 1920)	Russia, north Kurile region	690	Avdeev (1986)
Tripartisoma ovale	*Pareledone charcoti* (Joubin, 1905)	Antarctica, Ross Sea	100–120	Avdeev (1983)
	Pareledone harrissoni (Berry, 1917)	Antarctica, Ross Sea	85	Avdeev (1983)
	Pareledone turqueti (Joubin, 1905)	Antarctica, Ross Sea	390	Avdeev (1983)
Tripartisoma trapezoidale	*Pareledone harrissoni* (Berry, 1917)	Antarctica, Ross Sea	65	Avdeev (1983)
			85–120	Avdeev (1983)

[1] Record in list of symbiotic copepods associated with “British” invertebrates, probably referring to Farran’s (1914) original report (which was based on material collected outside current British territorial waters). The Irish Free State, renamed “Ireland” by the 1937 constitution, explicitly became independent and a republic not until 1949.

[2] The coordinates (52º02’N, 10º55’W) on the slide deposited in the National Museum of Ireland indicate that the two adult females it contains were collected off the west coast of Ireland (Co. Kerry) and hence are not types (Holmes & O’Connor 1990; Humes & Voight 1997); Farran’s type material was collected off the south-west coast of Ireland (Massy 1909).

Cholidyella intermedia (Bresciani, 1970)

This species was originally described as *Cholydia* [*sic*] *intermedia* from an unidentified preserved cirroteuthid cephalopod (suborder Cirrata) caught off the far north-east of Scotland during the early 1900s. Avdeev (1982a) transferred *C. intermedia* to *Cholidyella* and compared it with his new species, *C. incisa*. Bresciani (1970) exclusively found females (45 from a single host) and the male has as yet remained undescribed. The species is closely related to *C. nesisi* Avdeev, 1986.

OD: Bresciani (1970—as *Cholydia intermedia*): 11–15; Figs 1–16 (♀ only).
TL: Faroe-Shetlands Channel (62°14'N, 4°09'W); depth 382–403 m; in pallial cavity and on gills of an unnamed cirroteuthid cephalopod.
BL: 1,140 µm (♀).

Cholidyella incisa Avdeev, 1982a

Avdeev (1982a) obtained 74 females and 41 males from seven specimens of an unidentified *Graneledone* species collected at 1,240–1,500 m depth off the Pacific coast of Honshu, Japan. A single specimen of the same octopodan caught at 1,300 m depth off the southern Kuriles yielded eight females of *C. incisa*. The host was subsequently described as *Graneledone boreopacifica* by Nesis (1982) (*cf.* Avdeev 1986). The egg sac measures 461 × 360 µm.

OD: Avdeev (1982a—as *Cholydiella incisa*): 108–112; Figs 1–2, 3(А, В, Г, Д).
TL: Unconfirmed. Avdeev (1982a) combined the specimens obtained from both localities in the north-western Pacific as type material, but did not specify where the designated holotype was collected; attached to the gills of *Graneledone boreopacifica* Nesis, 1982 (Octopodidae).
BL: 1,026–1,172 µm (♀), 390–443 µm (♂).

Cholidyella breviseta Avdeev, 1986

Cholidyella breviseta appears to be widespread in the north-western Pacific where it utilizes exclusively *Opisthoteuthis californiana* Berry, 1949 and can be abundant locally. In one case Avdeev (1986) recorded 100 females and 400 males from the gills of 11 host individuals caught at 660–900 m depth off the north Kurile region. Ovigerous females carry a large, dorsoventrally depressed, egg sac. As in the previous species there is a marked size sexual dimorphism with females being three times as large as males.

OD: Avdeev (1986): 56–61; Figs 23–46.
TL: Unconfirmed. Avdeev (1986) listed type material from five localities in the Kurile region and off the islands of Hokkaido and Honsu, Japan (Table 8), but did not specify where the holotype was collected; attached to the gills of *Opisthoteuthis californiana* Berry, 1949 (Opisthoteuthidae).
BL: 1,290–1,400 µm (♀), 380–460 µm (♂).

Cholidyella nesisi Avdeev, 1986

Avdeev (1986) collected *C. nesisi* from the gills of two species of *Muusoctopus* (originally cited as *Benthoctopus*) caught off the Pacific coast of Honshu, Japan, *i.e. M. profundorum* and *M. fuscus*. On 11 specimens of *M. profundorum* he recorded 566 females and 216 males, suggesting this is probably the most common host of *C. nesisi*; only two males were recovered from the gills of a single *M. fuscus*.

OD: Avdeev (1986): 61–65; Figs 47–63.

TL: Japan, Pacific coast of Honshu, 985–1,500 m depth; on gills of *Muusoctopus profundorum* (Robson, 1932) (Enteroctopodidae).
BL: 940–1,070 µm (♀), 430–490 µm (♂).

Brescianiana Avdeev, 1982a

Brescianiana rotundata Avdeev, 1982a

Avdeev (1982a) obtained a total of 20 females from the gills of *Graneledone* sp. collected at three different localities in the north-western Pacific, *i.e.* off the east coast of Honshu, Japan (1,480 m), and off the northern (1,350 m) and southern (1,300m) Kurile Islands, Russia. Nesis (1982) subsequently described the host as *Graneledone boreopacifica* (*cf.* Avdeev 1986). The voluminous egg sac (1,330 × 820 µm) is almost as large as the body. The male of *B. rotundata* is as yet undescribed.

OD: Avdeev (1982a): 111, 113–116; Figs 3(Е, Ж), 4–6 (♀ only).
TL: North-western Pacific Ocean. Avdeev (1982a) fixed a holotype but did not disclose which of the three localities it was collected from; on gills of *Graneledone boreopacifica* Nesis, 1982 (Octopodidae).
BL: 1,411–1,653 µm (♀).

Tripartisoma Avdeev, 1983

The genus currently accommodates two species which can be separated by differences in the shape of the cephalic shield and pedigerous complex (fused somites beaing legs 2–4), the size of the maxillipedal basis and presence *vs* absence of the intercoxal sclerites of legs 2–3. Both species utilize members of the octopodid genus *Graneledone* and are found in the Antarctic.

Tripartisoma ovale Avdeev, 1983

This species is so far known only from the gills of three *Pareledone* species collected in the Antarctic Ross Sea. Of the hosts examined by Avdeev (1983), one of three *P. turqueti* (collected at 390 m depth), one of 13 *P. harrissoni* (collected at 85 m depth) and two of seven *P. charcoti* (collected at 100–120 m depth) were infected. The intensity was very low with one to two females per host. No males were found. The white egg sac is round and measures 528 × 458 µm.

OD: Avdeev (1983—as *Tripartisoma ovalis*): 1782–1784; Figs 4(6–9), 5 (♀ only).
TL: Antarctica, Ross Sea. Avdeev (1983) did not specify the type host or collection site; attached to the gills of its host (*Pareledone* spp.).
BL: 704–845 µm (♀).

Tripartisoma trapezoidale Avdeev, 1983

This species is known from a single locality in the Ross Sea and was found only on *Pareledone harrissoni*. Prevalence and intensity are very low. Avdeev (1983) obtained four females from the ventral surface of the head of only two of 13 hosts examined. The male is as yet undescribed. The egg sac is round, about 521 µm in diameter and white in live specimens.

OD: Avdeev (1983—as *Tripartisoma trapezoidalis*): 1778, 1780–1783; Figs 2(6), 3, 4(1–5).
TL: Antarctica, Ross Sea; 85–120 m depth; on ventral surface of head of *Pareledone harrissoni* (Berry, 1917) (Octopodidae).
BL: 884–903 µm (♀).

Yunona Avdeev, 1983

Yunona marginata Avdeev, 1983

Currently known only from the Antarctic Ross Sea, *Y. marginata* has been found on the gills of two species of *Pareledone* hosts. Of the specimens examined by Avdeev (1983), five of seven *P. charcoti* (collected at 65–120 m depth) and one of 13 *P. harrissoni* (collected at 65 m depth) were infected. The intensity was low with one to seven females per host. No males were found. *Yunona marginata* and *Octopinella tenax* are the only cephalopod-associated cholidyinids that have all body somites expressed (the same is found in *Neoscutellidium*). The egg sac is round (222 × 211 µm) and white in live specimens.

OD: Avdeev (1983): 1776–1779; Figs 1, 2(1–5) (♀ only).
TL: Antarctica, Ross Sea. Avdeev (1983) fixed a holotype but did not mention the type host or where it was collected; attached to the gills of its host.
BL: 901–1,042 µm (♀).

Octopinella Avdeev, 1986

Octopinella tenax Avdeev, 1986

Avdeev (1986) established *Octopinella* for a species which parasitizes the gills of a wide diversity of octopodids in the north-western Pacific Ocean, including *Muusoctopus* (as *Benthoctopus*) *hokkaidensis* (Berry, 1921), *M.* (as *Benthoctopus*) *profundorum*, *Sasakiopus* (as *Bathypolypus*) *salebrosus* (Sasaki, 1920), *Octopus longispadiceus* (Sasaki, 1917) and an unidentified species of the genus *Octopus* Cuvier, 1798. Highest intensities were recorded on *O. longispadiceus* caught off the Pacific coast of Honshu at 690–950 m depth (84 females and 43 males on two hosts) and on *M. profundorum* in the same area at 600–985 m depth (47 females and 12 males on eight hosts). Ovigerous females carry a dorsoventrally flattened egg sac containing 11 eggs, each about 16 µm in diameter.

OD: Avdeev (1986—as *Octopinella tenacis*): 51–56; Figs 1–22.
TL: Unconfirmed. Avdeev (1986) listed type material from five octopodid hosts and six localities in the northern Pacific (Table 8) but did not specify where the holotype was collected; attached to the gills of its hosts.
BL: 1,250–1,340 µm (♀), 1,130–1,210 µm (♂).

Avdeevia Bresciani & Lützen, 1994

Avdeevia antarctica Bresciani & Lützen, 1994

Bresciani & Lützen (1994) described *A. antarctica* from 80 females found on the gills of two male Antarctic octopodans belonging to *Megaleledone setebos* (Robson, 1932) [as *Megaleledone senoi* Taki, 1961]. The male has remained undescribed. The species is characterized by the extreme disproportion in size between the body and the appendages. The latter are of the same dimensions as in other cholidyinids but the body length and width are three to four times as large. Legs 3–6 are absent, and the caudal rami, present in the other genera of the subfamily, are completely lost. The cephalic appendages and maxillipeds do not diverge from the typical cholidyinid morphology. The complete lack of somite boundaries in the bean-shaped body makes *A. antarctica* the most highly modified harpacticoid known so far.

Adult females are immovably attached to the gill tissue using their hooked maxillae and maxillipeds. The body is partly enclosed within the folded surface of the gill lamellae, its posterior three-quarters being raised above the gill, with the egg sac protruding into the mantle cavity. The gill epithelium is probably perforated by means of the maxillulary arthrites and the toothed gnathobases of the mandibles. Both lateral and medial surfaces of the gills were found to be infested. Host blood is sucked into the foregut and further into the capacious midgut, possibly by contractions of the criss-crossing muscle fibers. Longitudinal sections showed that most of the midgut contained numerous spherical particles, representing ingested blood corpuscles and their semi-digested decomposition products. Bresciani & Lützen (1994) provided additional information on the internal anatomy, including the integument and the female reproductive system.

Ovigerous females carry a single sausage-shaped egg sac, protruding from a genital depression and borne on a solid stalk. The egg sac is often as long as the body, containing hundreds of eggs, each approximately 100 µm in diameter.

OD: Bresciani & Lützen (1994): 744–750; Figs 1–5 (♀ only).
TL: Antarctic Sea, Prydz Bay (66º59.9'S, 75º00.9'E), depth 385–388 m; on gills of an immature male of *Megaleledone setebos* (Robson, 1932) (Megaleledonidae).
BL: 3,200–4,200 µm (♀).

Genesis López-González, Bresciani & Huys, in López-González, Bresciani, Huys, González, Guerra & Pascual, 2000

Genesis vulcanoctopusi López-González, Bresciani & Huys, in López-González, Bresciani, Huys, González, Guerra & Pascual, 2000

López-González *et al.* (2000) based their description of *G. vulcanoctopusi* on 20 non-ovigerous females and three juveniles obtained from three male *Vulcanoctopus hydrothermalis*. The octopod host specimens were collected on the East Pacific Rise in an area (12º48.43–59'N 103º56.41–42'W; 2,631–2,647 m depth) situated north of the site commonly known as "Genesis". The discovery of *G. vulcanoctopusi* represents the deepest record of a cholidyinid and the first one infesting octopods at tropical latitudes.

The host is endemic to hydrothermal vents along the East Pacific Rise (González *et al.* 1998, 2008). Unlike other octopodids that serve as hosts to cholidyinids *V. hydrothermalis* does not occur on soft substrata but was collected on a cliff of basaltic rocks covered by oxidate sulphides. Although octopodids are generally regarded as solitary, those of *V. hydrothermalis* have been observed in groups of up to 12 during foraging (Voight 2005) or apparent mating aggregation (Rocha *et al.* 2002). Individual octopuses also wrap their arms around the mantles of smaller individuals, apparently in competition for prey (Voight 2005). Their density virtually assures close contact among conspecifics which might explain the high levels of infection by *G. vulcanoctopusi* and conceivably contribute to the spread of the parasite.

OD: López-González *et al.* (2000): 243–249; Figs 1–7.
TL: East Pacific Rise (12º48.43'N, 103º56.41'W); 2 m from east wall of main black smoker of the "Genesis" site; 2,647 m depth; embedded in integument of head and mantle of adult male of *Vulcanoctopus hydrothermalis* González & Guerra in González, Guerra, Pascual & Briand, 1998 (Enteroctopodidae).
BL: 2,500–2,800 µm (♀), juvenile stages (700–800 µm).

Amplipedicola Avdeev, 2010

Amplipedicola pectinata Avdeev, 2010

Avdeev (2010) recorded *A. pectinata* from the gills of two octopod hosts collected in the Bering Sea, *Muusoctopus* cf. *profundorum* (Robson, 1932) [as *Benthoctopus* cf. *profundorum*] and *Enteroctopus dofleini* (Wülker, 1910) [as *Octopus dofleini*]. The species is characterized by the unusual size sexual dimorphism. The dorsoventrally flattened egg sac contains 12–14 eggs, each measuring about 26 µm in diameter.

OD: Avdeev (2010—as *Amplipedicola pectinatus*): 1365–1368; Figs 1–2.
TL: Bering Sea. Avdeev (2010) did not specify the type locality or type hosts. Specimens were obtained from the

gills of three *Muusoctopus* cf. *profundorum* (Robson, 1932) collected at 500 m depth (61º15'N, 175º34'E) and one *Enteroctopus dofleini* (Wülker, 1910) caught at 129 m depth (55º42'N, 167º01'E) (Enteroctopodidae).
BL: 122–144 µm (♀), 276 µm (♂).

(iii) Bivalve hosts

Many copepod species have been reported as inhabitants of marine bivalves, however only two harpacticoids, both belonging to the genus *Tisbe* Lilljeborg, 1853, have been confirmed as genuine symbionts of this molluscan host group (Humes 1954; Huys & Song 2004).

Marchenkov (1997, 1999) recorded an undescribed species of unknown affinity ("Harpacticoida fam. gen. sp. 1") from the gills of the sandgaper *Mya arenaria* Linnaeus, 1758 (Myidae) in the entrance and northwestern part of the Kandalaksha Gulf in the White Sea. The same species was also recorded from the branchial tissues of the Iceland scallop *Chlamys islandica* (O.F. Müller, 1776) (Pectinidae) in the Onega Gulf. The presence of this copepod is possibly accidental since Marchenkov (1997, 1999) obtained it also from the branchial sac of the solitary tunicate *Molgula retortiformis* Verrill, 1871 and from the tunic of the colonial ascidiacean *Synoicum pulmonaria* (Ellis & Solander, 1786).

Donsiellinid copepods are typically (but not exclusively) associated with teredinid and gribble-bored wooden wharf-piles and sunken decaying wood (Hicks 1988a) and an intimate relationship with their limnoriid companions has been established in many cases. Although teredinids are known to act as hosts to copepods (Stock 1959; Humes & Turner 1972), the nature of a similar association between donsiellinids and shipworms has not been assessed so far.

Family Tisbidae

Tisbe Lilljeborg, 1853

Volkmann (1979b) provided a key to *Tisbe* species displaying unusual endopodal armature on leg 1 which includes the species below.

Tisbe celata Humes, 1954

Humes (1954) reported this species from the mantle cavity of *Mytilus edulis* Linnaeus, 1758 in New Brunswick where it appears to be very common. The mantle cavities of 79% of 265 *M. edulis* contained *T. celata* whereas this species was not found in 203 *Mya arenaria* Linnaeus, 1758 collected from the same area. Each mussel had an average of two copepods with the number encountered in a single mussle ranging from 1–41. Adults of both sexes and immature males were obtained. Ovigerous females carry a large dorsoventrally flattened egg sac, measuring about 290 × 270 µm and containing approximately 45 eggs (each about 54 µm in diameter and pale orange in colour) (Humes 1954). According to Humes (1954) the presence of copepodid stages on the gills suggests that *T. celata* is a genuine associate that probably breeds in the mussel rather than a free-swimming species accidentally introduced into the mantle cavity. When the mussels were opened and dissected, dislodged copepods tended to return to the torn off gill fragments. Both Humes (1954) and Volkmann (1979b) stated that *T. celata* is probably a facultative parasite, however, observations by Yeatman (1966) indicated that the symbiotic relationship between the copepod and its bivalve host may be commensal. *Mytilus edulis* obtained from Frenchman Bay, Mount Desert Island, Maine carried many *T. celata* but virtually no ciliates while mussels from Blue Hill Bay had no copepods but considerable numbers of *Peniculistoma* (as *Conchophthirus*) *mytili* (De Morgan, 1925), a symbiotic ciliate of the edible mussel. Yeatman (1966) examined the gut contents of *T. celata* and found remains of *P. mytili* in three out of nine specimens, suggesting that at least some of the copepod's diet consists of symbiotic ciliates.

Both Kulachkova (1985) and Fateev *et al.* (2000) recorded *Tisbe* sp. from the mantle cavity of cultured *M. edulis* in the Kandalaksha Gulf of the White Sea. Krapivin (2012) suggested that these records may in reality refer to *Microsetella norvegica* but this is unlikely. According to Song *et al.* (2010) *T. celata* is one of the more abundant species in the phytal harpacticoid community associated with *Ulva pertusa* Kjellman, 1897 in Pohang on the east coast of Korea. Given the radically different habitat and geographical origin this record will require confirmation.

A second symbiotic *Tisbe* species, closely related to *T. celata*, was observed in the South American blue mussel *Mytilus edulis platensis* Orbigny, 1846 (as *M. e. chilensis* Hupé, 1854), collected in Argentina (Huys in Huys & Song (2004)); this is the same species referred to by Cremonte *et al.* (2015) as *Tisbe* sp.

OD: Humes (1954): 816–824; Plates I–III (Figs 1–32); Tables I–IV.
AD: Volkmann (1979b): 192–195, 276–277; Fig. 33A–F.
TL: Canada, New Brunswick, St. Andrews; mantle cavity of *Mytilus edulis* Linnaeus, 1758 (Mytilidae) obtained from intertidal rocks, sandy gravel and wharf piling in the immediate vicinity of the St. Andrews Biological Station (formerly Atlantic Biological Station).
BL: 929–979 µm (♀), 765–800 µm (♂) [Humes 1954]; 920–1,000 µm (♀), 700–800 µm (♂) [Volkmann 1979b].

(iv) Gastropod hosts

Copepods associated with gastropods are very infrequently recorded and harpacticoid records are particularly rare. Four of the five records discussed below are to be considered anecdotal until new evidence corroborates their authenticity. Limpets (Patellidae) retain water in their pallial cavities when becoming exposed during low tide and thus provide protection against desiccation. At least one species of harpacticoid has exploited this unusual intertidal microhabitat by becoming a facultative inquiline.

Risbec (1928) reported an ectoparasitic copepod, occurring together with *Paralichomolgus orbicularis* Monod, 1928, on the nudibranch *Platydoris cruenta* (Quoy & Gaimard, 1832) (family Discodorididae) in New Caledonia. Monod (1928) reproduced Risbec's illustrations and provisionally assigned the species to the Harpacticidae while Monod & Dollfus (1932) listed it as "Harpacticoidea Gen. ?". Although Risbec (1928) tentatively attributed the species to "… la famille des Harpacticidés …", his sketches (Fig. 1*bis* (5–6)) of the dorsal and ventral habitus of an ovigerous female with paired egg sacs leave little doubt that he was dealing with a non-harpacticoid copepod. Monod & Dollfus (1932: 189) also stated that Risbec (1928) had observed copepods between the gills of another New Caledonian doridid nudibranch *Doris immonda* Risbec, 1928 [as *Platydoris immonda*] which he provisionally had attributed to the Harpacticoida. However, no evidence could be found in Risbec's report to support this claim. An unidentified species of harpacticoid was described living in association with the freshwater snail *Lanistes carinatus* (Olivier, 1804) (Ampullariidae) in Egypt (El-Bahy 1998). However, the precise nature of this association was not investigated, although it was characterized as having no ill effect on the apple snail and may simply be a commensal relationship. Sullivan & Yeung (2011) observed harpacticoid copepods in the tissues of the pulmonate gastropod *Biomphalaria glabrata* (Say, 1818) (Planorbidae), the intermediate snail host of the digenetic trematode *Schistosoma mansoni* Sambon, 1907. All copepods were heavily encapsulated by hemocytes and were dead, indicating that the tissue invasion was probably accidental rather than symbiotic or predatory. The scale of the hemocytic response also suggested that such invasions would be capable of causing considerable histopathology and hemolymph loss, in addition to providing a portal of entry for opportunistic pathogens. Sullivan & Yeung (2011) claimed that high densities of harpacticoid copepods may be a contributing factor to mortality in laboratory snail colonies.

Family Miraciidae

***Amphiascus* Sars, 1905c**

See p. 486 for a key to species.

Amphiascus waihonu (Hicks, 1986b)

Hicks (1986b) described *Paramphiascopsis waihonu* based on 30 females, 33 males and nine copepodids, all of which were found inside a spent embryo case ("mermaid's purse") of an undisclosed species of skate (Elasmobranchii: Rajiformes). The embryo case was retrieved from a depth of 1,116 m off the south-east coast of New Zealand, establishing a new bathymetric record for the genus *Amphiascus* (= *Paramphiascopsis*). Together with the copepods were forty specimens of a new species of a prosobranch gastropod of the genus *Choristella* Bush, 1897 (family Choristellidae) which was subsequently described by McLean (1992) as *C. marshalli*. Members of the Choristellidae are considered obligatory inhabitants of elasmobranch embryo cases (Kuroda *et al.* 1971). It has been reported that the inner wall of egg cases that contained *C. marshalli* were eaten by the gastropods (McLean 1992) although it is not clear whether their diet consists of the bacteria associated with the decomposition of the biogenic substratum, rather than the direct food source provided by the egg case itself.

Egg cases are composed of layers of structural protein collagen, which exhibits unique chemical and physical properties when deployed in egg cases. Elasmobranch embryos develop within the egg cases for up to nine months, during which there is little evidence of deterioration of the collagen layers (Wourms 1977). Although the duration of spent egg cases in the benthos is unknown they undoubtedly persist for a number of years, providing a persistent and reliable food source (McLean 1992) for associated organisms. However, the collagenous spent embryo case of a skate represents an unusual substratum for harpacticoids and it is unlikely that they would feed on such a food source. There is some circumstantial evidence that the occurrence of *A. waihonu* is in some way linked to the presence of the gastropod and only incidentally to the skate embryo case. Inspection of one of the two cases retrieved by Hicks (1986b) contained no harpacticoids while those that were collected came from inside a case that also contained *Choristella marshalli*. Webber *et al.* (2010) considered an association with the gastropod unlikely, suggesting instead that both are most probably feeding on detritus and decay products within the case.

Hicks (1986b) noted slight variability among females in the segmentation of the antennary and mandibular exopods, the relative length of the P1 endopod, the endopodal armature of leg 3 and the dorsal spinular ornamentation of the genital double-somite. Similar variability was observed among males in the armature of P3 endopod and P5 exopod, and the spinular patterns on the abdominal somites.

OD: Hicks (1986b—as *Paramphiascopsis waihonu*): 390–395; Figs 1–24.
TL: New Zealand, South Island, Canterbury Bight (44°55.0'S, 174°04.2'E); depth 1,116 m; inside spent skate (Rajiformes) embryo case together with *Choristella marshalli* McLean, 1992 (Gastropoda, Lepetellidae).
BL: 790 ± 30 μm (♀); 710 ± 20 μm (♂).

Family Porcellidiidae

Villiers *et al.* (1998) examined samples of seven species of *Patella* Linnaeus, 1758 (probably *Scutellastra* Adams & Adams, 1854—see below) collected at De Hoop Nature Reserve on the south coast of South Africa. In some of them they observed an undescribed species of *Porcellidium* Claus, 1860 sheltering under the limpet shells. An SEM photograph was provided but the species remained undescribed.

Family Tisbidae

Scutellidium Claus, 1866

Although members of this genus are considered characteristic indicators of the marine algal biotope (*e.g.* Pallares & Hall 1974; Hicks 1977a), one of the 20 currently valid species (Wells 2007) is known as a facultative inquiline associated with patellid gastropods in South Africa.

Scutellidium patellarum Branch, 1974

During investigations on the biology of *Patella* in South Africa, Branch (1974) found large numbers of a new species, *Scutellidium patellarum*, in association with five species of limpets. All host species have subsequently been assigned to the genus *Scutellastra* on both morphological and molecular grounds (Ridgway *et al.* 1998; Koufopanou *et al.* 1999). The complete sequence of developmental stages (nauplii, copepodids and adults) are associated with the limpets, being restricted to the pallial cavity where they move between the gills and over the foot without affecting the hosts. Occasionally they can be found on the external surface of the shell. *Scutellidium patellarum* was predominantly associated with *Scutellastra argenvillei* (Krauss, 1848) and *S. cochlear* (Born, 1778), with respectively 80% and 45% of the limpets harbouring copepods (up to 160 per limpet). There appears to be a marked correlation between host size and the number of copepods on these two limpet species (Branch 1975a). Occasional specimens also occurred in the pallial cavities of *Scutellastra barbara* (Linnaeus, 1758), *S. longicosta* (Lamarck, 1819), *S. tabularis* (Krauss, 1848), *Cymbula granatina* (Linnaeus, 1758), *C. miniata* (Born, 1778) and *C. oculus* (Born, 1778) (Branch 1974, 1975a). The apparent preference of *S. patellarum* for *P. argenvillei* is probably due to its zonation pattern, being restricted to the lower regions of the shore, rather than reflecting genuine host specificity.

Branch (1974, 1975b) obtained additional material from various other localities in the Western Cape Province, including Lambert's Bay, Elands Bay, Langebaan, Cape Point, Dalebrook, Kalk Bay and Hangklip. Based on these records he suggested that the species assumes a predominantly cold-water west coast distribution. This requires further research since the distribution range of some limpet hosts extends along the east coast as far northwards as Durban (*S. cochlear*) or Richards Bay (*S. longicosta)* (Branch *et al.* 2010).

It is difficult to define the nature of the relationship between the copepod and the gastropod host. According to Branch (1975a) *S. patellarum* appears to be a scavenger, feeding on the limpet faeces as well as algal fragments and possibly mucus produced by the hosts. However, under laboratory conditions, *S. patellarum* is capable of surviving and breeding without their hosts for three weeks, fed on dry shavings of *Ecklonia maxima* (Osbeck) Papenfuss, 1940 and small amounts of wet algae. Other sympatric species, such as *Scutellidium ringueleti* Pallares, 1969 and *Scutellopsis macrosetus* (Branch, 1975b), were found on littoral algae adjacent to the limpets, but never associated with the latter (Branch 1975a).

At all collection sites females grossly outnumbered males, comprising 95–98% of the adult population. Ovigerous females and larval stages can be found throughout the year and no marked peaks of reproduction were observed. It is noteworthy that the complete series of developmental stages are found under the limpets, clinging tenaciously to the host when water movement occurs. Adults and copepodids have strong raptorial setae and suctorial setal pads while the nauplii have a large midventral labral sucker. The naupliar sucker-disc was described in detail by Branch (1974) who confirmed its presence in all naupliar stages of *S. patellarum*. A similar circular suction disc had previously been documented for nauplii of *Scutellidium longicauda* (Philippi, 1840) (*cf.* Brian 1919; Gurney 1933), *S. idyoides* (Brady, 1883) and *S. arthuri* Poppe, 1884 (*cf.* Clogston 1965). This unique naupliar attachment device is probably diagnostic for all species in the genus with the notable exception of *S. hippolytes* (Krøyer, 1864) which is radically divergent in lacking the labral sucker (Dahms 1993a) as well as in displaying unusual copepodid characters (Dahms 1993b). Given the high density of limpets in the cochlear zone, short-range dispersal of *S. patellarum* could occur by direct transfer from host to host.

Branch (1975a) discovered a negative correlation between the intensity of *S. patellarum* on a limpet, and that of the polyclad turbellarian *Notocomplana erythrotaenia* (Schmarda, 1859) [as *Notoplana patellarum* (Stimpson, 1856)]. Although he considered a direct cause-and-effect relationship between the two distributions unlikely, he believed that avoidance of the predatory polyclads is certainly of survival value to the copepods. Gut contents analysis of five *N. erythrotaenia* taken from under the limpets *P. argenvillei* and *P. cochlear* revealed that all had two to five *S. patellarum* in their guts, suggesting that small crustaceans probably comprise the principal diet of the flatworm (Branch, 1975a).

Branch (1975a) noted the regular occurrence of one peritrich and two suctorian species of ciliates on the body of *S. patellarum*. One of the suctorians (an ophryodendrid) was found only on the proximal segments of the antennule.

Sexual dimorphism is first expressed at copepodid IV with males and females being distinguishable by small differences in the morphology of the antennule and leg 5, and by size. The single median egg sac contains 10–44 eggs, measuring each about 42 µm in diameter. Live specimens are suffused with a red colour over the entire body.

OD: Branch (1974): 180–198; Figs 1–82; Tables I–V.

TL: South Africa, Western Cape Province, Cape Town, Kommetjie (30º20'S, 18º20'E); pallial cavity of limpets (type host not specified).

BL: 125 µm (NI), 130–155 µm (NII), 153–195 µm (NIII), 188–207 µm (NIV), 208–236 µm (NV), 233–270 µm (NVI), 288–305 µm (CoI), 302–325 µm (CoII), 406–582 µm (CoIII), 512–721 µm (CoIV♀), 556–596 µm (CoIV♂), 671–721 µm (CoV♀), 721–910 µm (♀), 601–720 µm (♂).

Bryozoa

Four members of three unrelated families (Ectinosomatidae, Laophontidae, Tegastidae) are known to live in association with cheilostomatid bryozoan hosts (Gymnolaemata). According to Soyer (1968) the three species encountered in the Banyuls area (Médioni & Soyer 1966, 1968) appear to demonstrate significant host specificity while the association of the widely distributed *Tegastes falcatus* (Norman, 1869) with bryozoans has so far only been reported from the White Sea (Ivanenko *et al.* 2008a, 2008b). Ivanenko & Smurov (1997) recorded unidentified harpacticoids from *Flustra foliacea* in the Kandalaksha Bay of the White Sea; according to Ivanenko *et al.* (2008b) they do not belong to *T. falcatus* or any other member of the Tegastidae. Hicks (1980) noted that *Heterolaophonte denticulata* Roe, 1958 and a number of other laophontid species (*H. minuta* (Boeck, 1873), *Laophonte serrata* (Claus, 1863), *Paralaophonte spitzbergensis* Mielke, 1974) in Robin Hood's Bay, North Yorkshire, were preferentially found on the red alga *Mastocarpus stellatus* (Stackhouse) Guiry, 1984). He assumed these species may associate with cheilostomatid bryozoans such as *Electra pilosa* (Linnaeus, 1767), which is commonly found epizooitic on this rhodophyte (Ryland & Hayward 1977).

Family Ectinosomatidae

For latest key to genera see Kihara & Huys (2009).

Peltobradya Médioni & Soyer, 1968

Peltobradya bryozoophila Médioni & Soyer, 1968

The species was obtained from washings of the cheilostomatid *Schizomavella linearis* (Hassall, 1841) (Bitectiporidae) collected at 15 m depth off Banyuls-sur-Mer. Although Médioni & Soyer (1968) found only three females and two males, the discovery of numerous copepodid stages made them assume that *P. bryozoophila* completes its entire life cycle on the host. The dorsoventrally flattened body, large cephalothorax and short swimming legs with strong outer exopodal spines were considered as adaptations facilitating adherence to the bryozoan substratum. Live observations showed that *P. bryozoophila* moves actively over the host's surface and rarely loses contact with it (Médioni & Soyer 1968).

Ventham (2011) recorded *P. bryozoophila* from three different locations along the coast of West Sussex, southern England. The species was found on a cobble encrusted with the cheilostomatid bryozoan *Cellepora pumicosa* (Pallas, 1766) (Celleporidae) at 19.6 m depth off Selsey Bill. It was also obtained from two samples collected 8 km SSW of Worthing, one at 6.7–11.4 m depth and one at 8.0–11.6 m depth. In both cases Ventham (2011) presumed that *P. bryozoophila* was associated with the cyclostomatid *Patinella radiata* (Audouin, 1826) [as *Lichenopora radiata* (Audouin, 1826)] and/or the cheilostomatid *Flustra foliacea* (Linnaeus, 1758), the only bryozoans present in the mixed material (including red algae and the hydroid *Tubularia indivisa* Linnaeus, 1758).

Gheerardyn *et al.* (2008b, 2009) discovered a single specimen of an as yet undescribed species of *Peltobradya* Médioni & Soyer, 1968 in the coral degradation zone of *Lophelia pertusa* reefs at 800–1,005 m depth in the Porcupine Seabight (north-eastern Atlantic Ocean). Gheerardyn *et al.* (2010) speculated that the prehensile first legs of members of *Peltobradya* facilitated an epifaunal life style on hard biogenic substrata, explaining their absence from the soft-bottom deep-sea floor.

OD: Médioni & Soyer (1968): 318–325; Figs 1–4.

TL: France, Languedoc-Roussillon, Pyrénées-Orientales Department, vicinity of Banyuls-sur-Mer, Cap Rédéris; on *Schizomavella linearis* (Hassall, 1841) (Bryozoa, Gymnolaemata, Cheilostomatida) collected from coral sandy bottom at 15 m depth

BL: 255–285 µm (♀), 260–290 µm (♂).

Family Laophontidae

Inermiphonte Huys & Lee, 2009

Key to species of *Inermiphonte* Huys & Lee, 2009

1. P4 exp-3 with three outer spines; P2 enp-2 ♂ with four elements; P3 enp-2 ♂ with three elements .... *I. hamondi* Huys & Lee, 2009.
   P4 exp-3 with two outer spines; P2 enp-2 ♂ with three elements; P3 enp-2 ♂ with two elements .... 2.
2. Antennule ♀ 7-segmented; P1 exopod 3-segmented; P2–P3 exp-2 with inner seta; P5 baseoendopod ♀ with five setae; P5 exopod ♂ with five setae; caudal ramus about 2.5 times as long as wide .... *I. danversae* (Hamond, 1969).
   Antennule ♀ 6-segmented; P1 exopod 2-segmented; P2–P3 exp-2 without inner seta; P5 baseoendopod ♀ with four setae; P5 exopod ♂ with four setae; caudal ramus about as long as wide .... *I. drachi* (Médioni & Soyer, 1966).

Inermiphonte drachi (Médioni & Soyer, 1966)

Médioni & Soyer (1966) originally described this species as *Laophonte ? drachi* from material obtained in washings of the cheilostomatid bryozoan *Turbicellepora armata* (Hincks, 1860) [as *Schismopora armata* (Hincks, 1860)]. The bryozoans were collected from the lower branches of *Cystoseira spinosa* Sauvageau, 1912 in a *Posidonia* seagrass bed off the coast of Argelès-sur-Mer, Languedoc-Roussillon, in southeastern France. Médioni & Soyer (1966) tentatively assigned *L. ? drachi* to the *inopinata*-group of *Laophonte* and noted some similarities with *L. ? platychelipusoides* Noodt, 1958 (currently placed in *Coullia* Hamond, 1973a; *cf.* Hamond 1973a; Huys 2009a). In an addendum to his paper, Hamond (1969) remarked that his "Laophontid male, ?gen., ?sp." and the male of *L. ? drachi* shared the same type of sexual dimorphism on the P3 endopod and that the latter species was obviously closely related to *L. danversae* Hamond, 1969. Huys & Lee (2009) removed all three species to a new genus *Inermiphonte* Huys & Lee, 2009 and provisionally regarded it as the sistergroup of *Harrietella* T. Scott, 1906c. They pointed out that *I. drachi* showed some important differences with the other two species such as the 6-segmented antennule in the female, the 2-segmented P1 exopod, the reduced inner distal setae on the female P2–P4 exp-3 (a character typical for *Inermiphonte* males), and the presence of three strong spines on the male P4 endopod. Due to these discrepancies *I. drachi* was placed as *species incertae sedis* in *Inermiphonte*. The three species can be differentiated by the key above.

The association with *T. armata* appears to be genuine since *I. drachi* was never found on the stipes or branches of the brown alga *C. spinosa* while it was almost always present on the epibiotic bryozoan. All developmental stages, including nauplii, were observed on *T. armata*, suggesting that the entire life cycle is completed on the bryozoan host. Copepodids and adults firmly attach themselves to the colonies using their maxillipeds and the prehensile first pair of swimming legs. Females in particular have a dorsoventrally flattened body, a characteristic viewed by Médioni & Soyer (1966) as an adaptation to life in close connection to the bryozoan substratum. Live observations revealed that postnaupliar stages move slowly over the host's surface and display a poor swimming ability, being unable to reattach once they are dislodged from the host (Médioni & Soyer 1966; Soyer 1968).

OD: Médioni & Soyer (1966—as *Laophonte ? drachi*): 1054–1063; Plates 1–5.

TL: France, Languedoc-Roussillon, Pyrénées-Orientales Department, Argelès-sur-Mer, off Plage du Racou; on *Turbicellepora armata* (Hincks, 1860) (Bryozoa, Gymnolaemata, Cheilostomatida) attached to lower branches of *Cystoseira spinosa* Sauvageau, 1912 (Fucales) at 10 m depth.

BL: 300–425 µm (♀), 310–410 µm (ovigerous ♀), 310–400 µm (♂).

Family Tegastidae

Tegastes Norman, 1903

Tegastes falcatus (Norman, 1869)

The species was originally described as *Amymone falcata* from brown algal washings (Laminariaceae) collected in Bressay Sound, Shetland Islands (Norman 1869). It was subsequently reported from sandy substrata (Brady 1880; Sars 1904b; Ventham 2011), plankton samples (Willey 1923; Wilson 1936a; Grainger & McSween 1976), seagrass beds (Mascart *et al.* 2015) and various algae such as *Ahnfeltia plicata* (Hudson) E.M. Fries, 1836, *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863, *Fucus vesiculosus* Linnaeus, 1753, *Plocamium cartilagineum* (Linnaeus) P.S. Dixon, 1967, *Ptilota serrata* Kützing, 1847 and *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, 2006 (Chislenko 1967; Hauspie & Polk 1974; McAlice & Coffin 1990). Brady (1880) reported *T. falcatus* amongst serpulid tube worms (*Filograna implexa* Berkeley, 1835) off Robin Hood's Bay, Yorkshire but this association is most likely accidental.

Recently, Ivanenko *et al.* (2008a, 2008b) found large numbers of nauplii and copepodid stages of *T. falcatus* in washings of the cheilostomatid bryozoan *Flustra foliacea* collected off the Karelian coast of the Kandalaksha Gulf, White Sea. The branching fronds of the bryozoan colonies serve as a substratum for an unidentified suctorian protist. Nauplii attach to the sessile suctorians and have been observed to feed on them (see above—Associations with Protozoa) (Ivanenko *et al.* 2008a). Copepodids also appear to prey on the ciliates using their maxillipeds and maxillae. Ivanenko and co-workers have expressed ambiguous views on the nature of the relationship between *T. falcatus* and its substratum, claiming that the copepods are either associated with the bryozoan host (Ivanenko *et al.* 2008b: 192), or with the protists at least during their naupliar phase (Ivanenko *et al.* 2008a: 280), or directly with the suctorians and only indirectly with the bryozoans during their copepodid phase (Ivanenko *et al.* 2008b: 213), or displaying solely predation (carnivory) on protists (Ivanenko *et al.* 2012: 246). The naupliar and copepodid phases of development were described by Ivanenko *et al.* (2008a) and (2008b), respectively. Ovigerous females carry a single egg sac contained in an incubatory chamber formed by the anteroventral face of the genital triple-somite complex and the baseoendopods of the fifth legs.

Species identification in the genus *Tegastes* is notoriously difficult and comparison between them is made very difficult by the males being as yet unknown. According to Ivanenko *et al.* (2008b) females of *T. falcatus* can be readily distinguished from other species of the genus by the lancet-shaped seta V on the caudal ramus, the shape of the two ventral, hook-like processes on the genital triple-somite complex. Males can be separated by the shape of these attenuations, as well as the shape of the beak-like structure formed by the last posterior thoracic somite (P6).

Ivanenko *et al.* (2008b) claimed that copepodid stages II–VI possess eight elements on the caudal ramus, all of which were interpreted as genuine setae, and not as attenuations of the caudal ramus. No other copepod has been reported with more than seven setae and all previous reports of supernumerary setae have proven to be erroneous (Huys & Boxshall 1991). It is likely that the additional element in *T. falcatus* (indicated as seta 8 in Ivanenko *et al.* (2008b: Fig. 17F)) is a tubular extension of the large pore commonly found along the posterior margin of the caudal ramus (*cf.* Back *et al.* (2010: Fig. 8F)). Similar elongate tube pores had previously been reported and misinterpreted as setae in some deepwater tisbids (Boxshall 1979; Huys & Boxshall 1991).

The verifiable and probable records of *T. falcatus* from the Hudson Bay, Baffin Bay, Norwegian Sea, White Sea, Barents Sea and Franz Josef Land hint at an almost continuous circumarctic distribution (Scott 1899, 1903a; Willey 1923; Wilson 1936a; Gorbunov 1946; Kamshilov 1957; Kamshilov & Zelikman 1958; Brotskaya 1962; Chislenko 1967, 1977; Grainger & McSween 1976; Ivanenko *et al.* 2008a, 2008b; Kornev & Chertoprud 2008). The lack of records from the Kara, Laptev, East Siberian and Chukchi Seas introduces an element of discontinuity but this may reflect only the lack of collecting in northern Asia. In the Northern Atlantic it has also been reported from northwestern boreal Europe with records from Norway (Boeck 1873; Sars 1904b), Scotland including the Orkney and Shetland Island (Norman 1869; Brady 1880; Scott 1888, 1897, 1905, 1906a, 1907a; Hardy & Barnett 1986), England including the Isles of Scilly (Brady & Robertson 1876; Brady 1880, 1904, 1905; Norman & Scott 1906; Norman & Brady 1909; Wells 1970b; Bossanyi & Bull 1971; Moore 1973; Ventham 2011), and northwestern France (Hauspie & Polk 1974). Note that since Brady (1880) had erroneously identified the species as *Tegastes sphaericus* (Claus, 1863) most pre-Langian British records of the latter that referred to his redescription were subsequently identified as *T. falcatus* (Lang 1948: 465). On the western seaboard of the Atlantic it has been recorded from the Gulf of Saint Lawrence (Tremblay 1944) and Damariscotta River, Maine (McAlice & Coffin 1990). Records from the western Mediterranean (Pesta 1957; Mascart *et al.* 2015) are uncertain and require confirmation (Bodin 1997; Ivanenko *et al.* 2008b). Both Wilson (1936a) and Ivanenko *et al.* (2008b) claim that the species was found in Sri Lankan waters but this is incorrect. The single record (as *Tegastes sphærica*) cited in Thompson & Scott's (1903: 258) *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar* refers to a locality in the Suez Canal and is to be considered doubtful.

OD: Norman (1869—as *Amymone falcata* Norman, 1869): 296 (text only).
AD: Boeck (1873—as *Amymone rubra* Boeck, 1873): 48; no illustrations. Brady (1880—as *Amymone sphærica* Claus, 1863): 28–30; Plate XLIX (Figs 1–11). Brady (1904—as *Amymone rubra* Boeck, 1873): 5; Plate I (Fig. 13). Sars (1904b): 69–70; Plate XLI. Pesta (1959): 115–117; Fig. 43. Chislenko (1967): 122–124; Fig. 33. Huys *et al.* (1996): 291; Figs 116E–F. Ivanenko *et al.* (2008a): 270–279; Figs 1–9 (naupliar stages NI–VI). Ivanenko *et al.* (2008b): 193–218; Figs 1–20, 21A–B (adults and CoI–V). Kornev & Chertoprud (2008): 144.
TL: Scotland, Shetland Islands, Bressay, Bressay Sound; among kelp (Laminariaceae).
BL: 500 µm (♀) [Boeck 1865]; 460 µm (♀) [Sars 1904b]; 480–520 µm (♀), 460–500 µm (♂) [Chislenko 1967]; 70 µm (NI), 82 µm (NII), 103–107 µm (NIII), 103–109 µm (NIV), 125–148 µm (NV), 147–158 µm (NVI) [Ivanenko *et al.* 2008a]; 240–280 µm (CoI), 270–310 µm (CoII), 300–360 µm (CoIII), 310–320 µm (CoIV♀), 310–370 µm (CoIV♂), 380 µm (CoV♀), 370–420 µm (CoV♂), 430–490 µm (♀), 410–480 µm (♂) [Ivanenko *et al.* 2008b]; 500–600 µm (♀) [Kornev & Chertoprud 2008].

Tegastes knoepffleri **Médioni & Soyer, 1968**

The original description was based on two females and three males recovered in washings of the cheilostomatid bryozoan, *Schizobrachiella sanguinea* (Norman, 1868) (Schizoporellidae) collected off the coast of Banyuls-sur-Mer. Médioni & Soyer (1968) did not make any live observations but claimed finding numerous copepodids, suggesting most of the life cycle is completed on the bryozoan host. The species does not appear to be closely related to its bryozoan-associated congener, *T. falcatus*, and has not been recorded again since its original description.

OD: Médioni & Soyer (1968): 326–334; Figs 5–9.
TL: France, Languedoc-Roussillon, Pyrénées-Orientales Department, vicinity of Banyuls-sur-Mer, "calanque" (cove) of Troc; on *Schizobrachiella sanguinea* (Norman, 1868) (Bryozoa, Gymnolaemata, Cheilostomatida) collected from coral sandy bottom at 15 m depth.
BL: 455–472 µm (♀), 443–450 µm (♂).

Chaetognatha

Chaetognaths or arrow worms are at a high risk of becoming parasitized due to their position in the oceanic food web, being both prey and predator. Juveniles and adults of most species mainly prey on copepods (Feigenbaum & Maris 1984) and, in turn, are consumed by fish and pelagic predators, including members of the copepod families Candaciidae (Wickstead 1959, Lawson 1977), Pontellidae (Ohtsuka 1985), Corycaeidae (Daponte *et al.* 2008) and Oncaeidae (Go *et al.* 1998, Ohtsuka *et al.* 1996). Since at least some of these copepods are most likely to perform simultaneously the roles of prey, predator and intermediate host, the nature of their observed association with chaetognaths is often difficult to determine (Daponte *et al.* 2008). There are only a few reports of chaetognaths being infested with copepods (Alvarino 1965; Pierrot-Bults 1990) and most are merely anecdotal in nature. Thomson (1947) reported a specimen of *Decipisagitta decipiens* (Fowler, 1905) (as *Sagitta decipiens*) from south-eastern Australia with an ectoparasitic copepod attached in the region of the "oviducal papilla"; no description or illustrations accompanied this record. Ghirardelli (1948) reported ectoparasitic copepods on *Ferosagitta hispida* (Conant, 1895) (as *Sagitta hispida*) in the Indian Ocean and *Zonosagitta bedoti* (Béraneck, 1895) (as *S. bedoti*) in the Gulf of Aden. In both cases the copepods were adult ovigerous females carrying paired dorsal egg sacs and had attached themselves with their maxilipeds to the dorsal surface of the host. Although Ghirardelli (1948) did not give any morphological description, his photograph (Tavola II, Fig. 3) indicates that he was not dealing with harpacticoids but most likely oncaeids. Alvariño (1965) observed a parasitic copepod in the rectum of *S. decipiens* from the Sea of Cortés and assumed that it had entered the digestive tract via the anus. No illustrations or other information were provided. Reimer *et al.* (1971) recorded parasitic copepods at different stages of development in the coelom of *Parasagitta elegans* (Verrill, 1873) collected in the North Sea. Since no illustrations were provided it remains unknown whether the authors were dealing with harpacticoids.

Members of the planktonic genus *Microsetella* Brady & Robertson, 1873 have been found to parasitize *Flaccisagitta enflata* (Grassi, 1881) in the Indian Ocean. Infested *F. enflata* were observed in plankton samples from the Zanzibar channel, the western Indian coast off Goa and Seychelles waters where 1.1–2.9% of the arrow worms were infested with *Microsetella* spp. (Øresland & Bray 2005). The copepods were identified as *Microsetella norvegica*, based on caudal seta length and leg 5 morphology; however, since not all specimens were identified to species level, some may have been *M. rosea* (Dana, 1847). Copepods were usually found in the body coelom or inside the gut, however, several specimens were also observed with the anterior part of their bodies embedded halfway into the chaetognath body wall, gut or anus, suggesting that they can enter the digestive tract without being eaten. Some specimens found inside the gut were enveloped in a peritrophic membrane, indicating that they entered via the mouth as prey items and passed to the posterior part of the gut by peristaltis. It is unlikely that copepods can come through the mouth without being killed since most chaetognath species are capable of subduing their prey with a tetrodotoxin venom (Thuesen *et al.* 1988; Thuesen 1991). The discovery of copepods with their anterior end only halfway into the arrow worm shows that not all *Microsetella* that are encountered in chaetognath gut analyses (*e.g.* Laing & Vega-Pérez 1995; Kehayias *et al.* 1996; Duró & Saiz 2000) should be regarded as prey items. Øresland & Bray (2005) also observed *M. norvegica* infesting the male and female reproductive organs and feeding on the spermatogonia and ova of the chaetognath host. This feeding behaviour appears to cause partial castration and corroborates Seifried & Dürbaum's (2000) conjecture that carnivory is widespread among members of the family Ectinosomatidae. Finally, some copepods were found halfway inside the head of *F. enflata*, suggesting that *M. norvegica* may cause decapitation in chaetognaths by inflicting injuries to the neck region. While decapitation had previously been attributed to holoplanktonic typhloscolecid polychaetes (Feigenbaum 1991; Øresland & Pleijel 1991) it now appears that some pelagic harpacticoids can cause similar damage. The precise mechanism and reason for this phenomenon remain as yet unknown.

Crustacea

The Crustacea have more harpacticoid associates than any other group of macro-invertebrates, approximately 92 species, representing at least ten families, at present count (Tables 1, 3). About 119 crustacean species are known to serve as hosts to harpacticoid copepods, including amphipods, isopods, crayfish, lobsters, anomurans, brachyurans, palinurids, axiideans and barnacles. A total of 38 independent colonization events can be identified (Table 3) but this number is likely to be a significant underestimate of the real success of harpacticoids entering into symbiotic relationships with crustacean hosts. The symbionts are usually associated with the gills or the external surface of the carpace of their hosts, or inhabit the confined spaces occupied by tubicolous amphipods and particularly hermit crabs.

(i) Amphipod hosts

Copepods utilizing amphipods as hosts are extremely rare. Some members of the siphonostomatoid family Nicothoidae are ectoparasites of amphipods (*e.g.* Boxshall & Harrison 1988; O'Reilly 2003) but only one harpacticoid species is as yet known to have entered into a symbiotic association with this host category (Falck & Bowman 1994).

Family Canuellidae

Various members of the family Canuellidae have been reported as commensals of crustacean hosts, including one species of the genus *Parasunaristes* Fiers, 1982 which was found to be associated with an amphipod host. The family currently accommodates 17 valid genera, however, the generic assignment of at least two species is contentious. Wells & Rao (1987) admitted that there are significant differences in the male genital field between *Canuellina nicobaris* Wells & Rao, 1987 and other species of *Canuellina* Gurney, 1927. Huys (1995) pointed out that the taxonomic status of *C. nicobaris* remained unresolved and that the species keyed out as a member of *Ellucana* Coull, 1971b. Bodin (1997) and Wells (2007) included the species as *incertae sedis* in *Canuellina*. Previously, Fiers (1984b) had noted considerable differences between the two species of *Ellucana*, *E. longicauda* (Sewell, 1940) and *E. secunda* Coull, 1971b, and Por (1984b), without giving any reason, proposed to transfer the latter to *Canuellina*. Morphological comparison based on the male genital field, sexual dimorphism of leg 2 endopod and armature of leg 4 exopod indicates the presence of two lineages among the various species included in *Ellucana* and *Canuellina*, which do not accord with the current species compositions of these two genera. *Ellucana longicauda*, *C. nicobaris* and *C. onchophora* Por, 1967 (called hereafter the *Ellucana* lineage) have virtually identical male genital fields in which the opercula bear a long basal styliform element and a conspicuous uncinate spine along the inner margin, and a slender seta apically (*e.g.* Fiers 1984a: Fig. 2a). In *E. secunda* and the remaining *Canuellina* species (called hereafter the *Canuellina* lineage) the genital field is characterized by several chitinized areas and the absence of distinct triangular opercula. Although not a single accurate representation exists (*cf.* Por 1967—Plate V, Figs 15, 17; Wells 1967—Text-Fig. 14D; Coull 1971b—Fig. 16; Por 1983b—Fig. 16) there is no doubt that the two types are radically different. Members of the *Canuellina* lineage typically have extremely elongate, setiform elements on the distal and middle exopodal segments of leg 4 (in one case their setiform nature made Por (1967) inadvertently count them as inner elements, resulting in the erroneous formula 1.1.4 instead of 0.0.4 for *C. femur* Por, 1967; see his Table III) while species of the *Ellucana* lineage have the typical outer spines as found in most other canuellids. No sexual dimorphism is expressed on the P2 endopod in members of the *Canuellina* lineage while this is clearly the case in both *E. longicauda* and *C. nicobaris*, and possibly in *C. onchophora*. Males of all three species have an analogous modification of the distal exopod segment of leg 4 and display a similar chirocer antennule in which the segment posterior to the geniculation is considerably more swollen than in members of the *Canuellina* lineage. It is here proposed to formally transfer *C. onchophora* and *C. nicobaris* to the genus *Ellucana*, and assign *E. secunda* to the genus *Canuellina*.

Krishnaswamy (1957) described *Canuella* (*Canuella*) *indica* from several females dredged off Chennai, India. The morphology of the antennary exopod indicates that the species is related to *Brianola* Monard, 1926a but the highly reduced swimming leg armature probably prevents its assignment to that genus. Against all nomenclatural rules Becker (1972: 49) proposed a new binomen for the Indian species which he named "*Indicanuella krishnaswamyi*". Since the name was contained in an unpublished dissertation it constitutes an unavailable binomen. Unfortunately the generic name *Indicanuella* has entered the peer-reviewed literature as a *nomen nudum* on a number of occasions (*e.g.* Bodin 1979; Mielke 1979; Por 1984b; Pointner 2015) and in one case the combination *Canuella* (*Indicanuella*) *indica* was coined (Mielke 1994). Por (1984b) considered Krishnaswamy's (1957) description inadequate but admitted that Becker's (1972) generic assignment was probably justified on account of the unusual swimming leg morphology. In his latest tabular keys Wells (2007) continued considering *C. indica* as *species incertae sedis* in the genus *Canuella* Scott & Scott, 1893c. In accordance with the provisions of ICZN for new names published after 1999 (Arts 13.1.2, 13.3 and 16.1) Krishnaswamy's (1957) generic name is here expressly made available as *Indocanuella* **gen. nov.** by fixing *C.* (*C.*) *indica* as the type species by original designation, consequently taking the authorship and publication date of the present paper. In order to satisfy the provisions of ICZN Art. 13.1 a generic diagnosis is given below:

Canuellidae. Rostrum elongate, with rounded apex. Caudal rami elongate and narrow; with one long and one short apical seta. Antennary exopod very small, probably 6-segmented, with reduced armature; endopod 2-segmented. Mandibular exopod indistinctly 4- segmented. Legs 1–4 with 3-segmented rami. Leg 2 enp-1 without anterior apophysis fitting into groove on enp-2. Leg 3 with distinct spinous process on outer distal corner of enp-1 and -2. Leg 4 endopod about as long as exopod. Setal formulae of swimming legs as follows:

	Exopod	Endopod
Leg 1	0.0.022	1.0.121
Leg 2	0.0.021	0.0.121
Leg 3	0.0.022	1.1.121
Leg 4	0.0.021	1.0.121

Leg 5 with 3 setae in female. Male unknown.

Key to genera of Canuellidae

1. Distal segment of P4 endopod with two setae/spines . . . . *Microcanuella* Mielke, 1994.
Distal segment of P4 endopod with three setae/spines . . . . 2.
Distal segment of P4 endopod with four setae/spines. . . . . 7.
2. P1 exp-3 and enp-3 with six and four setae/spines, respectively; P2 exp-3 and enp-3 with four elements, respectively . . . . *Galapacanuella* Mielke, 1979.
P1 exp-3 and enp-3 with seven and six setae/spines, respectively; P2 exp-3 and enp-3 with 6–7 and five elements, respectively . . . . 3.
3. P2 exp-3 with six elements; distal segments of both rami of P3 with four setae/spines; P4 exp-2 without inner seta. . . . . 4.
P2 exp-3 with seven elements; P3 exp-3 and enp-3 with five and three setae/spines, respectively; P4 exp-2 with inner seta . 5.
4. Outer elements on P4 exp-1 and -2 short and spiniform; male genital field with triangular opercula bearing basal styliform element, conspicuous uncinate spine and slender seta; P2 enp-3 and P4 exp-3 sexually dimorphic . . . . . . *Ellucana* Coull, 1971b[1].
Outer elements on P4 exp-1 and -2 elongate and setiform; male genital field with different morphology and armature, displaying distinct chitinized patches; P2 enp-3 identical in both sexes, P4 exp-3 occasionally sexually dimorphic. . . . . *Canuellina* Gurney, 1927.
5. P4 endopod 2-segmented . . . . 6.
P4 endopod 3-segmented . . . . *Sunaristes* Hesse, 1867.
6. Maxilla sexually dimorphic, allobasal claw strongly chitinized, dark brown and recurved in ♀, much smaller, straight and with blunt teeth in ♂; antennule with enormous subchela in ♂ . . . . *Parasunaristes* Fiers, 1982.
Maxilla not sexually dimorphic, allobasal claw short and accompanied at base by four accessory setae; antennule with moderately developed subchela in ♂. . . . . *Intersunaristes* Huys, 1995.
7. P1 exopod 2-segmented . . . . *Canuellopsis* Lang, 1936b.
P1 exopod 3-segmented . . . . 8.
8. P3 exp-3 with four setae/spines. . . . . 9.
P3 exp-3 with five setae/spines. . . . . 10.
9. P2 exp-3 with three setae/spines . . . . *Indicanuella* **gen. nov.**
P2 exp-3 with four setae/spines. . . . . *Brianola* Monard, 1927.
P2 exp-3 with five setae/spines. . . . . *Nathaniella* Por, 1984b.
P2 exp-3 with six setae/spines. . . . . *Ifanella* Vervoort, 1964.
P2 exp-3 with seven setae/spines . . . . *Intercanuella* Becker & Schriever, 1979.
10. P4 exp-3 with four setae/spines. . . . . 11.
P4 exp-3 with five setae/spines. . . . . 12.
11. P1-bearing somite fused to cephalosome; P4 exp-3 without inner seta . . . . *Coullana* Por, 1984b.
P1-bearing somite not fused to cephalosome; P4 exp-3 with inner seta. . . . . *Scottolana* Huys, 2009b.
12. P4 enp-2 without inner seta. . . . . 13.
P4 enp-2 with inner seta . . . . *Elanella* Por, 1984b.
13. Female caudal rami distinctly longer than wide; P3–P4 coxa with inner seta; usually free-living . . . . *Canuella* Scott & Scott, 1893c.
Female caudal rami not longer than wide; P3–P4 coxa without inner seta; endosymbionts of spatangoid sea-urchins . . . . *Echinosunaristes* Huys, 1995.

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[1] Sewell (1940) divided the genus *Canuella* into two subgenera. *Canuella perplexa* Scott & Scott, 1893c, *C. furcigera* Sars, 1903, *C. scotti* Sewell, 1940, *Sunaristes inopinata* Thompson & Scott, 1903 and *S. longipes* Thompson & Scott, 1903 were retained in the nominotypical subgenus while a new subgenus *Canuella* (*Ellucana*) was proposed for a new species *Canuella* (*Ellucana*) *longicauda* (occasionally misspelled *longicaudata*, *e.g.* Por & Marcus 1973 (pp. 254–255); Por 1984b (p. 17)) and *Sunaristes curticaudata*. Coull (1971b) and Por & Marcus (1973) independently attributed generic rank to *Canuella* (*Ellucana*).

> The generic name *Ellucana* Sewell, 1940 is, however, currently unavailable. Under normal conditions, when a nominal taxon in the genus group is raised in rank, the name-bearing type remains the same (ICZN Art. 61.2.2), however, since Sewell (1940) neglected to fix a type this rule does not apply. The first author to satisfy the provisions of ICZN Art. 13.1 is Coull (1971b) who indirectly fixed the type by stating that "… *Ellucana secunda* differs from the genotype, *E. longicauda*, in the segmentation …" and by providing a description of characters that serve to differentiate it from other canuellid genera. The name *Ellucana* should be attributed to Coull (1971b) and Huys' (2009: Table 4) claim that *Canuella longicauda* Sewell, 1940 was fixed by monotypy in the subgenus *Canuella* (*Ellucana*) by Sewell (1940: 136) is incorrect. Fiers' (1982: 24) subsequent designation loses in priority.

***Parasunaristes* Fiers, 1982**

Thompson & Scott (1903: 257), with considerable foresight, stated that the reduced P4 endopod in *Sunaristes curticaudata* Thompson & Scott, 1903 may eventually necessitate the removal of this species to a new genus. Fiers (1982) reviewed the taxonomy of *Sunaristes* Hesse, 1867 and on the basis of the 2-segmented condition of the P4 endopod transferred *S. curticaudata* and *S. dardani* Humes & Ho, 1969a to a new genus *Parasunaristes*. *Ellucana chelicerata* Por & Marcus, 1973 and a new species *Parasunaristes cucullaris* Fiers, 1982, were also included in this genus. Por (1984b), being unaware of Fiers' (1982) paper, transferred *E. chelicerata* to *Sunaristes*, resulting in a new combination *Sunaristes cheliceratum* [*sic*] (Por & Marcus, 1973). Huys (1995) restricted the genus *Parasunaristes* to *P. chelicerata* (Por & Marcus, 1973) and the type species *P. cucullaris* by taking into account additional characters such as the shape of the cephalothorax and the morphology of the male antennule, maxilla, maxilliped, P1, male P2 and caudal ramus.

One of the characters employed by Fiers (1982) to distinguish *P. cucullaris* from *P. chelicerata* is the middorsal cap-like extension of the cephalic shield in the male. Huys' (1995) re-examination of the types of *P. chelicerata* revealed that the dorsal sensilla shown in Fiers' drawings (Figs XIV-6, XV-5) arise from short, paired, cuticular reinforcements along the hyaline posterior margin of the cephalic shield. Since these paired structures may easily be misinterpreted as somite contours Huys (1995) assumed that the shape and form of the cephalic shield are identical in both sexes, *i.e.* as illustrated by Fiers (1982) for the female of *P. cucullaris* (his Fig. XIV-5). According to Fiers (1982) *P. cuccularis* differs from *P. chelicerata* in the shape of the anal somite and the genital field.

***Parasunaristes chelicerata* (Por & Marcus, 1973)**

Por & Marcus (1973) originally described *P. chelicerata* from five specimens (three females, two males) obtained in sediment samples near Sinafir (= Sanafir) Island (northern Red Sea), at Port Taufiq (the southern outlet of the Suez Canal) and at two sites in the Great Bitter Lake. They suggested that *P. chelicerata* was introduced from the Red Sea into the Suez Canal. Falck & Bowman (1994) subsequently found the species in two localities (29°31'00"N, 34°56'00"E; 29°30'00"N, 34°55'00"E) on the Israeli coast of the Gulf of Elat (Aqaba) and added another record from Ras Mohammad (27°45'30"N, 34°15'30"E) at the southern tip of the Sinai Peninsula. Station depths varied between 2.7 and 22.9 m. At each of the sites *P. chelicerata* was found in about half (53 of 114) of the portable domiciles constructed by the epibenthic, tubicolous, corophioid amphipod *Siphonoecetes* sp. (family Ischyroceridae), a common species in subtidal sandy substrata in the northern Red Sea. Domiciles were composed of a secreted tube with embedded sediment particles, extending into the opening of usually a gastropod shell (86% of the cases), or less frequently a polychaete tube or another object. Extraordinary bilateral asymmetry in the size of the antennulary subchela was observed in a proportion of the males. Of 27 males examined, both subchelae were equal in 19 (70.4%), the right subchela was larger in six (22.2%) and the left subchela was larger in two (7.4%). Falck & Bowman (1994) suggested a role in mating behaviour for the sexually dimorphic maxillae but had no information on what that function might be. A similar sexual dimorphism has been reported for *Parasunaristes cucullaris*, a species known so far from free-living individuals only (Fiers 1982). The nature of the relationship between *P. chelicerata* and its amphipod host is unknown but the shelter offered by the latter must be advantageous to the copepod (Falck & Bowman 1994).

OD: Por & Marcus (1973—as *Ellucana chelicerata*): 251–254, 265–266; Figs 1–15, 44–50.

AD: Falck & Bowman (1994): 455–458; Figs 3–7.
TL: Egypt, Suez Canal, eastern shore of Great Bitter Lake.
BL: 1,360–1,400 µm (♀), 1,000–1,250 µm (♂).

(ii) Isopod hosts

Harpacticoids are known to infest three families of isopod hosts, two of which display boring activities. Members of four harpacticoid families have been positively identified as associates of isopods but only the Donsiellinae (Pseudotachidiidae) appears to have diversified. The most common hosts are gribbles or members of the Limnoriidae which bore into submerged wood and plant material for ingestion as food. The lignocellulose of wood is digested, most likely with the aid of cellulases produced by the gribbles themselves. Currently, the family accommodates 57 valid species in three genera (Boyko *et al.* 2015). The most destructive species are *Limnoria lignorum* (Rathke, 1799), *L. tripunctata* Menzies, 1951 and *L. quadripunctata* Holthuis, 1949a, all of which have successfully established themselves in European coastal waters (Borges *et al.* 2014). Due to dispersal while inhabiting wooden ships, it is uncertain where these three species originated and, consequently, this has similar implications for interpreting the phylogeography of their associated fauna. *Limnoria lignorum* and its symbionts may have been introduced to other areas as early as the sixteenth century, when fouling and wood-boring organisms from all continents started to cross oceans on ship hulls (Carlton & Hodder 1995; Wolff 2005). Switching between gribble hosts may also have occurred since limnoriids are often observed in association with other congeneric species engaged in interspecific competition. Additional host switching may have taken place when non-indigeneous copepod symbionts established associations with native hosts in the introduced range. For example, *Harrietella simulans* has been recorded from *L. tripunctata* in the Western Mediterranean, the Atlantic seaboard of North America, and Australia; however, it has also been observed on five other members of *Limnoria* Leach, 1814 (Table 9).

Family Ameiridae

Nitocra Boeck, 1865

Nitocra sphaeromata Bowman, 1988

Nothing is known about the biology of this species except that it occurs on the pleopods of its wood-boring host, *Sphaeroma peruvianum* Richardson, 1910 (family Sphaeromatidae). The association appears to be more intimate than between *Harrietella simulans* or donsiellinid copepods and their wood-boring hosts since *N. sphaeromata* was discovered on preserved *S. peruvianum* long after the collecting had been completed (Bowman 1988). The sphaeromatid host bores into the growing tips of aerial roots of the red mangroves *Rhixophora mangle* L. and *R. harrisonii* Leechman once roots have reached down to the high water line. Atrophy and breakage of the root tips caused by isopod boring results in a 50% decrease in aerial root growth rate (Perry & Brusca 1989). Since the isopods do not remain in one burrow throughout their lifetime it is highly probable that they contribute to the dispersal of *N. sphaeromata* via phoresis. The species is so far known only from the type locality but it is conceivable that its geographical range mirrors that of *S. peruvianum* which assumes a distribution along the eastern Pacific seaboard of Central and north-western South America. Santhakumari & Nair (1982) recorded unidentified ectocommensal harpacticoids on the wood-boring isopod, *Sphaeroma terebrans* Bate, 1866 in various localities along the south-western coast of India.

OD: Bowman (1988): 171–174; Figs 1–16.
TL: Costa Rica, Gulf of Nicoya, Punta Morales (ca. 10º04'N, 84º58'W); from pleopods of *Sphaeroma peruvianum* Richardson, 1910 (Sphaeromatidae) collected from its burrows in red mangrove aerial roots.
BL: 1,220–1,260 µm (♀), 1,100–1,160 µm (♂).

TABLE 9. Records of *Harrietella simulans* (T. Scott, 1894b) and their habitats (*L.* = *Limnoria*)

Country	Locality	Depth (m)	Habitat	Reference
Norway	Oslofjord, Drøbak	91	residue in collecting bottle	Sars (1920c)
	Trondheim	?	on *L. lignorum*	Stephensen (1936)
Ireland	Co. Down, Strangford Lough	1	on *L. lignorum*	Holmes & Jeal (1987)
	Co. Cork, Lough Hyne	0–19	on *L. lignorum*	Wouters & De Grave (1992)
		?	submerged wood	Holmes (1996)
United Kingdom	Firth of Forth, off West Wemyss	?	inside dead bivalve shells	Scott (1894b)
	Loch Fyne, off Inveraray	?	submerged decayed wood	Scott (1897)
	Firth of Forth	?	submerged decayed wood	Scott (1906a, 1907b)
	Firth of Clyde	?	submerged decayed wood	Scott (1906c, 1907b)
	Pembrokeshire, West Dale Bay	intertidal	on *L. lignorum*	Wells (1964), Crothers (1966)
	Norfolk, vicinity of Morston	inter/subtidal	sunken/stranded logs	R. Hamond (unpubl. data)
	Brighton, Roedean	intertidal	from *Polysiphonia fucoides*	Ventham (2011)
	Solent, remains of King Henry VIII's flagship *Mary Rose*	14	gribble-bored timbers	Hicks (1989)
The Netherlands	South Holland, Katwijk	intertidal	on *L. lignorum*	Vervoort (1950b), Pinkster (1968)
	South Holland, Noordwijkerhout	intertidal	on *L. lignorum*	Vervoort (1950b), Pinkster (1968)
	Zeeland, Vlissingen	intertidal	on *L. lignorum*	Faasse (2003)
France	Pas-de-Calais, Wimereux	intertidal	on *L. lignorum*	Pinkster (1968), Hicks (1988a)
	Pas-de-Calais, Wimereux, Audresselles, Pointe aux Oies	intertidal	on *L. lignorum*	Boer (1971)
	Hérault, Bassin de Thau	?	on *L. tripuncata*	Raibaut (1962b, 1967)
	Marseille harbour, Saumaty	?	on *L. tripunctata*	Pinkster (1967, 1968)
Canada	Baie des Chaleurs (48°24'N, 64°16'W)	57	on *L. borealis*	Brunel (1963)
U.S.A.	North Carolina, Beaufort Channel (34°33.4'N, 76°39.7'W)	intertidal	on *L. tripunctata*	Coull & Lindgren (1969)
	Massachusetts, Duxbury	intertidal	gribble-bored pine boards	Sleeter & Coull (1973)
Korea	Sacheon, Seogwipo and Taean	subtidal	submerged decayed wood	Kim (2013)
	Gosung	intertidal	washings of macroalgae	Kim (2013)
Australia	various localities, primarily in Victoria and New South Wales	intertidal	on *L. tripunctata* and *L. quadripunctata*	Hicks (1988a)
New Zealand	Bay of Plenty, off Whale Island (37°51'S, 177°15–19'E)	48–49	wood bored by *L. sexcarinata*	Hicks (1988a, 1989)
	off Kawhia (38°02.5–06.0'S, 174°36.9–37.0'E)	51	teredinid-bored log	Hicks (1989)
	Kaikoura, Baxter's Reef	10	wood bored by *L. carinata*	Hicks (1988a, 1989)
	Cook Strait ((40°56.4–59.8'S, 174°43.7–44.0'E)	144–182	wood bored by *L. sexcarinata*	Hicks (1988a, 1989)
	Otago Harbour, Portobello	intertidal	on *Limnoria carinata*	Hicks (1988a)
		intertidal	gribble-bored wharf piles	Hicks (1989)
	Wellington Harbour, Queen's Wharf	intertidal	gribble-bored wharf piles	Hicks (1989)

Family Laophontidae

Harrietella T. Scott, 1906c

Harrietella simulans (T. Scott, 1894b)

Due to scarcity of material Scott (1894b) provisionally assigned this species to the genus *Laophonte* as (?) *Laophonte simulans* but subsequently (Scott 1906c) fixed it as the type of a new genus *Harrietella*. The type material was obtained inside a dead bivalve (*Arctica* sp.) shell dredged in the Firth of Forth, but it was not until additional female specimens were collected in considerable numbers in Loch Fyne (off Inveraray) and the Firth of Clyde (Scott 1897, 1906a, 1906c) that the real habitat was recognized. All of Scott's specimens were recovered from the crevices of submerged and partly decayed wood; the surface of the logs was usually perforated by boring molluscs or crustaceans. The male was first described by Scott (1907b) from the Firth of Clyde. In his study of harpacticoids found living on the gribble, *Limnoria lignorum*, in Trondheim (western Norway), Stephensen (1936) illustrated a single male which he tentatively attributed to *Laophonte brevifurca* Sars, 1920b, a species so far known from a single female collected off Hvaler (Hvalør) in southern Norway (Sars 1920b). Nicholls (1941), Lang (1948) and Vervoort (1950b) independently recognized the conspecificity between Stephensen's (1936) male and *H. simulans*. Sars (1920c) found a single female in the bottom residue of a collecting bottle in which material obtained from a depth of 91 m near Drøbak in the Oslofjord had been preserved.

Stephensen (1936) was the first to suggest a commensal relationship between *H. simulans* and *L. lignorum* but such an association was refuted by Lang (1948) who believed that the copepod was more dependent on the gribble burrows, or the decaying wood, than on the isopod host itself. Vervoort (1950b) made live observations on *L. lignorum* from logs of wood washed ashore at Katwijk and Noordwijkerhout (The Netherlands), and confirmed that *H. simulans* attaches itself to various parts of the host's carapace, usually the telson, by means of the powerful maxillipeds and the endopods of the first legs. Occasionally they were observed on the legs and oral appendages of the host. Indicative of its commensal mode of life during at least some part of the copepodid phase is the fact that Vervoort found developmental stages of *H. simulans* on the isopod host. Raibaut (1962b, 1967) reported the first occurrence of *H. simulans* from the Mediterranean (Bassin de Thau) as well as its association with a different isopod host, *Limnoria tripunctata*. Wells (1964) found two males and three females of this species in association with *L. lignorum* in a piece of drift-wood stranded on the beach at West Dale Bay, Pembrokeshire (Wales). Pinkster (1968) re-examined Vervoort's (1950b) material, provided an updated description and added a new record from *L. lignorum* in wooden poles in Wimereux, Pas-de-Calais (France). He also added a second Mediterranean record from *L. tripunctata* in the harbour of Marseille. Wouters & De Grave (1992) found *H. simulans* in Lough Hyne (Co. Cork) in wood samples infested with the burrows of *L. lignorum*. It has also been recorded from Norfolk (England), both intertidally and subtidally, in stranded and sunken logs (R. Hamond, *in litt.*).

Holmes & Jeal (1987) found a single female in a light trap, along with 18 gribbles, in Strangford Lough (Co. Down). Based on previous observations (Vervoort 1950b; Pinkster 1968) that *H. simulans* lacks a nauplius eye, they concluded that the copepod must have entered the light trap upon one of the gribbles rather than having been attracted to it. Ventham (2011) recorded a single female from the filamentous red alga, *Polysiphonia fucoides* (Hudson) Greville, 1824, in the lower intertidal east of Brighton.There being no wood substrata in the vicinity of the sampling location he speculated that, as a vagrant, it had associated itself with the common intertidal phytal isopod *Idotea granulosa* Rathke, 1843 which was abundant in the sample.

Coull & Lindgren (1969) reported *H. simulans* for the first time from North America. They found it inside wood samples excavated by *L. tripunctata* in the Beaufort Channel, North Carolina. The authors confirmed the telson as the preferred attachment site for *H. simulans* while observed during laboratory experiments but noted that, *in situ*, no copepods were attached to the gribbles in the wood samples, suggesting that previous reports of physical association may be an artefact of the collecting methods employed. Being a poor swimmer, it would appear that *H. simulans* only uses *Limnoria* spp. as a substratum when isolated from its natural environment, the gribble burrows. Similar experiments conducted by Sleeter & Coull (1973) using material from Duxbury Bay, Massachusetts, also failed to reveal any direct commensal relationship between *H. simulans* and the gribble, other than that it feeds on the *Limnoria* faecal pellets that gradually pile up in the burrows. The copepods will attach themselves to *L. tripunctata* only when no other suitable substratum is available. Typically, copepods greatly outnumbered the gribble and often clusters of 10–20 copepods were discovered in abandoned burrows. Sleeter & Coull (1973) found that *H. simulans* was the most prevalent species in October, but by December, the co-occuring miraciid, *Paramphiascella fulvofasciata* Rosenfield & Coull, 1974, was the dominating form.

Brunel (1963) cited an unidentified laophontid associated with *Limnoria japonica* Richardson, 1909 in Chaleur Bay (Baie des Chaleurs), an arm of the Gulf of Saint Lawrence located between Quebec and New Brunswick. The species, which was found to co-exist with *Donsiella limnoriae* Stephensen, 1936 on the gribble host, almost certainly refers to *H. simulans*. Kussakin (1963) and Kühne (1976) pointed out that the host was misidentified and probably belongs to *Limnoria borealis* Kussakin, 1963. Kim (2013) recorded the species from Korea in washings of submerged wood (bored by limnoriids and teredinids) collected at Sacheon, Seogwipo and Taean, but also in washings of macroalgae at Gosung. The only records of *H. simulans* in the Southern Hemisphere are those by Hicks (1988a, 1989). In New Zealand he reported it from offshore gribble-bored wood in the Bay of Plenty, Baxter's Reef (Kaikoura) and Cook Strait, and from a teredinid-bored log off Kawhia. He also collected the species from intertidal wharf piles in Wellington Harbour and Otago Harbour. Although Hicks (1989) made no attempt at identifying the limnoriid hosts for all these records, some of them had already been referred to in his revision of the Donsiellinae (Hicks 1988a) in which he identified two new gribble species, *L. carinata* Menzies & Becker, 1957 and *L. sexcarinata* Kühne, 1975, as potential hosts for *H. simulans*. Finally, his re-examination of the badly gribble-bored oak timbers of King Henry VIII's flagship *Mary Rose*, sunk in the Solent, off Portsmouth in 1545, also revealed the presence of *H. simulans*. Given the worldwide distribution of limnoriids (Menzies 1957; Cookson 1991), the published records of *H. simulans* are still few (Table 9) but it seems likely that this scarcity is more apparent than real; due to its minute size and transparent nature this copepod is easily overlooked (Wells 1964).

Harrietella simulans often co-occurs with *Donsiella limnoriae* (Pseudotachidiidae) (*e.g.* Stephensen 1936; Pinkster 1967, 1968; Holmes & Jeal 1987; Wouters & De Grave 1992) or with other members of the Donsiellinae (Hicks 1988a). Unlike other members of the Laophontidae the female has paired egg sacs (Scott 1894b, 1906c, 1907b). Fiers (1992a) hinted at a relationship between the genera *Pseudonychocamptus* Lang, 1944 and *Harrietella* while Huys & Lee (2009) regarded a sistergroup relationship between the latter genus and *Inermiphonte* Huys & Lee, 2009 more likely. Descriptions of *H. simulans* vary in detail and considerable variability has been reported within and between populations. According to Hicks (1989) this morphological variability is a reflection of the great heterogeneity of the highly ephemeral and spatially non-continuous substrata occupied by the species. Although habitat heterogeneity may indeed be an underlying factor, the wide geographic and bathymetric ranges occupied by *H. simulans* may also point to a previously unrecognized species complex. Published reports on the swimming leg armature pattern of this species (Table 10) demonstrate that an adequate assessment of intraspecific variability is long overdue.

OD: Scott (1894b): 248–249; Plate VII (figs 24–32), Plate VIII (fig. 1) (♀ only).
AD: Scott (1906c): 464–465; Plate XI (figs 9–10). Scott (1907b): 209–211; Plate XIII (figs 1–5) (♂). Sars (1920c): 73–75; Plate XLIX. Stephensen (1936): 4–6; Fig. 1 (as *Laophonte* (*brevifurca* G.O. Sars ?)) (♂). Vervoort (1950b): 297–303; Figs 1–4 (♀). Pinkster (1968): 61–63; Figs 9–11. Coull & Lindgren (1969): 73–74; Fig. 1. Hicks (1989): 115–116; Fig. 9. Kim (2013); 32–34; Fig. 10.
TL: Scotland, Fife, north shore of Firth of Forth, off West Wemyss; dredging.
BL: 430 µm (♀) [Scott 1894b]; 510 µm (♀) [Sars 1920c]; 400 µm (♂) [Stephensen 1936]; 410–500 µm (♀) [Vervoort 1950b]; 500–680 µm (♀) [Pinkster 1968]; 510 µm (♀), 420 µm (♂) [Lee 2013].

Family Pseudotachidiidae

Lang (1944) established the subfamily Donsiellinae in the Laophontidae to accommodate *Donsiella limnoriae*, which lives in association with wood-boring isopods of the genus *Limnoria*. Hicks (1988a) removed the subfamily from the Laophontidae and placed it within the Thalestridae with closest affinities to the Pseudotachidiinae. Willen (2000) elevated the latter to family status and recognized the Donsiellinae as one of four subfamilies in the Pseudotachidiidae. Boxshall & Halsey (2004) rejected Willen's (2000) classification and phylogenetic analysis, principally on the grounds that she failed to identify apomorphies for the nominate subfamily Pseudotachidiinae. Pending a rigorous analysis Wells (2007) continued to use Willen's subfamily arrangement and this *status quo* is also adopted here.

TABLE 10. Variability recorded in armature pattern of P2–P5 in *Harrietella simulans* (T. Scott, 1894b) [apo = apophysis].

P2		P3		P4		P5 ♀		P5 ♂		Reference
exp	enp	exp	enp	exp	enp	exp	benp	exp	benp	
?	?	0.1.023	0.121	0.123	011	5	3	?	?	Scott (1894b)
0.1.022	0.020	?	?	0.0.023	011	?	?	4	1	Scott (1907b) [1, 2]
0.1.023	0.020	0.1.023	0.121	0.122	011	5	3	?	?	Sars (1920c)
0.1.122	0.020	0.0.122	0.12apo	0.023	121	?	?	4	0	Stephensen (1936) [3]
0.1.023	1.021	0.1.023	0.121	0.123	011	4	4/5	?	?	Vervoort (1950b)
1.1.023	0.020	0.0.013	0.122	0.123	011	5	3	4	0	Pinkster (1968)
?	?	0.1.023	0.120	0.123	011	?	?	?	?	Coull & Lindgren (1969)
?	?	0.1.022	0.12apo	0.123	011	5	3	4	1	Hicks (1989) [3, 4]
?	?	?	0.02apo	0.022	0/111	5	4	3	1	Hicks (1989) [3, 5]
0.1.022	0.020	0.1.022	0.120	0.022	020	5	3	3	1	Kim (2013)

[1] armature of P4 based on male.

[2] the figure legends contradict the text and illustrations with the male P4 being labelled as the female P4 (Fig. 4) and the male P5 as the male P4 (Fig. 5)

[3] armature of P2–P4 based on male.

[4] based on specimens from the Solent, southern England.

[5] based on specimens from off Kawhia, north-western New Zealand.

Hicks (1988a) collected a wealth of material from teredinid and gribble-bored wooden intertidal wharf-piles and from sunken decomposing logs trawled from offshore waters around New Zealand down to a depth of 1,514 m. Four new genera and eight new species of Donsiellinae were described, all of which appeared to be co-associates of wood-boring invertebrates and/or the specialized habitat prepared by them. However, recent studies showed that not all deepwater donsiellinids, in particular members of *Xylora* Hicks, 1988a, are associated with sunken wood (Table 11). Willen (2006) described *X. calyptogenae* Willen, 2006 from the Edison Seamount, a hydrothermally active submarine volcano in the New Ireland Fore-Arc system (Papua New Guinea). The specialised mouthpart morphology and the presence of a large prey organism, presumably a copepod, consumed either alive or dead, in the gut of one of the specimens, led her to suggest that *X. calyptogenae* employed a carnivorous feeding strategy rather than being associated with a biogenic substratum. *Xylora bathyalis* displays a similar mouthpart design (but see below for conspecificity of these two species) and is frequently the most dominant harpacticoid in deep sea water-logged wood substrata in New Zealand waters (Hicks 1988a). However, Huys & Lee (2000) subsequently reported several males and females of *X. bathyalis* from the "White Lady" site on the North Fiji Ridge at 2,765 m depth, the deepest record of the subfamily so far, indicating that its association with sunken wood is likewise not obligatory. Other reports have demonstrated since that *Xylora* species are common in hydrothermal vent habitats on the Mid-Atlantic Ridge and East Pacific Rise where decaying wood is absent (Gollner *et al.* 2006, 2007, 2010; Degen 2010; Degen *et al.* 2012; Cuvelier *et al.* 2014). Unidentified species were recorded from dead fragments of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758) at 880–1,005 m depth in the Porcupine Seabight (Gheerardyn *et al.* 2010) and from the permanent meiofauna associated with vestimentiferan tubeworm aggregations from hydrocarbon seeps of Atwater Valley (~2,200 m) in the Gulf of Mexico (Degen *et al.* 2012).

Hicks (1988a) suggested that *X. bathyalis* utilizes a habitat previously prepared in shallower water by limnoriids and teredinids, which ultimately becomes available to the copepods in deeper waters where they attain their highest abundance. Willen (2006) depicted an alternative "evolutionary" scenario for the Donsiellinae based on a different sequence of events and a gradual increase in intimacy between the copepods and their isopod cohabitants, starting from the more primitive deepwater taxa which live in the hydrothermal seafloor in the absence of decaying wood (some *Xylora* spp.), to species which are found in decomposing wood but are not necessarily associated with gribble (*X. bathyalis*), to eventually the morphologically more advanced genera which invaded shallow waters and entered into a permanent and probably obligatory association with their limnoriid hosts (*e.g. Donsiella* spp.). Irrespective of which pathway is more plausible, the acquisition of a flattened body, a robust prehensile P1 endopod and markedly reduced swimming legs would equip donsiellines extremely well for their specialized life style as close associates of gribble and the wood borings of shipworms (Hicks 1998a).

Key to genera of Donsiellinae Lang, 1944

1. Antennule of female 7-segmented; maxilliped with palmar seta on basis; P1 exp-3 with five elements; P1 enp-1 with inner seta; P2 exp-3 with five elements . . . . 2.
   Antennule of female 6-segmented; maxilliped without palmar seta on basis; P1 exp-3 with three or four elements; P1 enp-1 without inner seta; P2 exp-3 with four elements. . . . . 3.
2. P2–P3 endopods 3-segmented. . . . . *Xylora* Hicks, 1988a.
   P2–P3 endopods 2-segmented. . . . . *Oligoxylora* Hicks, 1988a.
3. P1 exopod 2-segmented, with three elements on distal segment . . . . *Apodonsiella* Hicks, 1988a.
   P1 exopod 3-segmented, with four elements on distal segment . . . . 4.
4. P4 endopod 1-segmented . . . . *Donsiella* Stephensen, 1936.
   P4 endopod absent. . . . . *Pseudonsiella* Hicks, 1988a.

Donsiella Stephensen, 1936

Originally proposed to accommodate the gribble-associated *Donsiella limnoriae* from Norway, the genus has seen the addition of four new species since, all of which are implicated either as direct associates of wood-boring isopods or of habitats occupied by them (Hicks 1988a) or as commensals of other limnoriids that excavate tunnels in the holdfasts and stipes of kelp (Hicks 1990). The genus presumably has a wordwide distribution due to dispersal while inhabiting wooden ships, explaining the geographically wide separation between, for example, *D. anglica* Hicks, 1988a from southern England and its closest relative *D. victoriae* Hicks, 1988a from eastern Australia. The Canadian records of *Donsiella* from *Limnoria borealis* (Brunel 1963; Brunel *et al.* 1998) probably refer to an as yet undescribed species (see below). Cuvelier *et al.* (2014) listed a donsiellinid from the Lucky Strike vent field under the name *Donsiella* cf. *bathyalis* but this species does not exist.

Key to species of *Donsiella* Stephensen, 1936

1. Caudal ramus distinctly longer than wide; P3 enp-1 ♀ with inner seta; distal unguiform projection on P2 enp-3 ♂ either bispinulose or with few spinules along outer margin; P4 endopod with two apical setae in both sexes . . . . 2.
   Caudal ramus only slightly longer than wide; P3 enp-1 ♀ without inner seta; distal unguiform projection on P2 enp-3 ♂ naked; P4 endopod with one apical seta in ♀ and one or two apical setae in ♂. . . . . 3.
2. Claws of P1 enp-2 spinulose along outer margin; P2–P3 enp-2 ♀ with one inner seta, one apical seta and one outer spine; seta on P3 enp-3 ♂ arising from terminal position; P5 baseoendopod ♀ with four setae . . . . *D. phycolimnoriae* Hicks, 1990.
   Claws of P1 enp-2 naked along outer margin; P2 enp-2 ♀ with one seta and one spine apically, P3 enp-2 ♀ with one apical seta; seta on P3 enp-3 ♂ arising from mediolateral position; P5 baseoendopod ♀ with three setae . . *D. bisetosa* Hicks, 1988a.
3. P2 enp-2 ♀ with one inner and three apical elements; P3 enp-2 ♀ with one inner and two apical elements; P3 ♂ without inner seta on enp-1 and two setae on enp-3 . . . . *D. limnoriae* Stephensen, 1936.
   P2–P3 enp-2 ♀ with one inner and one apical element; P3 ♂ with inner seta on enp-1 and one seta on enp-3. . . . . 4.
4. Distal unguiform projection on P2 enp-3 ♂ bifurcate at tip; seta on P3 enp-3 ♂ arising from mediolateral position; P4 endopod ♂ with two setae; P5 exopod ♀ typically with four elements (innermost occasionally absent). . . . . *D. victoriae* Hicks, 1988a.
   Distal unguiform projection on P2 enp-3 ♂ rounded at tip; seta on P3 enp-3 ♂ arising from terminal position; P4 endopod ♂ with one seta; P5 exopod ♀ with three elements . . . . *D. anglica* Hicks, 1988a.

Donsiella limnoriae Stephensen, 1936

Lang (1948) reillustrated certain parts from the syntypes and sent the figures to Stephensen for corroboration. Although Stephensen confirmed that his own interpretation was wrong, Lang (1948) also failed to clarify critical features of the antenna and mouthparts. Hicks (1988a) based his revised diagnosis and redescription on material collected at Wimereux (Pas-de-Calais), France (see Pinkster 1968) and concluded that the French specimens were identical to the syntypes from Trondheim, Norway. He recorded some variability in the armature of the antennary exopod and the number of setae on the female leg 5 exopod. According to Stephensen (1936) the nauplius eye is lacking and the single egg sac contains 8–13 eggs.

TABLE 11. Distributional records of members of the subfamily Donsiellinae (Pseudotachidiidae). Type localities indicated by *.

Species	Country	Locality	Depth (m)	Habitat	Reference
Apodonsiella indica	Australia	Cocos Islands (12°10'S, 96°55'E) *	?	on *Paralimnoria andrewsi*	Hicks (1988a)
Donsiella limnoriae	Norway	Trondheim *	?	on *Limnoria lignorum*	Stephensen (1936)
	Ireland	Co. Cork, Lough Hyne	?	with *Limnoria lignorum*	Wouters & De Grave (1992)
		Co. Galway, Rossaveel	?	on *Limnoria lignorum*	Holmes & O'Connor (1990)
		Co. Waterford, Dunmore East	5	on *Limnoria lignorum*	Holmes & Jeal (1987) [1]
	England	North Devon, Ilfracombe	?	on *Limnoria quadripunctata*	Krishnaswamy & Jones (1962) [2]
	Wales	Pembrokeshire, Milford Haven and off Point Wood thermograph raft	intertidal	on *Limnoria lignorum* and *L. quadripunctata*	Krishnaswamy & Jones (1962) [2], Crothers (1966) [2]
	Netherlands	Zeeland, Vlissingen and Neeltje Jans	intertidal	on *Limnoria lignorum*	Faasse (2003)
	France	Pas-de-Calais, Wimereux	intertidal	on *Limnoria lignorum*	Pinkster (1968), Hicks (1988a)
		Pas-de-Calais, Wimereux, Audresselles and Pointe aux Oies	intertidal	on *Limnoria lignorum*	Boer (1971)
		Marseille harbour, Saumaty	1.5–4	on *Limnoria tripunctata*	Pinkster (1967, 1968)
	Canada	Baie des Chaleurs (48°24'N, 64°16'W)	57	on *Limnoria borealis*	Brunel (1963) [3]
	U.S.A.	Pacific coast	?	no data	Gooding (in Krishnaswamy & Jones 1962), Carlton (2007)
Donsiella anglica	England	Hampshire, Calshot and Southampton *	?	on *Limnoria quadripunctata*	Krishnaswamy & Jones (1958, 1962)
		Isle of Wight, Cowes	?	on *Limnoria tripunctata*	Krishnaswamy & Jones (1958, 1962)
	Ireland	Lough Hyne, Co. Cork	?	submerged wood with *L. lignorum*	Holmes (1996)
Donsiella bisetosa	New Zealand	Cook Strait, SW of Kapiti Island	144–182	on *Limnoria sexcarinata*	Hicks (1988a)
		Wellington Harbour, Queen's Wharf *	intertidal	gribble-bored wharf piles	Hicks (1988a)
Donsiella victoriae	Australia	New South Wales, Goat Island	?	on *Limnoria* sp.	Hicks (1988a)
		New South Wales, Goat Island	?	on *Limnoria tripunctata*	Hicks (1988a)
		Victoria, Brighton Pier	?	on *Limnoria quadripunctata*	Hicks (1988a)
		Victoria, Port Arlington	?	on *Limnoria quadripunctata*	Hicks (1988a)
		Victoria, Queenscliff	?	on *Limnoria quadripunctata*	Hicks (1988a)
		Victoria, Sandringham	?	on *Limnoria quadripunctata*	Hicks (1988a)
		Victoria, Sandringham	?	on *Limnoria tripunctata*	Hicks (1988a)
		Victoria, South Channel Light	?	on *Limnoria quadripunctata*	Hicks (1988a)
		Victoria, St. Kilda *	?	on *Limnoria* sp.	Hicks (1988a)
		Western Australia, Bunbury	?	on *Limnoria* sp.	Hicks (1988a)

……*continued on the next page*

TABLE 11. (Continued)

Species	Country	Locality	Depth (m)	Habitat	Reference
Donsiella phycolimnoriae	Australia	Macquarie Island *	?	on *Limnoria stephenseni*	Hicks (1990)
Donsiella sp.	Canada	Saint Lawrence estuary	?	on *Limnoria borealis*	Brunel *et al.* (1998)
Oligoxylora cooksoni	Australia	Victoria, Lorne *	?	on *Limnoria quadripunctata*	Hicks (1988a)
Pseudonsiella aotearoa	New Zealand	Dunedin City, Portobello	intertidal	decaying wharf pile with *Limnoria carinata*	Hicks (1988a)
		Kaikoura, Baxter's Reef	10	decaying gribble-bored wood	Hicks (1988a)
		Wellington Harbour, Queen's Wharf *	intertidal	gribble-bored wharf piles	Hicks (1988a)
Pseudonsiella longicaudata	Korea	Kangwondo, Namae Port *	?	decaying wood with *Limnoria* sp. (probably *L. lignorum*)	Kim & Kim (1997)
Xylora bathyalis	New Zealand	lower Kaikoura Canyon	1,489–1,514	water-logged decaying wood	Hicks (1988a)
		Chatham Rise, NE of Mernoo Bank	800–810	Kowhai fragment (*Sophora microphylla*)	Hicks (1988a)
		W of Hokitika	1,142–1,147	water-logged decaying wood	Hicks (1988a)
		Moeraki Canyon, off Jackson Bay	833–891	water-logged decaying wood	Hicks (1988a)
		off Castlepoint (41°10'S, 176°26'E) *	1,174–1,208	water-logged decaying wood	Hicks (1988a)
		off Castlepoint (41°10'S, 176°31'E)	1,198–1,211	water-logged decaying wood	Hicks (1988a)
		SW of Castlepoint (41°26'S, 176°08'E)	1,120	water-logged decaying wood	Hicks (1988a)
		Canterbury Bight (44°35'S, 174°06'E)	880–900	water-logged decaying wood	Hicks (1988a)
		Canterbury Bight (44°47'S, 173°35'E)	952–962	water-logged decaying wood	Hicks (1988a)
		Canterbury Bight (41°59'S, 174°01'E)	1,178–1,190	water-logged decaying wood	Hicks (1988a)
		off Timaru	750–738	water-logged decaying wood	Hicks (1988a)
		NE of Chatham Island	1,174–1,180	water-logged decaying wood	Hicks (1988a)
		Western side of Cook Strait	144–182	decaying wood with *Limnoria sexcarinata*	Hicks (1988a)
	Papua New Guinea	New Ireland Fore-Arc system, Edison Seamount (3°19'S, 152°35'E)	1,446	sediment samples	Willen (2006) [4]
	North Fiji Ridge	"White Lady" site west of Fiji (18°50'S, 173°29'W)	2,765	slurp gun samples	Huys & Lee (2000)
	East Pacific Rise	Tica Field (09°50.4'S, 104°17.5'W)	~2,500	*Riftia/Bathymodiolus* aggregations	Gollner *et al.* (2006, 2007, 2010), Degen (2010), Degen *et al.* (2012)
		Riftia Field (09°50.7'S, 104°17.4'W)	~2,500	*Riftia pachyptila* patches	Gollner *et al.* (2006, 2007, 2010), Degen (2010)

……*continued on the next page*

TABLE 11. (Continued)

Species	Country	Locality	Depth (m)	Habitat	Reference
Xylora cf. *bathyalis*	Mid-Atlantic Ridge	Eiffel Tower edifice (Lucky Strike vent field)	1,689–1,697	wood and inorganic slate panels	Cuvelier *et al.* (2014) [5]
Xylora neritica	New Zealand	Bay of Plenty, off Whale Island	48–49	decaying wood with *Limnoria sexcarinata*	Hicks (1988a)
		W Cook Strait	144–182	decaying wood with *Limnoria sexcarinata*	Hicks (1988a)
		Dunedin City, Portobello *	intertidal	decaying wharf pile with *Limnoria carinata*	Hicks (1988a)
		Kaikoura, Baxter's Reef	10	decaying wood with *Limnoria carinata*	Hicks (1988a)
		Wellington Harbour, Queen's Wharf	intertidal	gribble-bored wharf piles	Hicks (1988a)
Xylora longiantennulata	Korea	Kangwondo, Namae Port *	?	decaying wood with *Limnoria* sp. (probably *L. lignorum*)	Kim & Kim (1997)
Xylora sp.	SW of Ireland	Porcupine Seabight (51°24.8–25.9'N, 11°45.9–46.45'W)	880–1,005	sediment and dead *Lophelia pertusa* fragments	Gheerardyn *et al.* (2010)
	Gulf of Mexico	Atwater Valley (27°38.7–38.8'N, 88°21.8–22.4'W)	~2,200 m	vestimentiferan aggregations	Degen *et al.* (2012)

[1] according to Hicks (1988a) not enough detail is provided to determine the accuracy of the identification but Holmes & O'Connor (1990) confirmed its identity; [2] Krishnaswamy & Jones's (1958, 1962) records of *D. limnoriae* from the Solent area were subsequently identified by Hicks (1988a) as *D. anglica*; it not clear whether the records from Ilfracombe and Milford Haven should also be attributed to this species or represent genuine *D. limnoriae*; [3] the host was identified as *Limnoria japonica* but this is almost certainly an error (Kussakin 1963; Kühne 1976); according to Hicks (1988a: 683) Brunel's specimens are clearly not *D. limnoriae*; [4] as *Xylora calyptogenae* Willen, 2006; [5] a second donsiellinid is listed under the name *Donsiella* cf. *bathyalis* but this species does not exist.

Originally described as living upon specimens of *Limnoria lignorum* from Trondheim, Norway (Stephensen 1936), it is now generally accepted that the association between the adults and the isopod host is obligatory. Laboratory experiments conducted on *D. limnoriae* by Pinkster (1968) demonstrated that in the absence of live specimens of *L. tripunctata* adult copepods failed to survive for longer than two days. The adults were only found clinging to the body of the gribble, while the larval stages (nauplii and copepodids) were found both on wood, clinging to *L. lignorum*, and swimming freely in the water. Hicks (1990) suggested that certain aspects of the reproductive cycle (precopulatory clasping, copulation, egg laying, eclosion of nauplii) may be timed to occur within the shelter of the host marsupium. Synchronicity between the life cycles of the isopod host and the copepod symbiont would enhance the success of the copepod nauplii to infect the young manca stages as they emerge from the maternal brood pouch. However, Pinkster's (1968) experiments showed that naupliar stages lived twice as long as adults in the absence of limnoriid hosts, suggesting that they may represent the free-swimming invasion pathway.

A compilation of the reliable records suggest a northwest European distribution from Norway to France (Table 11). More detailed investigation of the fauna of jetty piles and stranded drift-wood will probably show a much more widespread distribution of *D. limnoriae* (Wells 1964). Except for Krishnaswamy & Jones (1962) (repeated by Crothers 1966) who list *L. quadripunctata* as an alternative host, *D. limnoriae* appears to be predominantly associated with *L. limnorum*. A single Mediterranean outlier utilizing *L. tripunctata* has been recorded by Pinkster (1967, 1968). The discovery of the previously unnoticed *D. anglica* in southern England (Hicks 1988a) casts doubt on the validity of other, unillustrated, records of *D. limnoriae* from the British Isles. The record of R.U. Gooding (in Krishnaswamy & Jones 1962; adopted by Carlton 2007) from the Pacific coast of the United States requires confirmation.

OD: Stephensen (1936): 6–10; Figs 2–4.
AD: Lang (1948): 1338, 1445–1446; Abb. 594 (except for dorsal habitus, antennule, antenna and maxilliped of ♀, and P1 of ♂); Table XXIV. Hicks (1988a): 640–645; Figs 1–4.
TL: Norway, Sør-Trøndelag county, near Trondheim; on *Limnoria lignorum* (Rathke, 1799) (Limnoriidae).
BL: 250 µm (♀), 300 µm (♂) [Stephensen 1936]; 270 µm (♀), ♂ somewhat smaller [Hicks 1988a].

Donsiella anglica Hicks, 1988a

Krishnaswamy & Jones (1958) provided a concise redescription of what they assumed to be *D. limnoriae* from the Southampton area. Three females were found on 220 *Limnoria tripunctata* at Cowes, Isle of Wight, and three females and two males from 69 *L. quadripunctata* at Calshot. Their illustrations introduced a number of deviations from Lang's (1948) corrected description of *D. limnoriae*, particularly in the segmentation of the female antennule, and the dimensions and armature of the endopods of legs 2–3 in both sexes. Additional discrepancies were noted in their subsequent, more elaborate, report (Krishnaswamy & Jones 1962). Although many of these differences turned out to be based on observational errors, Hicks' (1988a) re-examination of the Southampton material revealed clear deviations in the armature of the endopods of legs 2–3 in the female and leg 3 in the male, and the number of setae on the exopod of leg 5 in the female. Since such differences cannot be attributed to intraspecific variability, Hicks (1988a) proposed distinct specific status for the material from the Solent area.

According to Krishnaswamy & Jones (1958, 1962) the association between *D. anglica* and their gribble hosts is intimate. Copepods are usually found on the ventral surface of the isopods, especially in the cavities either side of the bases of the legs, formed by the sternites and epimera. When disturbed they move rapidly over the body surface. Attachment to the host is primarily achieved with the prehensile leg 1 endopods

The discovery of a second *Donsiella* species in north-western Europe renders previous records of *D. limnoriae* in Ireland, England and Wales (Krishnaswamy & Jones 1962; Crothers 1966; Wouters & De Grave 1992) potentially doubtful since they contain insufficient information to confirm their authenticity. Hicks (1998a) doubted the accuracy of Holmes & Jeal's (1987) identification of *D. limnoriae* from Dunmore East, Co. Waterford but subsequent re-examination of the material has proven the identification to be correct (Holmes & O'Connor 1990). Holmes' (1996) record from Lough Hyne, Co. Cork confirmed the presence of *D. anglica* in Ireland.

OD: Krishnaswamy & Jones (1958): 1016–1017; Fig. 1 (as *D. limnoriae*).
AD: Krishnaswamy & Jones (1962): 301–303; Figs 1–2 (as *D. limnoriae*). Hicks (1988a): 645–646.
TL: England, Solent area; associated with *Limnoria quadripunctata* Holthuis, 1949a (Limnoriidae). Hicks (1988a) re-examined the two whole mounts deposited by Krishnaswamy & Jones (1958) in the Natural History Museum, London, *i.e.* a female (NHMUK reg. no. 1958.5.14.1) from Southampton and a male (NHMUK reg. no. 1958.5.14.2) from Calshot, which collectively constitute the type series of *D. anglica* (ICZN Art. 72.4.1.1). Since Hicks (1988a) did not designate a holotype both specimens of the type series are automatically syntypes and the type locality encompasses their respective places of origin (ICZN Art. 73.2.3).
BL: 240–280 µm (♀), 250–300 µm (♂) [Krishnaswamy & Jones 1962].

Donsiella bisetosa Hicks, 1988a

Having been recorded from only two localities in New Zealand, *D. bisetosa* already shows a remarkable bathymetric range, from intertidal gribble-bored wharf piles in Wellington Harbour to 144–182 m depth in Cook Strait. It occasionally cohabits with *Xylora bathyalis*, *X. neritica* and *Harrietella simulans* (Hicks 1988a). No variability was recorded. The species is most similar to *D. phycolimnoriae* in the shape of the elongate caudal rami, the presence of an inner seta on the distal endopodal segment of P3 in the female, and two apical setae on the P4 endopod in both sexes.

OD: Hicks (1988a): 650–654; Figs 8–10.
TL: New Zealand, Wellington Harbour, Queen's Wharf; intertidal gribble-bored wharf piles infested by *Limnoria sexcarinata* Kühne, 1975 (Limnoriidae).
BL: 390 ± 20 µm (♀), 380 ± 10 µm (♂).

Donsiella victoriae Hicks, 1988a

The species is known to be associated with at least two limnoriid hosts in intertidal environments in the Australian states of Victoria, New South Wales and Western Australia (Table 11). Hicks (1988a) reported both copepodids and adults clinging to the sternum of their gribble hosts, commonly found cohabiting with *Harrietella simulans*. Considerable variability exists between the females from southeastern Australia, including small variations in the proportions of P2–P3 endopods, the shape of the receptaculum seminis varying between perfectly rounded to egg-shaped, the maxillipedal palmar margin being straight or with slight excavation and the P5 exopod occasionally lacking the inner marginal seta. Males show substantial variability in the relative length of the two setae on leg 4 endopod, and in the spinulation pattern on the second abdominal somite. According to Hicks (1988a) the high degree of morphological variability can be seen as a reflection of the high level of habitat heterogeneity that characterizes the ephemeral and spatially non-continuous substrata used by this species.

Donsiella victoriae is morphologically closest to *D. anglica* but can be differentiated from its Northern Hemisphere counterpart by the shape of the distal unguiform projection on P2 enp-3, the position of the seta on P3 enp-3 and the number of setae on the P4 endopod in the male, and by the number of setae on the P5 exopod in the female.

OD: Hicks (1988a): 646–650; Figs 5–7.
TL: Australia, Victoria, St. Kilda (37°51'S, 144°58'E); on *Limnoria* sp. (Limnoriidae)
BL: 290 ± 20 µm (♀), 330 ± 30 µm (♂).

Donsiella phycolimnoriae Hicks, 1990

This is the only member of the genus described from a seaweed-boring limnoriid. Adults of both sexes were taken from the sternum of *Limnoria stephenseni* Menzies, 1957 collected in tunnels excavated in the holdfasts and stipes of *Durvillaea antarctica* (Chamisso) Hariot, 1892 and *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820 off

Macquarie Island. Large numbers of nauplii along with copepodids and adults (including ovigerous females) were observed in the marsupium of brooding females. Nauplii were distributed throughout the brood pouch, typically in close proximity to the surfaces of developing isopod embryos and prehatchlings. Hicks (1990) also observed adult males and female copepodids adopting a precocious mating posture, the first time this behaviour had been recorded in members of the Donsiellinae. He speculated that the copepod life cycle may to a certain extent be synchronized with the oviposition by the host into the marsupium. Such synchronicity would enable the nauplii to infect the young isopod manca stages as they emerge from the maternal brood pouch. The specimens found in the marsupia did not appear to have damaged the limnoriid eggs, as broken eggs or egg fragments were very rarely found (Cookson 1991).

Donsiella phycolimnoriae can readily be distinguished from its congeners by the spinulose claws on the endopod of leg 1. It is the largest species of the genus (500 µm *vs* ~250–390 µm in other species) and there appears to be a strong congruence between its body size and that of its host, *L. stephenseni*, at about 8.0 mm in length being the largest known limnoriid (Menzies 1957), other gribble species measuring in the region of 3.0–5.0 mm.

Hicks (1990) observed variability in the relative size of leg 4 endopod in both sexes, the conspicuousness of the exopod-baseoendopod articulation in the female leg 5, caudal ramus shape, morphology of the mandibular gnathobase and the lateral spinulation patterns on the urosome of both sexes.

OD: Hicks (1990): 451–455; Figs 1–3.
TL: Australia, Macquarie Island, Handspike Point; from sternum of *Limnoria stephenseni* Menzies, 1957 (Limnoriidae) in holdfasts of the bull kelp *Durvillaea antarctica* (Chamisso) Hariot, 1892 (Phaeophyceae: Durvillaeaceae).
BL: 560–600 µm (♀), 520–550 µm (♂).

Donsiella sp. *sensu* Brunel (1963)

Brunel (1963: 42–44; Fig. 3) reported one female and one male of *D. limnoriae* from *Limnoria japonica* at 57 m depth in the Baie des Chaleurs (48°24'N, 64°16'W) in the Gulf of Saint Lawrence. It is highly conceivable that Brunel (1963) has misidentified both the copepod (*cf.* Hicks 1988a: 683) and the isopod host (*cf.* Kussakin 1963; Kühne 1976). The extreme disparity in body size between both sexes [600 µm (♀), 320 µm (♂)] is unusual for the genus, the female also being twice (!) the size of the European *D. limnoriae*.

The caudal rami shown in Brunel's (1963) illustration of the female urosome are at least 2.5 times as long as wide, as opposed to the nearly squarish shape in *D. limnoriae*. The endopods of legs 2–4 also differ from the typical condition: (a) leg 2 endopod has the shape and setation as illustrated by Krishnaswamy & Jones' (1958) description which refers to *D. anglica* not *D. limnoriae*, (b) leg 3 endopod agrees in shape with that of *D. anglica* but differs in its armature (only one apical seta and no lateral seta on enp-2), and (c) leg 4 endopod is completely absent. The round egg sac is about 200 µm in diameter and contains 17 eggs.

According to Brunel's (1963) text description one of the claws on the distal endopod segment of the male leg 1 is twice shorter and three times wider at its base than the other claw. In addition, the male caudal rami are much shorter than in the female and more or less correspond to the condition observed in European *D. limnoriae*. Such sexual dimorphism has as yet not been observed in other donsiellinids and casts doubt on the alleged conspecificity of Brunel's specimens. The author also claimed that the endopods of legs 1–3 in the male are much longer (relative to the exopod) than in the female or the European specimens of *D. limnoriae*. Neither the vestigial P4 endopod nor leg 6 could be discerned in the male, leading Brunel to suggest that the male was immature. Brunel *et al.* (1998) listed *Donsiella* sp. as an associate of *Limnoria borealis* in their checklist of marine invertebrates of the Saint Lawrence River estuary but it is unclear whether this record refers to Brunel's (1963) report.

Apodonsiella Hicks, 1988a

Apodonsiella indica Hicks, 1988a

The species is known from a single male collected along with *Paralimnoria andrewsi* (Calman, 1910) from the Cocos Islands.

OD: Hicks (1988a): 659–662; Figs 15–16 (♂ only).
TL: Indian Ocean, Australia, Territory of the Cocos (Keeling) Islands, Onfara (12°10'S, 96°55'E); on *Paralimnoria andrewsi* (Calman, 1910) (Limnoriidae).
BL: 270 µm (♂).

Oligoxylora Hicks, 1988a

Oligoxylora cooksoni Hicks, 1988a

This species is known from a single adult female collected along with *Limnoria quadripunctata* in Victoria.

OD: Hicks (1988a): 675–678; Figs 25–26 (♀ only).
TL: Australia, Victoria, Lorne (38°32'S, 143°58'E); on *Limnoria quadripunctata* Holthuis, 1949a (Limnoriidae).
BL: 310 µm (♀).

Pseudonsiella Hicks, 1988a

The genus contains two shallow-water species from the western Pacific, both of which were found in decaying wood infested by *Limnoria* species. They can be differentiated by the key below.

Key to species of *Pseudonsiella* Hicks, 1988a

1. Caudal ramus about 1.1. times as long as basal (maximum) width; second segment of antennary exopod with four elements; P5 exopod ♀ with three setae; subapical seta on P3 enp-3 ♂ more than twice length of supporting segment .... *P. aotearoa* Hicks, 1988a.
Caudal ramus twice as long as basal (maximum) width; second segment of antennary exopod with three elements; P5 exopod ♀ with four setae; subapical seta on P3 enp-3 ♂ vestigial, shorter than length of supporting segment...*P. longicaudata* Kim & Kim, 1997.

Pseudonsiella aotearoa Hicks, 1988a

The species is so far endemic to New Zealand, having been recorded from two localities on the South Island and one locality on the North Island (Table 11) where it occurs in intertidal gribble-bored wharf-piles or 10 m deep submerged decaying wood. It appears to be associated with *Limnoria carinata* and is sometimes found to co-exist with *Harrietella simulans*. Hicks (1988a) observed variability in the strength of the ventrolateral spinules on the abdominal somites between specimens from either end of their known range (Dunedin, Wellington). He also expressed doubts about the number of segments in the mandibular endopod, stating that in certain orientations there appears to be "… a distinct yet diminutive terminal segment from which arises the three or four apical setae". It is likely that the second segment represents the confluent bases of the apical armature segments rather than a true segment. A similar condition has been reported in members of the Paramesochridae (Huys & Boxshall 1991: 117).

OD: Hicks (1988a): 654–659; Figs 11–14.
TL: New Zealand, Wellington Harbour, Queen's Wharf; intertidal gribble-bored wharf piles.
BL: 310 ± 20 µm (♀), 290 ± 20 µm (♂).

Pseudonsiella longicaudata Kim & Kim, 1997

Except for the differentiating characters outlined in the key above, *P. longicaudata* can also be distinguished from the type species by the shape of the female antennulary segments 2–4 which are comparatively longer, and by the presence of four setae on the mandibular basis instead of three in *P. aotearoa*. The latter character is potentially unreliable because of the basal juxtaposition of the innermost and adjacent setae in donsiellinids. Hicks (1988a) admitted difficulties in discerning the exact number of basal setae in some specimens of *Donsiella victoriae* and *Apodonsiella indica*, hence it is possible that the 3-setae condition in *P. aotearoa* is based on an observational error. According to Kim & Kim (1997) the antennary and mandibular exopod can display variability, being either 2-segmented (typical condition) or 1-segmented. The species co-exists with *Xylora longiantennulata* in the same gribble-bored wood fragments. Although the limnoriid host was not specified it is likely to be *Limnoria lignorum* whose presence in Korea was confirmed by Kühne (1976). The single egg sac contains nine eggs.

OD: Kim & Kim (1997): 1–6, 8; Figs 1–4 [reproduced in Lee *et al.* (2012): 252–255; Figs 177–178].
TL: Korea, East Sea (Sea of Japan), Kangwondo; Namae Port (37°45'N, 123°35'E); washings of decaying wood infested by *Limnoria* sp. (probably *L. lignorum* (Rathke, 1799)) (Limnoriidae).
BL: 630 µm (♀), 570 µm (♂).

Xylora Hicks, 1988a

The genus currently accommodates three valid species, of which *X. bathyalis* Hicks, 1988a appears to be ecologically and bathymetrically largely separated from its two congeners, *X. neritica* Hicks, 1988a and *X. longiantennulata* Kim & Kim, 1997, and in fact all other members of the Donsiellinae. Other, as yet undescribed, species are known to exist in deeper waters. For example, Gheerardyn *et al.* (2010) recorded an unidentified *Xylora* species in sediment samples and among dead *Lophelia pertusa* fragments at 880–1,005 m depth in the Porcupine Seabight (51°24.8–25.9'N, 11°45.9–46.45'W) southwest off Ireland.

Willen (2006) described a fourth species, *X. calyptogenae*, based on female specimens collected at 1,446 m depth from the Edison Seamount, a hydrothermally active submarine volcano south of Lihir Island, Papua New Guinea. The species was considered morphologically distinct from the closely related *X. bathyalis* based on the following discrepancies with Hicks' (1988a) original description: (1) lateral seta of mandibular exopod modified in *X. calyptogenae* but not so in *X. bathyalis*; (2) maxillulary endopod well developed and distinct *vs* "rudimentary", represented by short spinulose outer seta; (3) small seta on maxillipedal endopod present *vs* absent; (4) inner setae of P enp-1 serrate *vs* not serrate; (5) inner setae on P2–P3 enp-2 strongly serrate *vs* not serrate; (5) female genital field of different shape; (6) female P6 with three *vs* two setae; and (7) female P5 with hyaline field at inner margin *vs* without hyaline field. In the absence of a proper specimen-based comparative analysis such differences are subtle at best and of little or no significance in establishing new species. Re-examination of *X. bathyalis* material from the "White Lady" site west of Fiji revealed that Hicks' (1988a) illustrations contained slight observational errors with regard to the characters listed above. Willen's (2006) specimens showed complete congruence with the Fiji material in the morphology of the P5, the spinular patterns on the urosome and the armature of P2 endopod (the vestigial middle seta on enp-3 was overlooked by Hicks). Since there is no justification for maintaining *X. calyptogenae* as a distinct species it is here formally relegated as a junior subjective synonym of *X. bathyalis* and excluded from the key below. Note also that Wells' (2007: 695) claim that both *X. bathyalis* and *X. neritica* possess two inner setae on P3 enp-2 in the female is incorrect. Hicks (1988a) clearly showed only one inner seta in *X. neritica* (as indicated by his setal formula on p. 671 and his Fig. 23c) while his report of a short "spinule-like" proximal seta in *X. bathyalis* is incorrect; in reality this element represents a strong spinule as illustrated in Willen's (2006: Fig. 6B) description of *X. calyptogenae* and explains why it is occasionally absent in *X. bathyalis* (see Hicks 1998a: Variability, p. 668).

Key to species of *Xylora* Hicks, 1988a

1. Inner seta of P1 enp-1 originating in distal half of segment; ventral posterior margins of abdominal somites with spinular rows; P6 ♂ with two setae; caudal ramus about as long as proximal (maximum) width . . . . *X. bathyalis* Hicks, 1988a.
Inner seta of P1 enp-1 originating in proximal third of segment; ventral posterior margins of abdominal somites without spinular rows; P6 ♂ with one seta; caudal ramus longer than proximal (maximum) width . . . . 2.
2. P5 endopodal lobe ♀ with three setae; P5 ♂ with total of four setae (including outer basal seta); apex of P2 enp-3 ♂ unidentate; caudal ramus 1.2 times as long as proximal (maximum) width . . . . *X. neritica* Hicks, 1988a.

P5 endopodal lobe ♀ with four setae; P5 ♂ with total of five setae (including outer basal seta); apex of P2 enp-3 ♂ bifurcate; caudal ramus 1.8 times as long as proximal (maximum) width . . . . *X. longiantennulata* Kim & Kim, 1997.

Xylora bathyalis Hicks, 1988a

This species appears to be reasonably common and abundant in harpacticoid copepod communities inhabiting deepwater wood substrata down to 1,514 m around New Zealand and is almost invariably found in situations where recoverable specimens of limnoriids are few (Hicks 1988a). This might suggest that *X. bathyalis* utilizes a habitat previously prepared in shallower water by wood-boring crustaceans and molluscs, which ultimately becomes available to them in deeper water, supporting Coull & Lindgren's (1969) claim that microhabitat (at least for this species) is the primary determining factor for habitation rather than dependence on the wood-borers themselves. However, *X. bathyalis* has since been found in slurp gun samples at 2,765 m depth on the North Fiji Ridge (Huys & Lee 2000), in sediments of a hydrothermally active submarine volcano at 1,446 m depth in the New Ireland Fore-Arc system (Willen 2006) and in aggregations of *Riftia pachyptila* Jones, 1981 and *Bathymodiolus* spp. at around 2,500 m depth in two vent fields of the East Pacific Rise (Gollner *et al.* 2006, 2007, 2010; Degen 2010), showing that it can survive in the absence of water-logged wood. Cuvelier *et al.* (2014) reported *Xylora* cf. *bathyalis* on wood and slate panels deployed around the Eiffel Tower edifice (Lucky Strike vent field) on the Mid-Atlantic Ridge at 1,689–1,697 m depth.

Xylora bathyalis shows an impressive bathymetric range (144–2,765 m) which appears to exceed by far the known depth range of wood-boring limnoriids. The deepest occurring limnoriid species appear to be those boring into water-logged wood at 1,514 m in the lower Kaikoura Canyon (42°38.3'S, 173°46.4'E) (Hicks 1988a; Cookson 1991). In shallower depths *X. bathyalis* has been found to cohabit with *X. neritica*, *Donsiella bisetosa* and *Harrietella simulans* in decaying wood infested by *Limnoria sexcarinata*.

The wood-associated *X. bathyalis* populations in New Zealand waters showed considerable morphological variability which is to be expected in a species displaying a wide bathymetric range and distribution, living as it does on isolated wood "habitat islands" (Hicks 1988a). Variability was recorded in (1) body size of both sexes, within and between populations; (2) form of mandibular gnathobase and segmentation of exopod; (3) extent of medial spinule rows on ventral surface of female urosome; (4) relative proportions of terminal claws on enp-2 and robustness of enp-1 of leg 1; (5) shape of female P5 baseoendopod, and extent of spinules and position of setae; (6) shape of female P5 exopod and degree of expression of suture between exopod and baseoendopod; (7) nature of the bifurcation on male P2 enp-3; and (8) relative proportions of the male P6 setae.

OD: Hicks (1988a): 662–668; Figs 17–20.
AD: Willen (2006—as *X. calyptogenae* Willen, 2006): 258–268, 271; Figs 1–9 (♀).
TL: New Zealand, North Island, off Castlepoint (41°09.9'S, 176°26.5'E); from decaying wood at 1,174–1,208 m depth.
BL: 630 ± 80 µm (♀), slightly smaller (♂) [Hicks 1988a]; 600 µm (♀) [Willen 2006].

Xylora neritica Hicks, 1988a

The species shares with most other donsiellinids the intertidal, shallow-water habitat of wharf pile borings, yet unlike the latter has a bathymetric range which extends to about 150 m. At the deeper end of the range it appears to co-exist with *X. bathyalis*. Other cohabitants frequently encountered with *X. neritica* include *Harrietella simulans*, *Donsiella bisetosa* and *Pseudonsiella aotearoa*. The known limnoriid hosts are *L. carinata* and *L. sexcarinata*.

Hicks (1988a) reported female variability in the relative proportions of the segments 6–7 of the antennule, the width of the maxillipedal basis, the proportions of P1 enp-1 and the claws on enp-2, the stunting and loss in some cases of setae on P3 enp-3 and both basoendopod and exopod of P5, and shape of P5 baseoendopod. Male variability appeared to be restricted to the extent of the spinule rows on the dorsal surface of the first abdominal somite and some "pathological deformities" of the P2 endopod and caudal rami. Hicks (1988a) provided a detailed morphological comparison between *X. bathyalis* and *X. neritica* in his Table 1.

OD: Hicks (1988a): 668–674; Figs 21–24.
TL: New Zealand, South Island, Dunedin City, Portobello; from decaying wharf pile.
BL: 530 ± 30 µm (♀), slightly smaller (♂).

Xylora longiantennulata Kim & Kim, 1997

Kim & Kim (1997) identified two different size classes among females, type 1 with a long abdomen, being 1.76 times as long as wide, and type 2 with a shorter abdomen, being only 1.45 times as long as wide. The species co-exists with *Pseudonsiella longicaudata* in the same gribble-bored wood fragments. The *Limnoria* host was not identified but probably belongs to *L. lignorum*. The single egg sac contains 8–15 eggs. The species differs from its congeners by the elongate segments 2–4 in the female antennule, a remarkable convergence shared with the co-associated *P. longicaudata*.

OD: Kim & Kim (1997): 5, 8–12; Figs 5–8 [reproduced in Lee *et al.* (2012): 256–258; Figs 179–180].
TL: Korea, East Sea (Sea of Japan), Kangwondo; Namae Port (37°45'N, 123°35'E); washings of decaying wood infested by *Limnoria* sp. (probably *L. lignorum* (Rathke, 1799)) (Limnoriidae).
BL: 750–820 µm (♀), 640–710 µm (♂).

Family Tachidiidae

This small family is predominantly benthic with four of the six genera being typically found in mud or fine muddy sands in shallow, marine and oligohaline waters. The sole species of *Cithadius* Bowman, 1972 is an external associate of an anthurid isopod in North America.

Key to genera of Tachidiidae Boeck, 1865

1.	P1 rami 2-segmented; planktonic	*Euterpina* Norman, 1903.
	P1 rami 3-segmented	2.
2.	P4 rami 2-segmented; distal exopod segment of P4 (exp-2) with four elements; P2 endopod not sexually dimorphic; associated with isopods	*Cithadius* Bowman, 1972.
	P4 rami 3-segmented; distal exopod segment of P4 (exp-3) with five elements [1]; P2 endopod sexually dimorphic; free-living	3.
3.	P1 exp-3 with five elements; P2 enp-2 with inner spinous apophysis in ♂	4.
	P1 exp-3 with six elements; P2 enp-2 without inner spinous apophysis in ♂	6.
4.	P1 enp-3 with four elements; P5 with seven elements in ♀ and five elements in ♂	*Neotachidius* Shen & Tai, 1963.
	P1 enp-3 with five elements; P5 with nine elements in ♀ and six or seven elements in ♂	5.
5.	P2 enp-2 ♂ with straight, distally directed spinous apophysis overlapping deep notch of elongate enp-3; P5 ♂ with seven elements	*Tachidius* Lilljeborg, 1853.
	P2 enp-2 ♂ with inwardly directed spinous apophysis, enp-3 short, without lateral notch; P5 ♂ with six elements	*Sinotachidius* Huys, Ohtsuka, Conroy-Dalton & Kikuchi, 2005.
6.	Female with genital double-somite; antennule ♀ robust and short, at most 6-segmented; P2–P4 exp-1 a small segment without inner seta [2]; P5 ♀ a small plate, either free or incorporated in the somite, with 4–5 setae; lateral integumental windows on P5-bearing somite absent	*Microarthridion* Lang, 1944.
	Female with separate genital and first abdominal somites; antennule ♀ slender and moderately elongate, 9-segmented; P2–P4 exp-1 of normal size and with inner seta; P5 ♀ a well developed bilobate plate with nine elements; lateral integumental windows on P5-bearing somite present	*Geeopsis* Huys, 1996 in Huys *et al.* (1996).

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[1] Wells (2007) scored six setae for *Sinotachidius vicinospinalis* Shen & Tai, 1964. Huys *et al.* (2005) claimed that Shen & Tai (1964) had illustrated either the P2 or the P3 and that the P4 has the common formula [1.1.122] for the exopod and [1.1.221] for the endopod; this interpretation appears to be confirmed by Tai & Song (1979), who labelled the P2 correctly and provided an illustration of the real P4.

[2] Note that Wells (2007) erroneously coded this seta as absent for legs 2–3 in *Cithadius*.

Cithadius Bowman, 1972

Cithadius cyathurae Bowman, 1972

Live observations indicate that the natural habitat of *Cithadius cyathurae* is the body surface of the cymothoidan estuarine isopod *Cyathura polita* (Stimpson, 1856) with a preference for the telson and the articulations between the segments of the posterior pereopods (Bowman 1972). The ectosymbionts also move easily over other parts of the body, including the ventral surface of the pereon, and do not seem to affect the host. Burbanck & Burbanck (1979) identified *C. cyathurae* on specimens of *C. polita* from Massachusetts and Georgia. Populations of *C. polita* are found along the Atlantic coast of North America from Saint John River, New Brunswick, Canada to Pointe au Chien in Lake Pontchartrain, Louisiana. It has been suggested that the distribution of *C. cyathurae* coincides with that of its anthurid host (Bowman 1972; Burbanck & Burbanck 1979). The reduced leg 4 with 2-segmented rami (progenesis), the apparent absence of sexual dimorphism in legs 2 and 5 (progenesis) and the separate genital and first abdominal somites in the female (postdisplacement) collectively suggest a paedomorphic development.

OD: Bowman (1972): 250–253; Figs 1–23.
TL: U.S.A., Maryland, Rhode River estuary, Fox Creek near Smithsonian Environmental Research Center (formerly Chesapeake Bay Center for Environmental Studies); on body surface of *Cyathura polita* (Stimpson, 1856) (Anthuridae).
BL: 540–580 µm (♀), 480–500 µm (♂).

(iii) Crayfish hosts

Various copepods are well-known symbionts associated with freshwater crayfish of the families Astacidae and Cambaridae (Alderman & Polglase 1988; Edgerton *et al.* 2002; Huys *et al.* 2014). They are common in Europe and eastern North America but there have been no reports of copepod infestations of crayfish hosts in western North America, eastern Asia, Australia and Madagascar. Two species of the family Canthocamptidae are associated with cambarid hosts in eastern North America and two species (and two subspecies) of the family Ameiridae have been recorded as symbionts of astacid hosts in western Eurasia (Table 12). Unidentified harpacticoids were recorded from the carapace of the invasive spiny-cheek crayfish, *Orconectes limosus* (Rafinesque, 1817) in various localities in the Czech Republic (Ďuriš *et al.* 2006). Reid *et al.* (2006) reported harpacticoids associated with the burrows of the South American *Parastacus defossus* Faxon, 1898 (Parastacidae) in Brazil (see below—pholeteros). The possible use of crayfish tunnels as refuges may have led to the development of various degrees of commensalism between certain harpacticoid species and crayfish (Reid 2001).

Family Ameiridae

Nitocra Boeck, 1865

Nitocra hibernica (Brady, 1880)

This species is found in coastal and estuarine waters throughout the Arctic and Atlantic coasts of Europe, the Baltic and Ponto-Caspian basins, as well as in fresh water and brackish inland waters across Europe, including the British Isles (*e.g.* Brady 1880; Gurney 1932). Its distribution also encompasses central Asia and the Caucasus (Defaye & Dussart 2011). The species was first recorded in North America in 1973, where it appeared to be introduced into Lake Ontario with ballast water from Europe (Hudson *et al.* 1998). Since then, it has become one of the most commonly collected nearshore harpacticoids in the Great Lakes. Although *N. hibernica* is generally considered a free-living species, it has been recorded from crayfish hosts on a number of occasions, illustrating the development of various degrees of commensalism between harpacticoids and freshwater decapod hosts.

TABLE 12. Ameiridae associated with crayfish hosts.

Ameirid (sub)species	Crayfish host	Country	Locality	Reference
Nitocra divaricata divaricata	*Astacus astacus*	Bulgaria	Byala reka River, Kalofer	Bassamakov (1973) [1]
			Stryama River, Stoletovo/Karlovsko	Bassamakov (1973) [1]
			Kolarov River, Rakovo	Bassamakov (1973) [1]
			western provinces	Subchev & Stanimirova (1998) [1]
		Czech Republic	Lučina River, Šenov/Domaslavice	Straškraba (1956) [1]
			Morávka River, Raškovice	Straškraba (1956) [1]
			Olomouc Region, Domašov nad Bystřicí/Bělkovice-Lašt'any	Štěrba (1964) [1]
			South Moravian Region, Luleč/ Kořenec	Štěrba (1964) [1]
		Kosovo	(Kosovska) Mitrovica	Kiefer (1938) [2]
		Poland	Poznań region	Jakubisiak (1939) [1,3]
		Romania	Hunedoara county, Paroş Cave	Chappuis (1926) [3]
			County Cluj, Someşul Mic River	Chappuis (1926) [3]
			Someş and Mureş Rivers	Chappuis (1927) [2]
		Slovakia	Banská Bystrica Region, Nová Baňa	Štěrba (1964) [1]
			Trenčín Region, Kostolné	Štěrba (1964) [1]
	Astacus leptodactylus	Belarus	Pińsk, Lake Zawiszczowskie	Jakubisiak (1939) [1]
		Bulgaria	Veleka River	Subchev & Stanimirova (1998) [1]
		Russia	Saratov Oblast, Saratov	Borutzky (1931) [4]
			Volgograd Oblast, Krasnoarmeisk	Borutzky (1931) [4]
		Ukraine	Bug River	Boshko (1975)
			Sula River	Boshko *et al.* (1977) [1]
			Uday River	Boshko (1978) [1,5]
	Astacus sp.	Bulgaria	Ablanitsa/Chepinska Rivers	Subchev & Stanimirova (1998) [1]
			Belasica Mountain range	Subchev & Stanimirova (1998) [1]
			Danube River	Subchev & Stanimirova (1998) [1]

......*continued on the next page*

TABLE 12. (Continued)

Ameirid (sub)species	Crayfish host	Country	Locality	Reference
	Austropotamobius torrentium	Austria	Vienna and vicinity	Defaye (1996)
		Bulgaria	eastern and central provinces	Subchev & Stanimirova (1998) [1,6]
		Germany	Hesse, Odenwald	Defaye (1996)
	host unknown [7]	Romania	Hunedoara county, Paroş Cave	Chappuis (1923), Pleşa (1969)
			Mureş-Voşlăbeni River	Damian-Georgescu (1970) [8]
	free-living	Czech Republic	South Moravian Region, Drahanská vrchovina	Štěrba (1954, 1964) [1]
	free-living	Slovenia	Cape Piran	Marinov & Apostolov (1981) [9]
Nitocra divaricata caspica	*Astacus leptodactylus caspicus*	Turkmenistan	Caspian Sea, Krassnowodsk	Behning (1936)
Nitocra hibernica	*Astacus astacus*	Bulgaria	Kolarov River	Bassamakov (1973) [1]
		Germany	Schleswig-Holstein, Dieksee and Schöhsee	Chappuis (1926) [3]
		Poland	lakes around Wągrowiec	Jakubisiak (1939) [3,10]
	Astacus leptodactylus	Bulgaria	Lake Shabla	Bassamakov (1975) [1]
		England	London, Serpentine and Long Water	Huys *et al.* (2014)
	Pacifastacus leniusculus	England	London, Serpentine and Long Water	Huys *et al.* (2014)
Nitocra sp.	*Astacus leptodactylus*	Ukraine	Dnieper River, Kakhovka	Koval' *et al.* (1975)
Nitocrella sp.	*Astacus leptodactylus*	Ukraine	Sluch River	Boshko (1976)
Unidentified harpacticoids	*Orconectes limosus*	Czech Republic	not specified	Ďuriš *et al.* (2006)

[1] as *Nitocrella divaricata* (Chappuis, 1923); [2] host cited as *Potamobius astacus* Linnaeus, 1758; [3] host cited as *Astacus fluviatilis* J.C. Fabricius, 1775; [4] host cited as *Potamobius leptodactylus* (Eschscholtz, 1823); [5] host cited as *Astacus (Pontastacus) leptodactylus* Eschscholtz, 1823; [6] host cited as *Astacus torrentium* (Schrank, 1803); [7] inside a jar labelled "*Pomatobius* sp."; probably referring to *Astacus astacus*; [8] this record is confusing since the author refers to it as Mureş-Voşlăbeni in Hunedoara county; although the River Mureş flows through this county, its tributary, the River Voşlăbeni is located far upstream near its source in Harghita county; [9] doubtful record from subtidal marine locality; [10] as *Nitocrella hibernica* (Brady, 1880).

Chappuis (1926) recorded a few specimens of *N. hibernica* from the gills of the noble crayfish, *Astacus astacus* (Linnaeus, 1758) (as *A. fluviatilis* J.C. Fabricius, 1775), in two lakes (Dieksee and Schöhsee) in northern Germany. Jakubisiak (1939) also found specimens of *N. hibernica* in *A. astacus* which he had collected from the ponds around Wągrowiec in north-western Poland. Bassamakov (1973) recorded a single female from the carapace of a noble crayfish collected in the Kolarov River in Bulgaria, and, in a subsequent paper (Bassamakov 1975), recorded its presence also on the body of the Turkish crayfish, *Astacus leptodactylus* Eschscholtz, 1823, in Lake Shabla in north-eastern Bulgaria.

Huys *et al.* (2014) reported a high prevalence of *N. hibernica* in the branchial cavities of *A. leptodactylus* in 2008 in the Serpentine and Long Water Lakes, Hyde Park, London. *Nitocra hibernica* was also found on the gills of three specimens of the invasive signal crayfish, *Pacifastacus leniusculus* (Dana, 1852a), collected in the Serpentine in August 2010, while it was not observed in the much larger sample of signal crayfish from Cripsey Brook in 2008. According to Huys *et al.* (2014) such discrepancy in prevalence may suggest that *N. hibernica* switched crayfish hosts in the Serpentine and Long Water Lakes following the decimation of the Turkish crayfish population. This is the first record of an indigenous copepod becoming associated with a non-indigenous crayfish host, a case of unusual host switching having previously been reported only for branchiobdellidans (Gelder *et al.* 1999). *Nitocra hibernica* was often found to co-occur with *Acanthocyclops* sp. in the gill chamber of *A. leptodactylus* in the Serpentine and Long Water Lakes, Hyde Park, London (Huys *et al.* 2014). Similar incidences of Cyclopidae in the gill chambers of crayfish have been reported by Kiefer (1927), Defaye (1996) and Nekuie Fard *et al.* (2011).

Noodt (1954b) observed variability in the spinulation pattern of the abdominal somites and the proportional lengths of the endopodal segments of leg 1.

OD: Brady (1880—as *Canthocamptus hibernicus*): 52–53, Plate XLVI (Figs 1–12).

AD: Herrick (1884—as *C. hibernicus*): 172–173; Plate K, Figs 3–4. Herrick & Turner (1895—as *C. hibernicus*): 134; Plate L, Figs 3–4. Richard (1893—as *C. hibernicus incertus* Richard, 1893): 440–443; Figs 16–22. Schmeil (1893): 78–84; Plate VII, Figs 1–16. Lilljeborg (1902—as *C. hibernicus*): 57–61; Plate IV, figs 6–9. Douwe (1909): 56–56; Figs 235–240. Haberbosch (1917): 596; Fig. 1. Donner (1928): 255, 299; Fig. 25. Jakubisiak (1931): 45–46 (and as *N. hibernica* var. *hyalina* Jakubisiak, 1931: 46; Plate I, Fig. 7). Gurney (1932): 72–79; Figs 496–515. Pesta (1932—as *Nitocra inuber* (Shmankevich, 1875)): 74–76; Fig. 4. Noodt (1954b): 29–30, 32; Tafel I (Figs 1–5). Damian-Georgescu (1960—as *Nitocrella hibernica* (Brady, 1880): 387–389; Figs 4–5. Dussart (1967): 206–209; Figs 76–77. Damian-Georgescu (1970—as *Nitocrella hibernica*): 17–19, 21, 68–71; Figs 6a, 7b, 8a–b, 9d, 23, 24. Apostolov (1973c—as *Nitocrella hibernica*): 293; Fig. 10. Bassamakov (1973—as *Nitocrella hibernica*): 52; Fig. 1. Bassamakov (1976): 69–70; Figs 1–2. Apostolov & Marinov (1988): 226–228; Fig. 88-3. Janetzky *et al.* (1996): 48–50; Abb. 14.

TL: Ireland. Brady (1880) based his description on specimens from the Mullingar Canal in Dublin and a lake near Newport (Co. Mayo) but did not specify a type locality.

BL: 650 µm (♀) [Brady 1880]; 560 µm (♀), 470 µm (♂) [Richard 1893]; 600–700 µm (♀), 500 µm (♂) [Schmeil 1893; Douwe, 1909; Pesta 1932]; 660–820 µm (♀), 580–660 µm (♂) [Lilljeborg 1902]; 600–700 µm (♀), 480 µm (♂) (variety *hyalina*: 410–430 µm (♀/♂)) [Jakubisiak 1931]; 670–720 µm (♀), 510–600 µm (♂) [Gurney 1932]; 620–730 µm (♀) [Noodt 1954b]; 560–750 µm (♀), 510–600 µm (♂) [Dussart 1967; Apostolov & Marinov 1988; Janetzky *et al.* 1996]; 600–650 µm (♀) [Damian-Georgescu 1970].

Nitocra divaricata divaricata Chappuis, 1923

In *Nitocra divaricata*, dependence on the hosts has become more obligatory; however, there appears to be some circumstantial evidence that the species can also survive outside the crayfish host (Štěrba 1954, 1964). The species was originally described from two females found in the residue inside a jar containing a preserved "*Potamobius* spec." specimen, collected on a stalagmite in Paros Cave, Transylvania, Romania. Chappuis (1923) initially considered the association with the decapod host accidental but revised his opinion upon the subsequent discovery of additional material from the gill cavity of the noble crayfish, *Astacus astacus* (as *A. fluviatilis*) collected in the same cave and in the River Someş near Cluj (Chappuis 1926). Contrary to Defaye's (1996) claim that Chappuis (1926) based the description of the male on specimens from Germany it was the Romanian material that was used for that purpose and probably also for Gurney's (1930b) supplementary description of the female. According to Chappuis (1926) adults and copepodid stages are not restricted to the gill chamber but also occur in large numbers on the carapace of the host. In contrast to Behning's (1936) observations on *N. divaricata caspica* (see below) only very few nauplii were encountered in or on the crayfish host, leading Chappuis to suggest that dispersal takes place primarily during the naupliar phase.

Borutzky (1931) cited Russian records by Arvid Behning (*in litt.*) from the Turkish crayfish, *Astacus leptodactylus*, collected in two localities in the southern Volga region, *i.e.* in the port of Saratov and in Sarepta (now Krasnoarmeysky Rayon, a district of Volgograd). Kiefer (1938) obtained it from a jar containing preserved *A. astacus* (as *Potamobius astacus* Linnaeus, 1758) collected in (Kos) Mitrovica in northern Kosovo.

Jakubisiak (1939) recorded all developmental stages of *N. divaricata* in *A. leptodactylus* from Lake Zawiszczowskie near Pińsk in Belarus. Specimens of *A. astacus* purchased at a market in the city of Poznań (and probably collected in nearby ponds) also contained (exclusively female) *N. divaricata*, leading Jakubusiak (1939) to suggest that the commensal copepod was probably not a rarity in the lakes, ponds and canals in western Poland. *Astacus leptodactylus* is indigeneous to the Ponto-Caspian region but was deliberately introduced into fourteen European countries, *e.g.* Poland, Italy, Germany, England, Spain and France, where it escaped into the wild and established large populations in a number of localities (Skurdal & Taugbol 2001). Jakubisiak (1939) argued that *N. divaricata* was introduced in Poland together with Turkish crayfish and subsequently switched hosts to the native *A. astacus*.

Straškraba (1956) reported the species from *A. astacus* in two rivers in the north-eastern Moravian-Silesian region of the Czech Republic. According to Štěrba (1969) the species occurs in three of the four zoogeographical regions of former Czechoslovakia. Štěrba (1954, 1964) recorded a single free-living male from a subterranean stream in the Moravian Karst (Moravský kras) to the north of Brno in the eastern part of the Czech Republic but later assumed that it had accidentaly been washed out of the gill cavity of its host (Štěrba 1965). His male differed from typical *N. divaricata* by the longer caudal rami and the shorter endopod of leg 1. The first records from Bulgaria are those by Bassamakov (1973) who recorded *N. divaricata* from the carapace of *A. astacus* in three rivers. Subchev & Stanimirova's (1998) extensive survey showed that the species is widely distributed throughout the central and western provinces of Bulgaria and utilizes three or possibly four crayfish hosts (*A. astacus*, *A. leptodactylus*, *A.* sp. and the stone crayfish *Austropotamobius torrentium* (Schrank, 1803)). It appears to be most commonly associated with *A. astacus* and *P. torrentium* up to an altitude of 1,600 m. *Nitocra divaricata* also seems to be common in the rivers of the Ukraine (Boshko 1975, 1978; Boshko *et al.* 1977) where it utilizes *A. leptodactylus* as host. The Ukrainian records of *Nitocra* sp. (Koval' *et al.* 1975) and *Nitocrella* sp. (Boshko 1976) from the same crayfish host almost certainly refer to *N. divaricata*. Subchev *et al.* (2007) examined *A. astacus*, *A. leptodactylus* and *A. torrentium* from several localities in Greece but did not find any *N. divaricata* in the gill chamber. Their absence may be related to the presence of branchiobdellids which are known to prey on other epibionts, including copepods that live on the crayfish gills (Wierzbicka & Śmietana 1999). Defaye (1996) added the first records from Austria and Germany, redescribed the species in detail and observed slight variability in the number of spinules on the anal operculum and in the relative length of the caudal setae.

Marinov & Apostolov (1981) collected two females from a muddy substratum at 15 m depth near the Cape of Piran in south-western Slovenia. The shape of the P5 exopod and relative lengths of its setae indicate that this marine record does not refer to *N. divaricata* but to another member of the Ameiridae. Apostolov & Marinov's (1988: 230) illustrations of *N. divaricata* represent an amalgam of two species; the P5 (their Fig. 90-1c) was taken from Marinov & Apostolov's (1981) Piran material while the caudal rami and P4 exp-3 were reproduced from a different source. Pesce (1983) reported a single female from a phreatic habitat near Lecce, Apulia (Italy) which he provisionally identified as *Nitocra* cf. *divaricata*. No illustrations were given but the setal formula of leg 2 (enp-3 with an inner seta) suggests that he was dealing with a different species.

OD: Chappuis (1923): 2–25; Figs 1–3 (♀ only).

AD: Chappuis (1926): 516–520; Figs 1–4. Gurney (1930b): 110–111; Figs 17–20. Borutzky (1931): 76–77; Fig. 20. Jakubisiak (1939—as *Nitocrella divaricata*): 117–118. Straškraba (1956): 593–595; Fig. 2. Borutzky (1964—as *Nitocrella divaricata*): 114–115 (130–131 in original Russian version; published 1952); Fig. 48 (11–13). Štěrba (1964): 271–273; Figs 1–7. Dussart (1967): 214–215; Fig. 80. Damian-Georgescu (1970—as *Nitocrella divaricata*): 71–73; Fig. 25. Janetzky *et al.* (1996): 50–51; Abb. 15. Defaye (1996): 146–153; Figs 1–4).

TL: Romania, Transylvania, Hunedoara County, Pui commune, Paros-Peşter, Peşterea de la Paros; residue in jar containing preserved "*Potamobius* spec." specimen, collected on stalagmite in Paros Cave, at about 150 m from entrance.

BL: 600 µm (♀) [Chappuis 1923; Borutzky 1931; Jakubisiak 1939; Dussart 1967; Damian-Georgescu 1970; Janetzky *et al.* 1996]; ♂ somewhat smaller [Jakubisiak 1939]; 600–800 µm (♀), 500–700 µm (♂) [Štěrba 1964]; less than 600 µm (♂) [Dussart 1967]; 580 µm (♀), 570 µm (♂) [Defaye 1996].

Nitocra divaricata caspica **Behning, 1936**

Behning (1936) provided a concise description based on specimens obtained from the gill chamber of *Astacus leptodactylus caspicus* (as *caspius* [*sic*]) Eichwald, 1838 in the Bay of Krassnowodsk, on the southeastern shore of the Caspian Sea, Turkmenistan. Various varieties and subspecies of *A. leptodactylus*, including *A. l. caspicus*, have been described on the basis of indistinct and variable features but are no longer recognized (Ingle 1997). The Caspian subspecies of *N. divaricata* differs from the nominotypical form in the shorter P5 exopod and the length of some of its setae. Both adults and nauplii occured in large numbers, the latter clinging firmly to the gill filaments. Behning (1936) illustrated the first naupliar stage. No information was given on the possible association of this subspecies with the co-occuring Caspian crayfish, *Astacus pachypus* Rathke, 1837. The subspecies is sometimes erroneously referred to as "*caspia*" (*e.g.* Borutzky 1964: 115).

OD: Behning (1936): 248–249; Figs 3a (♀), 3b (nauplius I).

TL: Turkmenistan, shore of Caspian Sea, vicinity of Krassnowodsk; salinity 13.5–14.2‰; in gill chamber of *Astacus leptodactylus caspicus* Eichwald, 1838 (Astacidae).

BL: unknown.

Family Canthocamptidae

Attheyella **Brady, 1880**

The genus *Attheyella* Brady, 1880 is subdivided in six subgenera (Wells 2007; Huys 2009b; Defaye & Dussart 2011), *i.e. Attheyella* Brady, 1880 (type species: *Canthocamptus crassus* Sars, 1863), *Chappuisiella* Brehm, 1925 (type species: *Canthocamptus crenulatus* Mrázek, 1901), *Delachauxiella* Brehm, 1925 (type species: *Canthocamptus insignis* Delachaux, 1918), *Ryloviella* Borutzky, 1931 (type species: *Attheyella* (*Ryloviella*) *baikalensis* Borutzky, 1931), *Canthosella* Chappuis, 1931 (type species: *Canthocamptus muscicola* Chappuis, 1928) and *Neomrazekiella* Özdikmen & Pesce, 2006 (type species: *Canthocamptus dentatus* Poggenpol, 1874). The subgenus *Ryloviella* was established by Borutzky (1931) to accommodate the new species *A. baikalensis* but ignored by Lang (1948) on the irrelevant and unacceptable basis that the diagnosis was given in Russian (Wells 2007). Borutzky (1952) expanded the subgenus by including two North American crayfish associates, *Attheyella* (*Brehmiella*) *pilosa* Chappuis, 1929 and *A.* (*B.*) *carolinensis* Chappuis, 1932, and Alekseev (1989) added *Attheyella amurensis* Borutzky, 1936, which had previously been assigned to the subgenus *Brehmiella* Chappuis, 1929 (= *Neomrazekiella*). This composition was accepted by Wells (2007) but Defaye & Dussart (2011), for no apparent reason, maintained *A. amurensis* in the subgenus *Neomrazekiella.* The latter course of action is followed here since *A. amurensis* appears to be radically different from the other three species. It has been suggested that this species should be placed in the genus *Canthocamptus* Westwood, 1836 (*cf.* Chang 2001), and differences in the male caudal rami and legs 5 also raise the question whether Alekseev's (1989) material is conspecific with Borutzky's (1936) type population.

Females of the two North American *Attheyella* species can be separated by differences in the caudal rami (L:W ratio, spinular ornamentation), urosomal spinulation pattern, size of the distal endopod segment of leg 1, armature of leg 5 baseoendopod and shape of leg 5 exopod (Bowman *et al.* 1968). Wells (2007) distinguished males on the basis of their fifth legs.

Key to species of *Attheyella* (*Ryloviella*) Borutzky, 1931

FEMALES

1. P5 endopodal lobe with 3–4 setae . . . . *A.* (*R.*) *carolinensis* Chappuis, 1932.
   P5 endopodal lobe with five setae . . . . 2.
2. P5 exopod 2.5 times as as long as wide . . . . *A.* (*R.*) *baikalensis* Borutzky, 1931.
   P5 exopod 1.7 times as as long as wide . . . . *A.* (*R.*) *pilosa* Chappuis, 1929.

MALES

1. P5 exopod with four setae/spines . . . . *A.* (*R.*) *baikalensis* Borutzky, 1931.
   P5 exopod with five setae/spines . . . . 2.
2. Transverse spinule row around posterior margin of urosomites present ventrally and laterally, interrupted dorsally . . . .
   . . . . *A.* (*R.*) *carolinensis* Chappuis, 1932.
   Transverse spinule row around posterior margin of urosomites present ventrally, laterally and dorsally, continuous (circumsomitic) . . . . *A.* (*R.*) *pilosa* Chappuis, 1929.

Attheyella pilosa Chappuis, 1929 and *A. carolinensis* Chappuis, 1932

Hobbs (1952) observed canthocamptid harpacticoids on the exoskeleton of various unspecified crayfishes in the New River system of North Carolina, Virginia, and West Virginia but did not identify them. The first identified record of a canthocamptid associated with crayfish hosts is that by H. Yeatman (in Prins 1964) who found *Attheyella carolinensis* Chappuis, 1932 in a bottle containing specimens of the Teays River crayfish *Cambarus sciotensis* Rhoades, 1944 which had been collected from Sinking Creek, Craig County, Virginia. Although the copepod was originally described as typically free-living (Chappuis 1932; Coker 1934; Wilson 1936b; Carter 1944), its regular association with crayfish hosts was subsequently confirmed by Bowman *et al.* (1968) who added records from West Virginia, Virginia, North Carolina, South Carolina, Georgia and Kentucky.

Prins (1964) reported dense, reddish copepod assemblages from the pleopods, the bases of the coxae of the pereopods, the hairs around the sterna, and various other places on the undersurfaces of the cavespring crayfish, *Cambarus tenebrosus* Hay, 1903, and the rusty crayfish, *Orconectes rusticus rusticus* (Girard, 1852), taken from a spring stream in Doe Run, Meade County, Kentucky. The copepods were intially identified as *A. carolinensis* but proved upon re-examination to belong to the morphologically similar *A. pilosa* Chappuis, 1929 (Bowman *et al.* 1968). Prins (1964) also found *A. carolinensis* on *C. tenebrosus* taken from Hite Creek, Jefferson County, Kentucky, and in the bottom sediments of Morgan's Creek about five miles east of Doe Run, but the authenticity of these records has not been verified. Bowman *et al.* (1968) added new records of *A. pilosa* from Virginia, South Carolina, Georgia, Tennessee, Kentucky, Indiana and Illinois, however, their host information (and for those of *A. carolinensis*) remained remarkably vague. The authors concurred with Prins's (1964, 1968) earlier work by listing *C. tenebrosus* and *O. rusticus rusticus* as hosts of *A. pilosa* but did not cite any additional ones. In the case of *A. carolinensis* only the boxclaw crayfish, *Cambarus distans* Rhoades, 1944, was mentioned as a host in a single locality in south-eastern Kentucky. In one instance where both *Attheyella* species occurred in a single collection (near Cleveland, South Carolina) the associated crayfish species listed were the mitten crayfish *Cambarus asperimanus* Faxon, 1914, and an undescribed *Cambarus* species of the *C. bartonii*-group.

Bowman *et al.* (1968) recognized a predominant east-west separation (except for a few outliers) of the two *Attheyella* species, with a preponderance of *A. pilosa* west of the Appalachians and of *A. carolinensis* in the drainage systems of streams flowing to the Atlantic. *Attheyella pilosa* has since been recorded further west from the eastern part of Oklahoma within the Arkansas River drainage (Hunt & Stanley 2003). Exceptions to the east-west pattern can be explained by migration of crayfish (and their associates) between stream systems, either over land during damp conditions or underground via subterranean connections.

Prins (1964) and Bowman *et al.* (1968) studied the seasonal occurrence of *A. pilosa* on the two co-occurring crayfish species in Doe Run. The incidence of infestation was generally much higher in *C. tenebrosus*, possibly because of their habit of spending more time in burrows in the banks and on the channel bottom where they may be more accessible to the copepods. The host regularly moults throughout the year which might explain why no apparent seasonal variations in the incidence of infestation were recorded. Infestation of *O. rusticus* appears greatest during the coldest months, and least during the midsummer months. The degree of infestation presumably is correlated directly with torpidity and the nearly complete absence of molting activity during the coldest months. Bowman *et al.* (1968) inferred from these observations that the copepods do not return to the host when the old exoskeleton is shed in moulting. Prins (1968) regarded the infestation by *A. pilosa* as indirect evidence for biotope preferences of both crayfish hosts since the copepod was most abundant in silt within beds of vegetation. *Cambarus tenebrosus* usually was more heavily infested than *O. rusticus rusticus*, suggesting it spent more time in vegetation in which *A. pilosa* was more abundant. Conversely, *O. rusticus rusticus* was as heavily infested as *C. tenebrosus* only when it was collected from stands of macrophytes such as *Myriophyllum heterophyllum* Michaux, 1803 but this occurred rarely. Nauplii and copepodid stages appear to be free-living since only adult males and (ovigerous) females were observed on the crayfish hosts (Bowman *et al.* 1968). *Attheyella pilosa* is probably a multivoltine species that breeds during most or all of the year and has a short period between generations.

Attheyella pilosa **Chappuis, 1929**

OD: Chappuis (1929—as *Attheyella* (*Brehmiella*) *pilosa*): 53–54; Figs 5–11.
AD: Bowman *et al.* (1968): 572–577; Figs 1–2, 3a–j.
TL: U.S.A.; Chappuis (1929) based his description on specimens collected in two caves, Mammoth Cave in Kentucky (some ♂♂) and Donnaldson Cave in Indiana (♀♀ and ♂♂), but neither was designated as the type locality. Had the author explicitly fixed a female specimen as the type, the latter cave would consequently have become the type locality.
BL: 750 µm (♀), slightly smaller (♂) [Chappuis 1929]; 530–760 µm (♀), 460–680 µm (♂) [Bowman *et al.* 1968].

Attheyella carolinensis **Chappuis, 1932**

OD: Chappuis (1932—as *Attheyella* (*Brehmiella*) *carolinensis*): 226–229, Abb. 1–10.
AD: Coker (1934): 116–118; Plates 10–11. Bowman *et al.* (1968): 576–579; Fig. 3k–l.
TL: U.S.A., North Carolina, Chapel Hill; spring in Battle Park.
BL: 800 µm (♀), slightly smaller (♂) [Chappuis 1932]; 700 µm (♀), 580 µm (♂) [Coker 1934].

(iv) Lobster hosts

Marine lobsters (family Nephropidae) are hosts to harpacticoids on both sides of the North Atlantic. Two species belonging to different families utilize the American lobster but show a distinct niche segregation on the host. A third species is common on the gills of the European lobster and restricted to the British Isles so far.

Family Miraciidae

Sarsamphiascus **Huys, 2009b**

Huys (2009b) pointed out that *Amphiascus* is a senior objective synonym of *Paramphiascopsis* Lang, 1944 and consequently proposed a new genus *Sarsamphiascus* (type: *Dactylopus minutus* Claus, 1863) to accommodate all species previously placed in *Amphiascus*. Two species in the *varians*-group are associated with crustacean hosts, including *S. ampullifer* (Humes, 1953) which utilizes *Homarus americanus* H. Milne Edwards, 1837.

Key to species of the *Sarsamphiascus varians*-group

1. Caudal ramus similar in both sexes; P4 exp-3 with seven setae/spines; . . . . 2.
   Caudal ramus sexually dimorphic, setae I–II flask-shaped in ♀; P4 exp-3 with six setae/spines . .*S. ampullifer* (Humes, 1953).
2. First segment of antennule with conspicuous spinous projection on posterior distal corner in both sexes . . . .
   . . . . *S. denticornis* (Coull, 1971a).

First segment of antennule without processes in both sexes . . . . 3.

3. Abdominal somites without spinular or setular ornamentation . . . . *S. gauthieri* (Monard, 1936).

At least one abdominal somite ornamented with rows of setules or spinules . . . . 4.

4. Body size large (♀: 1,300 µm; ♂: 1,140 µm); mandibular exopod minute, indistinctly 2-segmented, each segment with one seta; P1 enp-1 3.5 times as long as enp-2 and enp-3 combined; P5 ♀ endopodal lobe extending to distal margin of exopod; P5 ♂ exopod with six elements; associated with Brachyura . . . . *S. elongatus* (Itô, 1972).

Body size much smaller (maximum 600–700 µm); other characters not combined . . . . 5.

5. P1 enp-1 about three times as long as enp-2 and enp-3 combined; small-sized (370 µm); bathyal . . . . *S. profundus* (Becker & Schriever, 1979).

P1 enp-1 at most 2.5 times as long as enp-2 and enp-3 combined; size 450–700 µm; littoral and subtidal . . . . 6.

6. P5 ♀ exopod with five elements; P5 ♂ endopodal lobe with three spines; hyaline frills of abdominal somites deeply incised . . . . *S. varians* (Norman & Scott, 1905).

P5 ♀ exopod with six elements; other characters not combined . . . . 7.

7. Antennary exopod 2-segmented; P5 ♀ endopodal lobe short, not extending beyond proximal quarter of exopod; abdominal ornamentation consisting of short, very dense rows or small groups laterally and dorsolaterally on somites 1–2, and laterally and ventrolaterally on somite 3 . . . . *S. angustipes* (Gurney, 1927).

Antennary exopod 3-segmented; P5 ♀ endopodal lobe longer, extending at least to halfway the exopod; abdominal ornamentation different . . . . 8.

8. Abdominal spinular ornamentation very sparse, represented by small groups dorsolaterally on somite 1 and laterally only (sometimes only 1–2 spinules) on somites 2–4; abdominal hyaline frills plain; P5 ♀ baseoendopod with elliptical hyaline field adjacent to base of exopod; caudal ramus setae IV–V not swollen at base . . . . *S. tenellus* (Sars, 1906c).

These characters not combined . . . . 9.

9. P5 exopod and baseoendopod without hyaline field in both sexes . . . . 10.

P5 exopod and baseoendopod with hyaline field in both sexes . . . . 11.

10. Abdominal somite 2 with ventrolateral spinule row; penultimate somite (abdominal somite 3) without spinular ornamentation; P5 ♀ endopodal lobe extending beyond halfway the exopod length, with conspicuous pore . . . . *S. polaris* (Sars, 1909a).

Abdominal somite 2 without ventrolateral spinule row; penultimate somite (abdominal somite 3) with lateral spinular row; P5 ♀ endopodal lobe not extending beyond halfway the exopod length, without conspicuous pore . . *S. propinquus* (Sars, 1906b).

11. P5 ♀ exopod with large hyaline field near inner margin; P5 ♂ exopodal setae I–II equally long . . . . . *S. lobatus* (Hicks, 1971).

P5 ♀ exopod without large hyaline field near inner margin but with small "lens" between setae V–VI ; P5 ♂ exopodal seta I distinctly shorter than seta II . . . . *S. tainui* (Hicks, 1989).

Sarsamphiascus ampullifer **(Humes, 1953)**

Humes (1953) recovered several hundred specimens of a new species, *Mesamphiascus ampullifer*, from the mouthparts of eight small adult American lobsters (*Homarus americanus*) purchased alive from a lobster market at Portsmouth, New Hampshire. Nauplii, copepodids and adults were found clinging to the setose, flattened inner edges of the proximal endites of the first maxillipeds. The copepods started crawling over the other mouthparts only when disturbed by mechanical probing or intense light. The strong niche preference was confirmed in other lobster specimens from a Boston fish market and a second undisclosed location. The small (about 28 mm^2) area made up by the enditic lobes of the first maxillipeds can sustain high numbers of *M. ampullifer*. Typically, over 100 copepods, including all developmental stages, can be recovered per lobster but the degree of infestation is occasionally much heavier, attaining up to 370 ind.host^{-1} (Humes 1953). The entire life cycle is obviously completed on the host, but laboratory experiments showed that *M. ampullifer* can survive for up to 41 days if separated from its symbiotic partner. Although the species appears to be a common associate of *H. americanus* in the New England area, it has not been recorded elsewhere in the U.S.A. since its original description.

The copepods are colourless, except for the bright red nauplius eye, and appeared to be slightly negatively phototactic (Humes 1953). The paired egg sacs are laterally flattened and extend slightly beyond the middle of the second abdominal somite. Each egg sac usually contains six eggs (occasionally 7–8), each measuring about 50 µm in diameter.

Humes (1953) assigned the species to *Mesamphiascus* Nicholls, 1941 but the heterogeneous nature of the latter genus was severly criticized by Vervoort (1964) who suggested establishing a new genus for the reception of *M. ampullifer* which "… will find its place in the immediate vicinity of *Amphiascus* G.O. Sars, 1905, sensu Lang, from which it is primarily differentiated by the setation of the 3rd exopodal segment of leg 4, having only 2 setae at the internal margin, while 3 occur in *Amphiascus*". Lang (1965) referred *M. ampullifer* to *Amphiascus* with great hesitation, claiming that it appears to be close to the species of the *varians*-group. Hicks (1971, 1989) formally placed it in this species complex despite significant differences in the armature of P4 exp-3 in both sexes, and the morphology of the P1 basis and P2 endopod in the male. Wells (2007) and Huys (2009b) considered the species as *incertae sedis* in the *varians*-group of *Amphiascus* and *Sarsamphiascus* Huys, 2009b, respectively.

OD: Humes (1953—as *Mesamphiascus ampullifer*): 365, 367, 372; Figs 29–63.
TL: U.S.A., New Hampshire, vicinity of Portsmouth harbour; on mouthparts of *Homarus americanus* H. Milne Edwards, 1837 (Nephropidae).
BL: 975–1.081 µm (♀); 870–890 µm (♂).

Family Tisbidae

Sacodiscus Wilson, 1924

The genus currently accommodates five valid, morphologically similar species, however only *Sacodiscus ovalis* (Wilson, 1944) is known to live exclusively in association with lobsters. It should be noted that *S. ovalis* does not key out correctly in Wells' (2007) tabular keys due to a number of erroneously coded characters. According to Humes' (1960) text and illustrations the species has 7:8:8 setae/spines on the distal exopod segment of legs 2–4, respectively, six setae on the distal endopod segment of leg 3, and one inner seta on the middle endopod segment of leg 3. Wells (2007) had coded these states as 6:7:7, 5, and 1, respectively, and introduced additional confusion by coding the second character as 5–6 in *Sacodiscus humesi* Stock, 1960 while the original description does not make mention of such variability and simply states that the condition is as in *S. fasciatus* (Norman, 1869). This implies that all congeners of *Sacodiscus* share the same armature formula on legs 1–4, and—as in the related genera *Tisbe* and *Scutellidium*—can only be discriminated by small morphological or morphometric differences. Since most species are inadequately described any identifications arrived at with the key below must be checked against the best available description.

Key to species of *Sacodiscus* Wilson, 1924

1. Antennary exopod distinctly 2-segmented . . . .*S. humesi* Stock, 1960.
   Antennary exopod 1-segmented or indistinctly 4-segmented showing partial surface sutures . . . . 2.
2. P5 exopod ♀ approximately 1.5 times as long as broad; . . . . 3.
   P5 exopod ♀ at least twice as long as broad . . . . 4.
3. P5 exopod ♀ with relatively straight distal margin; P5 exopod ♂ with five setae; body length 1,220–1,420 µm in ♀, 1,140–1,240 µm in ♂ . . . . *S. ovalis* (Wilson, 1944).
   P5 exopod ♀ with rounded distal margin; P5 exopod ♂ with four setae; body length 740–800 µm in ♀, 600 µm in ♂. . . . . *S. fasciatus* (Norman, 1869).
4. P5 exopod ♀ approximately three times as long as broad . . . . *S. littoralis* (Sars, 1904b).
   P5 exopod ♀ approximately twice as long as broad. . . . . *S. australis* (T. Scott, 1914).

Sacodiscus ovalis (Wilson, 1944)

Wilson (1944) described the new genus and species, *Unicalteutha ovalis*, based on specimens collected from the "outside surface" of American lobsters (*Homarus americanus*) in Placentia Bay, Newfoundland. Templeton & Tibbo (1945) subsequently reported it from lobsters in other regions of Newfoundland, including Notre Dame Bay and St. Mary's Bay. Copepods were found to be present on each of over 600 lobsters examined and as a rule were restricted to the ventral surface of the chelipeds. On average, 80% were situated in a small area on the chela and the remainder on the carpus and more proximal segments. The copepods were able to move quickly in a film of water on the surface of the lobster when the host was removed from the water and could hold fast to one spot fairly well. Sindermann (1990; also cited in Shields *et al.* 2006) stated that "… a harpacticoid, *Unicaleuthes*, occurs sometimes in large numbers on the exoskeleton of the American lobster, *Homarus americanus*". There is no doubt that this record is based on a *lapsus calami* and in reality refers to *U. ovalis*. Wilson (1944) placed *Unicalteutha* in the family Peltidiidae, recognizing a close relationship with *Alteutha* Baird, 1846 (*cf.* name), from which it differs in

"… the body proportions, the dorsal epimeral plates, the first and fifth legs, and the male antennae". However, his original description was deficient in various aspects (*e.g.* segmentation of female urosome and male antennule, armature of swimming legs and leg 5, shape and armature of caudal rami) and, most importantly, failed to document the unique morphology of the maxillules. Humes (1960) redescribed the adults and described the copepodid stages based on several hundreds of specimens from over 200 *H. americanus*, collected from the coast of New England (presumably Maine). Since his material was recovered from the sediment in the warm water in which the lobsters were killed, little can be said about the biology of the species. Humes also mentioned the presence of naupliar stages in the sediment residue but without rearing experiments these could not be identified with certainty. It is likely that at least the entire postnaupliar phase is completed on the exoskeleton of the host. The body form does not change markedly during copepodid development, the mouthparts of copepodid I exhibiting already the general morphology of the adult. Sexual dimorphism is first expressed at copepodid IV in the segmentation of the antennule and the armature of legs 5–6. The large spherical egg sac is flattened, extends far beyond the caudal rami and contains about 20 eggs in a single layer (Humes 1960). Wilson (1944) considered *U. ovalis* a "… commensal profiting by the well-known scavenger habits of its host".

Humes (1960) confirmed the conspecificity between his New England material and Wilson's (1944) holotype of *U. ovalis* (labelled "*Unicalteutha homari*") and specimens from Notre Dame Bay. He assigned *U. ovalis* to the genus *Sacodiscus* (a genus coincidentally proposed by Wilson (1924) himself as a replacement name for *Aspidiscus* Norman, 1869) in the family Tisbidae, relegating *Unicalteutha* to a junior subjective synonym of the latter genus. This course of action was endorsed by Lang (1965).

Humes (1960) identified *Sacodiscus ovalis* also from lobsters collected at St. Andrews (New Brunswick), the Magdalen Islands (Quebec) and Portsmouth (New Hampshire). Squires (1965) observed it on the claws or legs of almost all the Newfoundland lobsters he examined. The native range of *H. americanus* (and potentially *S. ovalis*) is the north-eastern American coast and waters from Cape Hatteras, North Carolina in USA to Labrador, Newfoundland and Straits of Belle Isle in Canada. American lobsters (including berried females) have been captured and genetically identified in Norway, Sweden, Denmark and the English Channel (Stebbing *et al.* 2012; van der Meeren *et al.* 2010). The introduction pathway to northern Europe has not been investigated, but is presumably based on release or escapees of American lobsters from live import, either legally and illegally. Additionally, they can carry various diseases and parasites, such as Gaffkaemia (*Aerococcus viridans* var. *homari* (Hitchner & Snieszko, 1947)), a lethal bacterial blood disease, which has led to regular outbreaks in holding facilities for imported lobsters in Europe (Shields *et al.* 2006). Many imported *H. americanus* carry with them encrusting organisms, like barnacles and polychaetes with no harmful effect on the lobsters, but with a potential for becoming invasive species themselves. Given the high incidence in its native range, it is conceivable that the harpacticoid epibiont, *S. ovalis*, has already been introduced in Scandinavian waters.

OD: Wilson (1944): 540–543; Plate 34 (figures 209–219).
AD: Humes (1960): 279–293; Figs 1–67 (adults and copepodids).
TL: Canada, Newfoundland, Placentia Bay; on exoskeleton of *Homarus americanus* H. Milne Edwards, 1837 (Nephropidae).
BL: 1,350 µm (♀), 1,200 µm (♂) [Wilson 1944]; 516–552 µm (CoI), 564–684 µm (CoII), 612–768 µm (CoIII), 828–960 µm (CoIV♀), 792–888 µm (CoIV♂), 936–1,164 µm (CoV♀), 948–1,164 µm (CoV♂), 1,220–1,416 µm (♀), 1,140–1,236 µm (♂) [Humes 1960].

Tisbe Lilljeborg, 1853

Tisbe elongata (A. Scott, 1896b)

This species was originally recorded as *Idya elongata* (*nomen nudum*) from the muddy sediment on the mussel scars between Morecambe and Heysham (Lancashire) (Scott 1896a: 131). A formal description of both sexes was given in a subsequent paper by Scott (1896b—see also 1896c and 1900). Gurney (1927) transferred *I. elongata* to the genus *Tisbe* and rediscovered it while examining the gills of a European lobster *Homarus gammarus* (Linnaeus, 1758) (as *Homarus vulgaris* Milne Edwards, 1837) in the Plymouth area (Gurney 1933). *Tisbe elongata* was encountered in high abundance, including most developmental stages, suggesting the gill chamber is probably its natural habitat. Gurney described the copepod as a "semi-parasite" which "… colourless and slender in form, had the sluggish and rather aimless movements which one would expect from a commensal removed from its natural habitat". Leigh-Sharpe (1935) listed the species as a commensal copepod in British waters, occurring on the gills of the European lobster; rather than being new this record probably was based on Gurney's (1933) report.

The symbiotic association with *H. gammarus* was confirmed by Gooding (1957) who reported *T. elongata* on lobsters from Plymouth and the Orkney Islands. All stages from nauplius V to adult were found among the gills. The copepods were very abundant on Plymouth lobsters, averaging nearly 50 per host, with each one examined over a period of about a year being infected. Gooding (1957) found *T. elongata* also to be very common on lobsters in the Orkney Islands. Bruce *et al.* (1963) recorded it from the gills of each of 12 lobsters from Port Erin, Isle of Man. Holmes & O'Connor (1990) found it on the gills of lobsters collected in Courtmacsherry Bay, Co. Cork in Ireland. According to Gotto (1993) it has also been observed along the Scottish coasts. The European lobster has a broad geographical distribution and it is likely that future examination of populations from outside the British Isles will result in a significant range extension of *T. elongata*. In its northern range, *H. gammarus* occurs from northern Norway (Lofoten Islands) to south-eastern Sweden and Denmark, but is absent in the Baltic Sea probably due to lowered salinity and temperature extremes. Its distribution southwards extends along the mainland European coast to about 30° N on the Atlantic coast of Morocco, including the Azores. It also occurs, though less abundantly, throughout the coastal and island areas of the Mediterranean and has been reported from the north-west coast of the Black Sea (Holthuis 1991).

Volkmann (1979b) and Wells (2007) ranked *T. elongata* a *species incertae sedis* for no apparent reason.

OD: Scott (1896b): 151–153; Plates IV (Figs 21–24) and V (Figs 1–5).
TL: England, Lancashire, intertidal mussel beds between Heysham and Morecambe; muddy sediment.
BL: 740 µm (♀), unknown for ♂.

(v) Anomuran hosts

Hermit crabs act as hosts to over 550 invertebrates, representing 16 phyla, in a variety of symbiotic relationships (Williams & McDermott 2004). This high number of symbionts is primarily due to their typical behaviour of inhabiting domiciles (usually empty gastropod shells) that serve as a refuge or space for settlement. The symbiotic relationships between anomurans and their associates are not always clearly defined and can change between commensalism, mutualism, and parasitism depending on biotic and abiotic environmental factors. According to Williams & McDermott (2004) about 20 copepod species are known as symbionts of anomuran hosts. McDermott *et al.* (2010) reviewed the diversity and natural history of hermit crab parasites but their treatise largely excluded the symbiotic harpacticoids.

Approximately 23 species of harpacticoids are associated with hermit crabs, 16 of them apparently being obligate commensals in the lumen of inhabited shells. Members of the families Canuellidae and Tisbidae are usually found in the apical whorls of the shells while species of the family Porcellidiidae are typically found crawling on the inside surface of the gastropod shells. Two new genera, belonging to the Ameiridae and Laophontidae, respectively, were recently discovered in washings of sand (mole) crabs (Blepharipodidae) in South Korea (R. Huys, unpubl. data). Data on the feeding biology of obligate copepod commensals of hermit crabs (*e.g. Sunaristes* spp., *Kioloaria* spp.) is lacking but it is likely that they feed on material brought in by the branchial currents of the crab hosts and/or their faeces (Williams & McDermott 2004).

Family Ameiridae

Pearse (1934a) reported *Cancrincola jamaicensis* from the gills of the diogenid *Paguristes puncticeps* Benedict, 1901 collected at Loggerhead Key, Dry Tortugas, Florida. Humes (1958) re-examined this material and concluded that it did not belong to the genus *Cancrincola*, perhaps being accidentally present.

A new genus and species of Ameiridae was recently obtained in washings of the oriental sand (mole) crab *Blepharipoda liberata* Shen, 1949 (Blepharipodidae) off the East Sea coast of South Korea (R. Huys, unpubl. data). The hosts are specialized burrowing crabs that typically live in shallow sandy habitats and were collected in a fisheries bycatch at two different ports, Sacheong Port (Gangneung; 37º50'10"N, 128º52'37"E) and Gajin Port (38º22'02"N, 128º30'43"E). On both occasions the ameirids occurred in large numbers, suggesting that the symbiotic association was genuine. Interestingly, in each case the new ameirid also appeared to cohabit with an as yet undescribed laophontid. The known distribution range of the host includes records from China, Korea and Japan (Boyko 2002).

Family Canuellidae

Symbiotic associations with hermit crab hosts have been documented for members of four canuellid genera, *i.e.* *Sunaristes* Hesse, 1867, *Brianola* Monard, 1927, *Coullana* Por, 1984b and *Intersunaristes* Huys, 1995. Lang (1948: 170) suggested that *Canuellina insignis* Gurney, 1927 (described from a single female taken at Port Said north of the Suez Canal) may also be associated with crustacean hosts (based on Fox's (1926: 49) report of the common presence of crabs in the habitat where it was collected) but subsequent records of this species (Por 1968, 1969, 1973; Por & Marcus 1973; Wells 1967) or any of the other five species of *Canuellina* (Por 1967, 1969, 1983b; Wells & Rao 1987) have failed to confirm such an association. See p. 519 for an updated key to canuellid genera.

Sunaristes Hesse, 1867

Hesse's (1867) description of *Sunaristes paguri* was overlooked by Müller (1884) who described the same species under the name *Longipedina paguri* and placed it in the subfamily Longipediinae in the family "Harpactidae". The synonymy between *Longipedina* and *Sunaristes* was first recognized by Scott & Scott (1897) and corroborated by Sars (1903) who restricted the family Longipediidae to *Sunaristes*, *Canuella* and *Longipedia* Claus, 1862. Since then the genus *Sunaristes* has served as a repository for any large canuellid species bearing a superficial resemblance to *S. paguri*, leading to a state of the greatest possible confusion (Hamond 1973b).

Thompson & Scott (1903) added three new species from Sri Lankan waters (*S. curticaudata*, *S. inopinata* and *S. longipes*) which were subsequently transferred to the genus *Canuella* by Scott (1909). The genus remained monotypic until Por (1964) described *S. bulbosus* Por, 1964, however, in a later paper (Por 1967) he transferred this species to the genus *Scottolana*. Humes & Ho (1969a) added two new species, *S. dardani* and *S. inaequalis*, both being found in association with diogenid hermit crab hosts in the Indian Ocean. Hamond (1973b) gave a key to the four species he recognized as valid: *S. paguri*, *S. dardani*, *S. inaequalis* and the newly described *S. tranteri* Hamond, 1973b. He considered *S. bulbosus* to be identical with Scott's (1909) material of *S. curticaudata* (but see Fiers (1982) for a dissenting opinion) and, being unable to place the species in any of the recognized genera, retained it in *Sunaristes*. Por (1984b) also tentatively reassigned this species to *Sunaristes*, concluding that the systematic status of *S. bulbosus* remains uncertain. He also added *Ellucana chelicerata* Por & Marcus, 1973 to *Sunaristes*, raising the number of species to six, but gave virtually no justification for this assignment and entirely ignored Fiers' (1982) revision of the genus. Fiers (1982) restricted *Sunaristes* to *S. paguri*, *S. inopinata*, *S. inaequalis* and *S. tranteri*, and allocated the remaining species (*S. curticaudata*, *S. dardani* and *E. chelicerata*) to a new genus *Parasunaristes*. Ho (1986a) added *S. japonica* Ho, 1986a (note that his original spelling *japonicus* is here amended to reflect agreement in gender; ICZN Art. 31.2) and expressed doubts about the inclusion of *S. inopinata* in *Sunaristes*, considering it no longer a valid species in his subsequent cladistic analysis (Ho 1988). *Sunaristes inopinata* is currently considered a member of the genus *Scottolana*, either as a *species incertae sedis* (Huys 1995; Bodin 1997) or as a valid species (Wells 2007). Finally, Mu & Huys (2004) removed *Sunaristes bulbosus* and assigned it to the genus *Scottolana*.

All known species of *Sunaristes* are endolithic symbionts in the gastropod shells inhabited by anomuran decapods. Hodda & Nicholas (1986) recorded an unidentified *Sunaristes* species in the meiofauna of the Hunter River estuary on the central coast of New South Wales, Australia. Rao (1980) recorded *Sunaristes* sp. as an "uncertain endemic" in a checklist of the interstitial harpacticoids from the Andaman and Nicobar Islands. Kondalarao (1984) also recorded *Sunaristes* sp. from five intertidal mudflat sites in the Gautami-Godavari estuary (Konaseema delta), Andhra Pradesh, India. Williams (in Williams & McDermott 2004) found specimens of *Sunaristes* inside shells inhabited by hermit crabs from the Philippines, Singapore, and Hong Kong. Björnberg (1999) suggested that the planktonic canuellid nauplii found in the São Sebastião channel, southeastern Brazil, belonged to a species associated with a benthic host, possibly a member of the genus *Sunaristes*.

TABLE 13. Comparative analysis of swimming leg ornamentation between various *Sunaristes* species. Surface spinulation patterns on exopodal and endopodal segments of P1–P4 (+: present; –: absent; exp = exopod; enp = endopod; 1–3 = proximal, middle and distal segments) for both sexes and their deviations (in parentheses) reported in the literature.

	P1		P2		P3		P4		References
	exp	enp	exp	enp	exp	enp	exp	enp	
	1 2 3	1 2 3	1 2 3	1 2 3	1 2 3	1 2 3	1 2 3	1 2 3	
FEMALES									
paguri	+ − −	+ + −	+ + −	− − −	+ + −	− − −	+ + −	− − −	Hamond (1973b), Humes & Ho (1969a)
inaequalis	+ − −	+ + −	+ + +	+ + −	+ + +	− + +[1]	+ + +	− + −[1]	Humes & Ho (1969a)
				(+ − −)		(+ + −)[2]		(− − −)	Humes (1972)
								(+ − −)	Ho (1986a)[3]
tranteri	+ − −	+ + −	+ + +	+ − −	+ + +	+ + −	+ + +	− + −	Humes (1981c)[5]
				(+ + −)				(− − −)	Hamond (1973b), Humes (1981c)
						(+ − −)		(+ − −)	Hamond (1973b)
								(+ + −)	Hamond (1973b)
japonica	+ − −	+ + −	+ + +	+ − −	+ + +	− + −	+ + +	− + −	Ho (1986a)
				(− − −)					Ho (1986a)
sp.[4]	+ − −	+ + −	+ + +	+ − −	+ + +	− − −	++ +	− − −	Hamond (1973b)
MALES									
paguri	+ − −	+ + −	+ + −	− + −	+ + −	+ + −	+ + −	− + −[6]	Humes & Ho (1969a)
								(+ − −)	Hamond (1973b)
								(+ + −)	Hamond (1973b), Humes & Ho (1969a)
						(− + −)			Humes & Ho (1969a)
						(− − −)			Humes & Ho (1969a)
inaequalis	+ − −	+ + −	+ + +	− + −	+ + +[7]	+ + +	+ + +	− + +	Humes & Ho (1969a)
								(− + −)	Humes & Ho (1969a)
						(+ + −)[2]		(+ + −)	Humes (1972)
								(+ + +)	Ho (1986a) [3]
tranteri	+ − −	+ + −	+ + +	− + −	+ + +	+ + −	+ + +	+ + −	Hamond (1973b)
				(− − −)				(− + −)[8]	Humes (1981c)
								(− − −)	Humes (1981c)
japonica	+ − −	+ + −	+ + +	− + −	+ + +	+ + −	+ + +	− + −	Ho (1986a)
				(− − −)		(− + −)		(+ + −)	Ho (1986a)
								(− − −)	Ho (1986a)

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[1] Humes & Ho (1969a) inadvertently reversed the spinulation formula for P3–P4 (see their Figs 37–38) and unfortunately this error has been perpetuated in the literature (Hamond 1973b; Ho 1986a); the (− + −) condition, which was interpreted as a rare deviation for the P4 endopod by Humes & Ho (1969a), in fact represents the typical condition.

[2] typical condition in New Caledonian populations.

[3] neither Humes & Ho (1969a) nor Humes (1972) refer to this condition; it is not clear whether Ho (1986a) had observed additional specimens that confirmed this deviation.

[4] *sensu* Hamond (1973b).

[5] Humes' (1981c) re-examination was based on a large number of specimens from six different hosts; the most common pattern observed among the Moluccan specimens is here adopted as the typical condition rather than the one observed in Hamond's (1973b) much smaller collection from the type locality.

[6] Humes & Ho (1969a) consider this the typical condition; since their sample size was significantly larger than that of Hamond (1973b)—who remained inconclusive on the matter—their judgement is adopted here.

[7] Ho (1986a) claims that [+ + −] is the typical condition (as in *S. paguri*) but this must be a slip of the pen.

[8] typical condition in Moluccan populations.

As pointed out by various authors (*e.g.* Hamond 1973b; Ho 1986a; Wells 2007) the five known species (four named) of *Sunaristes* are closely related, in particular the Indo-Pacific members of the genus. Surface spinulation patterns on the exopodal and endopodal segments of P1–P4 have occasionally been used to differentiate species but the variability encountered in these patterns makes them essentially unsound for this purpose (except for the consistent absence of surface ornamentation on P2–P4 exp-3 in *S. paguri*) (Table 13). Clearly, the range of variability in ornamentation (and sometimes armature) must be recognized in establishing the criteria for species differentiation in this genus. Additionial aberrations in the segmentation and armature have been recorded for most species and may be the result of damage inflicted by the host (Codreanu & Mack-Firă 1961).

Several authors have tried to differentiate species but the majority of these morphological comparisons is at least partly based on dubious characters (*e.g.* antennule segmentation) and may lead to the wrong identification. For example, even though Wells (2007) wisely advised to check any identification against the original description, one of the three characters used in his tabular key (seta on second exopodal segment of antenna naked or plumose) is scored incorrectly since this seta is expressed only in *S. japonica* (*cf.* Codreanu & Mack-Firă 1961; Ho 1986a). The antennary exopod of *Sunaristes tranteri* was originally described as 7-segmented with a pinnate seta on the second segment but Humes' (1981c) redescription showed it is 8-segmented and that the real second (unarmed) segment was overlooked by Hamond (1973b).

It is debatable whether the three (four if *Sunaristes* sp. *sensu* Hamond (1973b) is included] Indo-Pacific representatives of the genus represent genuine species or just geographically widely separated races (sometimes using the same host). Ho (1987, 1988) presented an attractive scenario of the vicariant events that led to the speciation and current distribution of the genus. Although his hypothesis makes biological sense in the light of paleontological (host fossil record) and paleoceanographic data, his analysis is clearly flawed because many of the character states listed in his Table 1 were not scored correctly for at least one species. Re-examination of *S. paguri*, *S. tranteri* and *S. inaequalis* revealed the following characters to be constant throughout the genus: antennary exopod with three long setae and one short pinnate seta on apical segment (characters 12 and 14), antennary endopod with seven elements on distal segment (characters 13 and 15), mandibular exopod with eight setae (characters 4 and 7), maxillulary exopod with seven setae (characters 4 and 17). The only autapomorphy for *S. inaequalis* (character 19) does not feature in his Table 1.

Given the few reliable and consistent differences between them, the characters summarized in Table 14 should be considered a modest attempt at separating the four named species of *Sunaristes*.

Sunaristes paguri **Hesse, 1867**

There is considerable disagreement in the literature over the number of segments in the female antennule with reports varying between five (Müller 1884; Scott & Scott 1897; Codreanu & Mack-Firă 1961), 5–6 (Lang 1948) and six (Sars 1903). Re-examination showed that the antennule is 4-segmented, conforming to the pattern found in all species of the *Sunaristes*-lineage [as described for *Echinosunaristes*; *cf.* Huys (1995: Fig. 2B–C); for segmental homologies see Huys & Boxshall (1991: 116, Table 2)]. Codreanu & Mack-Firă (1961) observed sexual dimorphism in the armature of the distal exopodal segment of the antenna, the female bearing four elements and the male only three. This observation is doubtful and requires confirmation. Their statement that the exopod is 7-segmented contradicts their illustration (Fig. 4) which shows eight well defined segments as in other members of the genus. Codreanu & Mack-Firă (1961) also recorded variability in the number of setae on the mandibular endopod (enp-2 typically with eight setae but occasionally with seven setae on the right side in Pontic basin individuals) and maxillary endopod (7–8). The reports of an additional apical segment in the maxilliped by Scott & Scott (1897) and Sars (1903) are based on observational errors. Lang's (1948: 28) claim that there are eight setae on the caudal ramus was refuted by Codreanu & Mack-Firă (1961). Hamond (1973b) pointed out that Por's (1967: Table III) armature formula [exp: 1.1.4; enp: 0.1.3] for leg 4 is erroneous.

The distribution of *Sunaristes paguri* is confined to north-west Europe, the Mediterranean and the Black Sea where it is associated with hermit crabs of the families Paguridae and Diogenidae, and usually occupies the apical whorls of the gastropod shell inhabited by the host (Table 15). In north-west Europe *S. paguri* is almost exclusively found in association with the common hermit crab *Pagurus bernhardus*, which is by far the most common shallow water anomuran in that region. Norman & Scott (1906) summarized their own and other records of *S. paguri* as "… always in washings from shells inhabited by the common Hermit Crab (*Pagurus Prideauxi*) …" but this must be a slip of the pen (Hamond 1973b). *Sunaristes paguri* can be locally absent even if its host is abundant as in Norfolk (Hamond (1971) in Hamond (1973b)) but seasonality may be an important factor. The only other indisputable hosts of *S. paguri* in north-west Europe are *Pagurus cuanensis* Bell, 1845 (inhabiting shells of *Turritella communis* Risso, 1826) and *Diogenes pugilator* (R. Bourdon in Hamond (1973b)).

TABLE 14. Differentiating characters between species of *Sunaristes* Hesse, 1867.

	paguri	*inaequalis*	*tranteri*	*japonica*
Antenna exp-2 seta	absent	absent	absent	present
Antenna enp-1	2 setae	1 seta	1 seta	1 seta
P2–P4 exp-3 outer margin	no spinules	spinulose	spinulose	spinulose
P4 enp-1 inner seta	> endopod	< endopod	≥ endopod	> endopod
Caudal ramus L:W	≈ 3.3	≈ 2.7	≈ 2.3	≈ 1.8

Apostolov (1972) and Apostolov & Marinov (1988) included *S. paguri* in their catalogues of Bulgarian harpacticoids but did not give any records. Thompson & Scott (1903) found a few specimens in general washings of marine invertebrates taken off the coast of Sri Lanka and Scott (1909) reported a single male from Indonesian New Guinea (Raja Ampat Islands, between Salawati and Misool; 01°42.5'S, 130°47.5'E; depth 32 m). Both these records require verification (Humes & Ho 1969a; Humes 1972; Hamond 1973b) and almost certainly refer to one of the Indo-Pacific congeners (possibly *S. tranteri*) and not to the European *S. paguri*.

Müller (1884) observed a high prevalence on the Isle of Sylt, Germany, with over half of the whelk shells (*Buccinum undatum* Linnaeus, 1758) inhabited by *Pagurus bernhardus* also containing *S. paguri*. Jensen & Bender (1973) found the species also in shells of the common periwinkle *Littorina littorea* (Linnaeus, 1758) used by *P. bernhardus* in the Gullmarfjord. Ovigerous females occur at the beginning of July in the Gullmarfjord (Lang 1948), at the end of July in the western Wadden Sea (Stock 1952) and during the entire month of August in the Black Sea (Codreanu & Mack-Firă 1961). Each egg sac contains 80–90 eggs (up to 77 µm in diameter), arranged in two layers of four rows each (Codreanu & Mack-Firă 1961). Newly hatched nauplii soon leave the host and, upon completion of the naupliar phase, moult into the first copepodid stage before entering a new occupied shell. Lang (1948) assumed males died after mating and females probably underwent the same after eclosion of the nauplii is completed, however, this has been disputed by Codreanu & Mack-Firă (1961). The development time from nauplius to the first copepodid stage was estimated at 2–3 weeks by Lang (1948). Lang (1948: 145, Abb. 97b) described the first nauplius stage and reinterpreted Gurney's (1930c: Fig. 8) "Longipediidae, Genus II. Nauplius stage I" from the mouth of the River Lynher (Cornwall) as the second nauplius stage of a canuellid, most probably *S. paguri*. Codreanu & Mack-Firă (1961) provided data on copepodid development (CoII–V). According to Monard (1935b) the gut and egg sacs can have a deep violet colour. Lang (1948) described the colour of the nauplius eye (pp. 118–119), ovaries and egg sacs (p. 34) as deep blue-violet while Codreanu & Mack-Firă (1961) observed a difference in colour between the nauplius eye (red) and the eggs (deep violet).

According to Stachowitsch (1980) populations of *S. paguri* in the Gulf of Trieste often share the apex of its host's gastropod shell (usually *Aporrhais pespelecani* (Linnaeus, 1758)) with the sipunculid *Aspidosiphon muelleri muelleri*. Turquier (1965) observed a similar co-existence with the corophiid amphipod *Monocorophium sextonae* (Crawford, 1937) along the north-western coast of France. Codreanu & Mack-Firă (1961) suggested that the spionid polychaete *Polydora ciliata* (Johnston, 1838) is likely to compete for space with *S. paguri* since both occupy the apical whorls of the gastropod shell (*Nassarius reticulatus* (Linnaeus, 1758)) off the Romanian coast. Another space-limiting factor is the presence of parasites attached to the abdomen of the anomuran host such as the peltogastrid rhizocephalan *Septosaccus rodriguezii* (Fraisse, 1878) [as *S. cuenoti* Duboscq, 1912] and the epicaridean isopod *Parathelges racovitzai* Codreanu, 1940, which were observed in the same shells occupied by *S. paguri* (Codreanu & Mack-Firă 1961). Lang (1948) remarked that *S. paguri* appears to avoid smaller *Buccinum* shells in the Gullmarfjord, the critical shell height being around 41 mm. Codreanu & Mack-Firă (1961) also suggested there is a correlation in size between *S. paguri* and the shell utilized by the hermit crab. Diogenid hosts in the Mediterranean and Black Sea often inhabit shells belonging to smaller gastropod species (*Nassarius mutabilis* (Linnaeus, 1758) and *N. reticulatus*) which may offer an explanation for the smaller body size of *S. paguri* in these basins compared to the Atlantic populations.

Lang's (1948: 110) experiments showed that *S. paguri* can sustain significant damage, surviving decapitation up to at least 24 h. In individuals where the prosome was separated from the urosome, the hindgut maintained its peristaltic movement in the urosome while the prosome continued swimming around with the mouthparts showing no sign of dysfunction. Another experiment whereby somites were removed one by one until only the anal somite was left showed that the rectum and anal opening continued contracting and dilating. Lang (1948: 128) considered this as indirect evidence for the presence of an anal ganglion but failed to locate it in his serial sections.

TABLE 15. Known hosts and distribution records of *Sunaristes paguri* Hesse, 1867

Host family and species	Country	Region	Locality	Reference(s)
Family Diogenidae				
Paguristes eremita (Linnaeus, 1767)	Italy	Friuli-Venezia Giulia	Gulf of Trieste	Stachowitsch (1980) [1]
Diogenes pugilator (Roux, 1828)	France	Côtes d'Armor (Bretagne)	Saint-Efflam (Plestin-les-Grèves)	Hamond (1973b)
		Bouche-du-Rhône	Marseille	Codreanu & Mack-Firă (1961)
	Romania	Constanţa County	Agigea and Mangalia	Codreanu & Mack-Firă (1961) [2]
Clibanarius erythropus (Latreille, 1818)	France	Pyrénées-Orientales	Banyuls-sur-Mer	Stock (1960)
Family Paguridae				
Pagurus bernhardus (Linnaeus, 1758)	Norway	Østfold	Hvaler	Sars (1903) [3]
	Sweden	Bohuslän	Gullmarfjord (Strömmarna)	Lang (1948)
		West coast	locality unknown	Bresciani & Lützen (1962)
			Kristineberg	Jensen & Bender (1973)
	Germany	Schleswig-Holstein	Isle of Sylt	Müller (1884)
	The Netherlands	Noord Holland	between Hoek van Holland and Wijk aan Zee	Leenhouts (1950a)
		Noord Holland	western part of Wadden Sea	Stock (1952)
		Noord Holland	off Callantsoog	Stock (1952), Lucas (1958)
		Noord Holland	Wadden Sea (Dove Balg, Vlieter, Texelstroom)	Lucas (1958)
		Noord Holland	Wadden Sea (Midden Vlieter)	J.H. Stock in Humes & Ho (1969a)
			Wadden Sea	present account [4, 5, 6]
		Noord Holland	Hoek van Holland	Faasse (2003)
		Zuid Holland	Katwijk aan Zee	J.A.W. Lucas in Leenhouts (1950b), Vervoort (1950a)
		Zeeland	Westerschelde estuary	Stock (1952), Faasse (2003), present account [7]
			Zeehondenplaat	present account [8]
		West coast	From Schouwen to Hoek van Holland	Lucas (1958)
	Scotland	Highland	Cromarty Firth	Scott & Scott (1894, 1897), Scott (1906b)
	England	Devon	Starcross	Norman & Scott (1906)
			Mewstone reefs	Marine Biological Association (1931, 1957)

……continued on the next page

TABLE 15. (Continued)

Host family and species	Country	Region	Locality	Reference(s)
		Merseyside	Liverpool Bay	A. Scott in Herdman (1896)
			Mersey estuary	Scott & Scott (1897), A. Scott (1896b, 1909)
		Sussex	Cuckmere Haven	Ventham (2011)
	Ireland	County Mayo	Blacksod Bay	Farran (1913) [9]
		County Cork	Dunmanus Bay	Holmes & O'Connor (1990)
		County Kerry	Tralee Bay	Holmes & O'Connor (1990)
	France	Finistère (Bretagne)	Brest harbour	Hesse (1867)
		Finistère (Bretagne)	Roscoff	Monard (1935), Turquier (1965)
		Finistère (Bretagne)	Penpoull	present account [10]
		Calvados (Normandie)	Grandcamp-Maisy	Chevreux (1908)
		Manche (Normandie)	Pirou	Turquier (1965)
	Locality unknown			Sars (1919) [11]
Pagurus cuanensis Bell, 1845	France	Finistère (Bretagne)	Roscoff	Hamond (1973b)
	Italy	Friuli-Venezia Giulia	Gulf of Trieste	Stachowitsch (1980)
Paguridae *indet.*	Great Britain			Leigh-Sharpe (1935) [12]

[1] As *Paguristes oculatus* (J.C. Fabricius, 1775).

[2] Codreanu & Bălcescu (1968a, 1968b) subsequently established the subspecies *Diogenes pugilator orientalis* for Black Sea and Adriatic populations of the host species but this course of action has been disputed by Ingle (1993) who considered *D. pugilator* a very variable species.

[3] One female dredged from gravelly sand at a few fathoms depth; the host is likely to be *P. bernhardus*.

[4] Based on examination of material deposited in former Zoölogisch Museum Amsterdam (ZMA): Noord Vlieter, *ca.* 25 m (1 ♀ – ZMA Co. 100.047); Noord Vlieter, 5.5–8.5 m (4 ♀♀ – ZMA Co. 100.050); Scheer, 8–11 m (1 ovigerous ♀ – ZMA Co. 100.053); Noord Texelstroom, 14–16 m (1 ♀, 1 ♂ – ZMA Co. 100.055); Midden Vlieter, 6 m (3 ♀♀, 1 ovigerous ♀, 5 ♂♂, 54 copepodids – ZMA Co. 100.056). All material collected by J.H. Stock, 30 June 1950.

[5] Based on examination of material deposited in former Zoölogisch Museum Amsterdam (ZMA): Noord Vlieter, 19–24 m (2 ♀♀, 1 ♂, 1 copepodid – ZMA Co. 100.045); 2 km east of Baak Vogelzand (11 ♀♀, 2 ovigerous ♀♀, 3 ♂♂ – ZMA Co. 100.046); Scheer, 8–11 m (1 ovigerous ♀ – ZMA Co. 100.053); Noord Vlieter, 21–24 m (6 ♀♀, 1 copepodid – ZMA Co. 100.048). All material collected by J.H. Stock, 27 July 1950.

[6] Based on examination of material deposited in former Zoölogisch Museum Amsterdam (ZMA): Staart van Schieringhals (1 ♀ – ZMA Co. 100.283). All material collected by J.H. Stock, 14 July 1955.

[7] Based on examination of material deposited in former Zoölogisch Museum Amsterdam (ZMA): mouth of Westerschelde estuary (1 ♀ – ZMA Co. 100.083; 1 ♀ – ZMA Co. 100.113); collected by J.H. Stock, 23 October 1951 and 31 October 1951, respectively.

[8] Based on examination of material deposited in former Zoölogisch Museum Amsterdam (ZMA): 3 ♀♀ (ZMA Co. 100.049); collected by J.H. Stock, 20 July 1950.

[9] One male washed from weeds between tide-marks; the host is likely to be *P. bernhardus*.

[10] Based on examination of material deposited in former Zoölogisch Museum Amsterdam (ZMA): littoral zone, near St. Pol-de-Léon; 1 ovigerous ♀ (ZMA Co. 102.390); collected by J.H. Stock, 07 September 1972.

[11] Sars (1919) based his redescription of the male on a single female which he had received from Jules Richard without any mention of an associated host; it is likely that this specimen came from a French locality.

[12] Record in list of parasitic and commensal copepods associated with British invertebrates. Origin or authenticity unknown.

TABLE 16. Records of *Sunaristes inaequalis* Humes & Ho, 1969a in the Indo-Pacific, including diogenid hosts and locality data [data from Humes & Ho (1969a) and Humes (1972)]

Host	Locality
Madagascar	
unidentified hermit crabs	Ankify, opposite Nosy Komba
Dardanus megistos	Nosy Bé, Antsakoabe
	Ambariobe island, between Nosy Bé and Nosy Komba
Eritrea	
Clibanarius carnifex	Dahlak Archipelago, Andeber (= Entedebir), Landing Bay
New Caledonia	
Calcinus latens	Nouméa (Rocher à la Voile; 20°18'24"S, 166°25'50"E)
Clibanarius virescens	Nouméa (Ricaudy Reef)
Dardanus scutellatus	behind reef at Poe, near Bourail (21°40'00"S, 165°27'00"E)
Dardanus megistos	west of Paita, near Nouméa (22°07'00"S, 166°12'00"E)
	Port Ngea (north-west side) (22°18'18"S, 166°26'47"E)

OD: Hesse (1867): 205–209; Planche 4 (Figs 11–25).

AD: Müller (1884—as *Longipedina Paguri*): 20–21; Tafel III. Scott & Scott (1897): 490–492; Plate XI (Figs 1–10), XII (Figs 2–7). Sars (1903): 15–16; Plates VI–VII. Sars (1919): 19–20; Plate XII. Lang (1948): 28, 33–35, 38, 48, 50–53, 55–57, 60, 63–64, 75–76, 78–80, 82–87, 89–101, 110–111, 118–119, 121, 123, 125, 128, 134, 141, 145, 161–162; Abb. 6a, 11b, 21a–b, 24a, 27a, 32b, 54, 58a–c, 61a, 66b, 70a, 71a, 72–73, 74, 75a, 76a, 84, 88c, 92b, 97b (nauplius I), 101. Stock (1952): 70; Figs a–b. Codreanu & Mack-Firă (1961): 471–483; Figs 1–7; Tables I–III. Humes & Ho (1969a): 12, 14, 16; Figs 43–45; Tables I–II. Apostolov & Marinov (1988): 60–61; Fig. 17-3. Huys *et al.* (1996): 132–133, 340; Fig. 52; Appendix Table 1.

TL: France, Brittany (Bretagne), Finistère, Brest; gastropod shells inhabited by pagurid hermit crabs (most likely *Pagurus bernhardus* (Linnaeus, 1758)). Bourdon (*in litt.* in Hamond (1973b)) revealed that Hesse (1867) had collected the crabs from the harbour in Brest ("la rade de Brest").

BL: 5,000 µm (sex not specified; this measurement probably includes the caudal ramus setae) [Hesse 1867]; 2,700 µm (♀), 2,300 µm (♂) [Müller 1884; Scott & Scott 1894]; 3,000 µm (♀), 2,000 µm (♂) [Scott & Scott 1897]; 3,000 µm (♀) [Sars 1903]; 2,150 µm (♂) [Sars 1919]; 1,600–2,600 µm (♀), 1,400–2,200 µm (♂), 1,050–1,100 µm (CoII), 1,150 µm (CoIII), 1,200–1,500 µm (CoIV♀), 1,100–1,500 µm (CoIV♂), 1,550–1,950 µm (CoV♂) [Codreanu & Mack-Firă 1961].

Sunaristes inaequalis **Humes & Ho, 1969a**

Sunaristes inaequalis is exclusively associated with diogenid hosts. In the eastern Indian Ocean it is found with *Dardanus megistos* (Herbst, 1804) in Madagascar and with *Clibanarius carnifex* Heller, 1861 in Eritrea (Humes & Ho 1969a). Humes (1972) reported three new hosts in New Caledonia: *Calcinus latens* (Randall, 1840), *Clibanarius virescens* (Krauss, 1843) and *Dardanus scutellatus* (H. Milne Edwards, 1848). The high incidence of *S. inaequalis* with *D. scutellatus* suggests a preference for that host. The known records of *S. inaequalis* are summarized in Table 16.

Humes (1972) observed variability in the segmentation (exopods of P1 and P3), armature (P1 exp-3 with three instead of four setae; P2 exp-3 with two instead of three spines) and ornamentation (Table 13) of the swimming legs. Occasionally the female P5 bears five or six setae instead of four (including the outer basal seta).

OD: Humes & Ho (1969a): 11, 13, 15–17; Figs 33–42; Tables I–II.

AD: Humes (1972): 264–265 [no figures].

TL: Madagascar, Diana Region; on sand flat at Ankify, on the mainland of Madagascar, opposite Nosy (Nossi) Komba; washings of several unidentified small hermit crabs, intertidal.

BL: 1,930–2,490 µm (♀), 1,340–1,510 µm (♂).

TABLE 17. Known diogenid hosts and distribution records of *Sunaristes tranteri* Hamond, 1973b in the Maluku Islands [data from Humes (1981c)].

Host	Island	Locality	Coordinates	Depth
Dardanus guttatus (Olivier, 1812)	eastern Seram (= Ceram)	Pulau Parang	03°17’00”S, 130°44’48”E	3 m
	east central Halmahera	Karang Mie	00º20’07”N, 128º25’00”E	2 m
Dardanus lagopodes (Forskål, 1775)	Banda	SW shore of Goenoeng Api	04º31’45”S, 129º51’55”E	0.5 and 10 m
			04º31’55”S, 129º52’12”E	15 m
	western Seram	Pulau Marsegoe	02º59’30”S, 128º03’30”E	3 m
	eastern Seram	Pulau Parang	03°17’00”S, 130°44’48”E	5 m
	Ambon	Natsepa	03º27’05”S, 128°17’00”E	3 m
Calcinus gaimardii (H. Milne Edwards, 1848)	Banda	SW shore of Goenoeng Api	04º31’45”S, 129º51’55”E	10 m
Calcinus latens (Randall, 1840)	Banda	SW shore of Goenoeng Api	04º31’55”S, 129º52’12”E	15 m
Calcinus minutus Buitendijk, 1937	Banda	SW shore of Goenoeng Api	04º31’45”S, 129º51’55”E	10 m
			04º31’55”S, 129º52’12”E	15 m
Calcinus sp.	Banda	SW shore of Goenoeng Api	04º31’45”S, 129º51’55”E	10 m
Ciliopagurus strigatus (Herbst, 1804)[1]	Banda	SW shore of Goenoeng Api	04º31’45”S, 129º51’55”E	10 m
			04º31’55”S, 129º52’12”E	15 m

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[1] as *Trizopagurus strigatus* (Herbst, 1804)

Sunaristes tranteri Hamond, 1973b

In addition to the type host *Diogenes senex*, *S. tranteri* is known to live in association with another seven diogenid hermit crab hosts in the Maluku Islands (= Moluccas, Indonesia) (Humes, 1981c) (Table 17).

Hamond (1973b) observed variability in maxillulary armature, *i.e.* the numbers of setiform elements on the preacoxal arthrite (four or five) and epipodal setae (typically two, occasionally with a third small one) on the coxa. Hamond interpreted the female antennule as indistinctly 6-segmented but the first unarmed segment merely represents a pedestal and the second one has two internal semicircular, transverse ribs possibly marking an ancestral subdivision. Humes (1981c) corrected the antennary setal formula to [1, 4, 7] for the endopod and [1, 0, 1, 1, 1, 1, 1, 4] for the exopod. He also found that 12.5% of the females and 31.3% of the males in the Moluccan populations showed abnormal spinulation patterns on the swimming legs and that the endopodal segmentation of leg 4 can occasionally be reduced to two segments. Hamond (1973b) showed a spinule row on the coxa of leg 4 (a species discriminant used by Humes & Ho (1969a)) but this character was not observed by Humes (1981c) in his Moluccan material, rendering it unreliable for identification purposes.

Wells & Rao (1987) reported two females from a coarse sandy beach on Middle Andaman (Rangat Bay; 12º28’40”N, 92º57’18”E); this is the only record from outside a hermit crab host (and probably refers to Rao’s (1980) earlier record in a checklist of the interstitial harpacticoids from the Andaman and Nicobar Islands). Their specimens were attributed to *S. tranteri* because they were more similar in the surface spinulation of P1–P4 to this species than to any other. Wells & Rao (1987) confirmed that the first exopodal segment of the mandible has two inner setae. Hamond (1973b) mistakenly claimed that the proximal seta arose from the basis between the rami. They also stated that there can be either seven or eight setae on the second segment of the mandibular exopod [*sic*]; it is clear that the authors meant the endopod. The Andaman specimens have only two epipodal setae on the maxillule (being also the typical condition in Hamond’s type material) but differ from the type material in the relative lengths of the distal setae of P3 exp-3 and inner seta of P4 enp-1.

OD: Hamond (1973b): 167–176; Figs 1–21; Table 1.

AD: Humes (1981c): 3–6; Figs 1–5. Wells & Rao (1987): 4–5 [no figures].

TL: Australia, New South Wales, Cronulla (southern metropolitan Sydney); swimming pool of former CSIRO Division of Fisheries and Oceanography (approx. 34º04’30”S, 151º08’53”E) which empties directly into Gunnamatta Bay during low tide; washings of hermit crabs (*Diogenes senex* Heller, 1865; family Diogenidae) inhabiting empty gastropod shells of primarily *Pyrazus ebeninus* (Bruguière, 1792).

BL: 2,300 µm (♀), 1,900 µm (♂) [Hamond, 1973b]; 1,280–2,000 µm (♀), 1,020–1,780 µm (♂) [Humes, 1981c—note that the author erroneously gave the upper extreme of the size range as 780 µm].

Sunaristes japonica Ho, 1986a

In Japan *S. japonica* is known from four hermit crab hosts and has been recorded from both the Sea of Japan coast (Ishikawa and Niigata Prefectures) and the Pacific coast (Wakayama Prefecture) of Honshū Island (Ho, 1986a). Kim (1998) recorded *S. japonica* from two hermit crab hosts in Korea, collected in Daejin (about 100 km north from Gangneung). An additional record from Korea was mentioned by Kim (2013) who collected it in washings of an unidentified hermit crab from Jeju Island. Except for *Clibanarius bimaculatus* (De Haan, 1849) all hosts are members of the Paguridae (Table 18).

The species is most closely related to its Indo-Pacific congeners, *S. inaequalis* and *S. tranteri*, from which it can be distinguished by the armature of the antennary exopod, bearing a small plumose seta on segment 2. Kim (1998) shows the exopod as 7-segmented but this may be an observational error. The other antennary character used by Ho (1986a) is the armature of exp-8, consisting of a short spiniform seta and three long setae in *S. japonica* (instead of 3–4 long setae in the other species). Neither Humes & Ho (1969a) nor Hamond (1973b) showed the setae on this segment at their full length; re-examination revealed that the *japonica*-condition is exhibited in all species of *Sunaristes*, including *S. paguri* (*cf.* Codreanu & Mack-Firă, 1961: Fig. 4). The spinules typically present on P2 enp-2 and P3 enp-1 in male *S. japonica* can be absent in some specimens (resembling the typical female condition). Additional variability in male endopodal spinulation was observed in the P4 with spinules typically absent on enp-1 but present in some specimens; spinules typically present on enp-2 were occasionally lacking (Table 13). No such variability in endopodal spinulation was recorded for the female, except for the occasional lack of spinules on P2 enp-1.

TABLE 18. Host and locality records of *Sunaristes japonica* Ho, 1986a. Japanese records after Ho (1986a), Korean ones after Kim (1998) and Kim (2013)*.

Hermit crab host	Prefecture/Province	Locality
Japan		
Clibanarius bimaculatus (De Haan, 1849)	Wakayama	Shirahama
Pagurus filholi (De Man, 1887) [1]	Niigata	Sado Island, Tassha Bay
	Wakayama	Shirahama
Pagurus japonicus (Stimpson, 1858)	Ishikawa	Noto-ogi, Tsukumo Bay
Pagurus similis (Ortmann, 1892)	Niigata	Sado Island, Tassha Bay
	Ishikawa	Noto-ogi, Tsukumo Bay
Korea		
Pagurus lanuginosus De Haan, 1849	Gangwon-do	Daejin
Pagurus middendorffii Brandt, 1851	Gangwon-do	Daejin
Pagurus rubrior Komai, 2003*,[2]	Gyeongsangbuk-do	Uljin

[1] as *Pagurus geminus* McLaughlin, 1976

[2] Kim (2013) states his specimens were obtained from washings of hermit crabs and then cites *P. rubrior*, *P. japonica* ans *P. filholi* (as *P. geminus*) in the ecology section.

OD: Ho (1986a—as *S. japonicus*): 22–31; Figs 1–24; Table 1.

AD: Kim (1998): 824–827; Figs 407–408. Kim (2013): 57–61; Figs 20–22.

TL: Japan, Honshū. Ho (1986a) collected the species from three different localities and four different hosts (Table 18) but did not specify the type locality. Contrary to the statement in his paper (p. 22) the holotype was never deposited in the National Museum of Natural History, Washington, D.C. (T.C. Walter *in litt.*, 24 Feb 2010) and hence the precise type locality remains unknown.

BL: 2,550 µm (♀), 2,200 µm (♂) [Kim 1998]; 3,000 ± 700 µm (♀), 2,300 ± 500 µm (♂) [Kim 2013]. Ho (1986a) did not give measurements. Deduction from his Figs 3–4 gives a size of about 8.3 mm for the female and about 6.5 mm for the male, indicating that his scale bars are wrong.

***Sunaristes* sp. *sensu* Hamond (1973b)**

Hamond (1973b) examined two females but did not give any text description or illustrations. According to his key to female *Sunaristes* spp. the Auckland species is most closely related to *S. inaequalis* but can be distinguished by the absence of spinules on P2–P4 enp-2 and the longer inner seta on P4 enp-1 (setal length:total endopod length = 3:2, as opposed to 3:4 in *S. inaequalis*). Ho (1986a) rightly doubted the distinctiveness of this species since the endopodal spinulation of P2–P4 can show significant variability (and aberrations), particulary in *S. tranteri* and *S. inaequalis* (Table 13).

OD: Hamond (1973b): 177 (*cf.* key to females).

TL: New Zealand, Auckland harbour; washings of *Pagurus novizealandiae* (Dana, 1851b) (as *P. novaezealandiae*) (Paguridae).

BL: Unknown.

***Canuella* Scott & Scott, 1893c**

***Canuella perplexa* Scott & Scott, 1893c**

Stock (1952) recorded *C. perplexa* as a commensal of the hermit crab *Pagurus bernhardus* in the western Wadden Sea (Noord Texelstroom, Scheer) and found ovigerous females in late June. Examination of the canuellid material held in the collections of the former Zoölogisch Museum Amsterdam (ZMA), revealed the presence of four vials containing *C. perplexa*, collected from *Buccinum* shells inhabited by *P. bernhardus* (7 ♀♀—ZMA Co. 100.042; 13

♀♀—ZMA Co. 100.043; 3 damaged ♀♀—ZMA Co. 100.044; 2 ♀♀, 6 ♂♂—ZMA Co. 100.054). Lucas (1958) also recorded it from the same host off the Dutch coast but no locality was specified; Faasse (2003) appears to infer that Lucas's material also came from the western Wadden Sea. A single specimen collected by J.H. Stock east of Yerseke on the southern shore of the Oosterschelde (Eastern Scheldt) and initially identified as *S. paguri* turned out to be a copepodid V ♀ of *C. perplexa* (ZMA Co. 200646; coll. 04 April 1993; 6 m depth). Neither Stock (1952) nor Lucas (1958) specified whether *C. perplexa* and *Sunaristes paguri* co-existed in the same gastropod shell, however, one vial (ZMA Co. 100.083) contained one adult female of *S. paguri* and one adult male of *C. perplexa*, both collected from the mouth of the Westerschelde estuary. In contrast to members of *Sunaristes*, which are obligate endolithic commensals, these cursory records suggest that the typically free-living *C. perplexa* only occasionally displays a predilection for the shelter offered by the hermit crab's "mobile home". The Dutch records above and Jakubisiak's (1932) record from *Maja brachydactyla*, are more likely accidental associations or contaminations since species of *Canuella* are known to be good swimmers, living near or in the upper few cm of sandy deposits (Băcesco *et al.* 1957; Vincx & Heip 1979).

OD: Scott & Scott (1893c): 91–92; Plate II (Figs 1–3).

AD**: Brady (1880—as *Longipedia coronata* Claus, 1863—♀ only): 6–8; Plates XXXIV (Figs 3, 9), XXXV (Figs 1, 3, 9). Scott (1893): 201–202; Plate II (Figs 21–35). Sars (1903): 17–18; Plates VIII–IX. Lang (1948): 27–28, 163–164; Abb. 1, 102(1). Pesta (1920): 595, 161; Fig. H3. Pesta (1926): 607; Abb. 1–5. Monard (1928): 289–291; Fig. II-2. Pesta (1932): 10–11; Fig. 3. Stock (1952): 70; Figs c–d. Dussart (1967): 153–155; Fig. 52. Bodin (1970): 391–392; Plate 3. Mielke (1975): 16–17; Abb. 5. Ceccherelli & Rossin (1979): 99. Vincx & Heip (1979): 283–294; Figs 1–9; Table 1. Glatzel (1988): 106–112; Plates I (Figs 1–4), II (Figs 9–12), III (Fig. 17). Huys & Boxshall (1991): 114–115, 117–118, 120, 127, 133, 135, 137, 145–146, 149–150, 352, 355, 360; Figs 2.4.7B, 2.4.13C–D, 2.4.15A, 2.4.17B, 2.4.25D, 2.4.26A, 2.4.29A–E, 2.4.30A–B, 2.4.32B–C, 3.12.1D, 3.15.3B. Hosfeld (1995/1996): 176, 178–186; Figs 9–43. Huys *et al.* (1996): 123, 125, 129–130; Figs 49, 50, 51(A, E).

TL: Scotland, Fife, northern shore of Firth of Forth, Largo Bay.

BL: 1,400 µm (♀) [Brady 1880; Scott 1893; Scott & Scott 1893c]; 1,300 µm (♀), 1,250 µm (♂) [Sars 1903; Pesta 1920, 1932]; 900–1,300 µm (♀) [Lang 1948; Dussart 1967]; 970 µm (♀), 1,030 µm (♂) [Mielke 1975]; 1,100–1,200 µm (♀), 940–1,100 µm (♂) [Ceccherelli & Rossin 1979]; 79 µm (NI), 110 µm (NII), 146 µm (NIII), 149 µm (NIV), 164 µm (NV), 205 µm (NVI), 300 µm (CoI), 344 µm (CoII), 453 µm (CoIII), 698 µm (CoIV), 860 µm (CoV) [Vincx & Heip 1979].

** Note that partial redescriptions based on specimens from the Black Sea (Por 1960; Damian-Georgescu 1970; Apostolov 1972, 1973a, 1973c; Apostolov & Marinov 1988), Egypt (Gurney 1927) and Madagascar (Dussart 1982) are not included here since re-examination revealed that these populations are not conspecific with *C. perplexa*, representing as yet undescribed species.

***Brianola* Monard, 1927**

The genus currently accommodates seven valid species in addition to one unnamed species partly illustrated and described by Huys *et al.* (1996). *Brianola reichi* Por, 1964 and *B. pori* Hamond, 1973b (see below) had previously been transferred to the genera *Nathaniella* Por, 1984b and *Coullana*, respectively (Por 1984b; Huys 1995). The binomen "*Brianola minima*", first proposed by Por (1969: 170, 172) for an undescribed species from the Elat coast, is a *nomen nudum*. Apostolov's (2008) description of *Brianola* sp., based on a single female from the Aegean Sea, is not sufficiently detailed for any decision on its taxonomic status to be made other than that it does not belong to *B. stebleri* (Monard, 1926a). Three species are known as occasional guests of hermit crabs in Europe (Hendrickx & Fiers 2010) and Australia (Hamond 1973b) but have also been recorded in sediment samples independent of any anomuran host. Various undescribed species have been reported from Queensland (Coull *et al.* 1995; Gilby *et al.* 2012), the Philippines (De Troch *et al.* 2008), Vietnam (Chertopud *et al.* 2009), Zanzibar (Gheerardyn *et al.* 2008a; Callens *et al.* 2012) and Brazil (Rocha *et al.* 2011).

Wells' (2007) tabular key to the Canuellidae contains some erroneously coded characters in relation to *B. curvirostris* Božić, 1968, *B. exigua* Por, 1967 and *B. vangoethemi* Fiers, 1982. The first species was coded as having an inner seta on P4 exp-2 but Božić (1968) neither listed nor illustrated this seta in the original description.

The number of elements on P1–P4 enp-3 was scored as 5:4:4:5 in *B. exigua* but Por (1967) clearly illustrated six and five elements on P1–P2 enp-3, respectively, and Hamond's (1973b: 199) reinterpretation of the original description of leg 4 showed that its distal segment in reality bears four elements (instead of five), as in all other members of the genus. The adjusted formula should therefore be 6:5:4:4, being effectively identical with that of *B. hamondi* Wells & Rao, 1987. Note that Wells (2007: 335) had also corrected the original formula of P1 exp-3 for the latter species. Although Wells & Rao (1987) did not compare *B. hamondi* with *B. exigua* there is no doubt that both species are morphologically very similar and can only be differentiated by a few reliable characters. Finally, according to Wells (2007: 340) *B. vangoethemi* lacks the inner coxal seta on leg 1 but Fiers (1982) clearly showed its presence in his Plate II (Fig. 4). The genus contains four pairs of closely related species, some of which may turn out to be conspecific upon re-examination of the type material. Based on the published descriptions they can be separated by the key below.

Key to species of *Brianola* Monard, 1927

1.	P1 exp-3 with four elements	2.
	P1 exp-3 with five elements	3.
	P1 exp-3 with six elements	6.
2.	Rostrum without surface ornamentation; P4 enp-1 inner element very short and stout, rather bulbous in shape	*B. hamondi* Wells & Rao, 1987.
	Rostrum covered with spinules/setules; P4 enp-1 inner element well developed, as long as segment	*B. exigua* Por, 1967.
3.	P1 enp-3 with four elements	4.
	P1 enp-3 with six elements	5.
4.	Caudal ramus about 2.5 times as long (measured along outer margin) as maximum width	*B. stebleri* (Monard, 1926a)
	Caudal ramus about twice as long as maximum width	*Brianola* sp. *sensu* Huys *et al.* (1996).
5.	Proximal inner seta of P1 enp-3 well developed; P4 enp-1 with inner seta present	*B. sydneyensis* Hamond, 1973b.
	Proximal inner seta of P1 enp-3 vestigial; P4 enp-1 without inner seta	*B. vangoethemi* Fiers, 1982.
6.	Antennary exopod with eight setae in total; area between genital apertures of ♀ with four long spinules; pseudoperculum with median fringe of eight serrations; body length ♀ 700 µm	*B. curvirostris* Božić, 1968.
	Antennary exopod with five setae in total; area between genital apertures of ♀ without any spinules; pseudoperculum with median fringe of 25–30 serrations; body length ♀ 970 µm	*B. elegans* Hamond, 1973b.

Brianola stebleri (Monard, 1926a)

Monard (1926a) based his original description of *Brianella stebleri* on several females collected from a muddy substrate in the Étang des Eaux Blanches in southern France. Since the generic name *Brianella* Monard, 1926a was a junior homonym of *Brianella* Wilson, 1915 (Lernaeopodidae) Monard (1927) himself subsequently replaced it by *Brianola* Monard, 1927. The author also added records from the Lake of Tunis (Monard 1935a), Roscoff (Monard 1935b) and Bou Ismaïl (formerly known as Castiglione, Algeria) (Monard 1937). The male remained undescribed until Raibaut (1962b, 1967) illustrated the antennule and rostrum, and Por (1964) provided additional information on the genital field. The species appears to be widely distributed throughout the Mediterranean showing a distinct preference for coastal lagoons and other shallow water habitats characterized by muddy substrata including Lagune du Brusc, Marseille (Bodin 1964), the Bassin de Thau (Raibaut 1962b, 1963a, 1965, 1967), the Bassin d'Arcachon (Castel 1980, 1985, 1986; Castel & Lasserre 1976, 1979), the Venice Lagoon system (Villano & Warwick 1995; Warwick & Villano 2000), Stagni di Porto Pino in Sardinia (Ceccherelli & Mistri 1990), the Bay of Piran (Marcotte & Coull 1975; Marinov & Apostolov 1981), Iraklion harbour, Greece (Lampadariou *et al.* 1997) and the Israeli coast (Por 1964). It has also been recorded from the Portimão lagoon, Algarve in Portugal (Petkovski (1964b), representing the westernmost record of the species. Gaudy (1978) found the species abundantly in culture tanks on the island of Embiez. Monard (1935b) mentioned that the species had been recorded from Canada but I have been unable to trace that record in the published literature.

Until recently the only record of *B. stebleri* outside the Mediterranean and southern Portugal was that by Monard (1935b) who collected the species from the "vivier" (holding tanks) of the biological station at Roscoff, Brittany. Monard questioned its validity because the antennary exopod was larger, the caudal ramus showed two longitudinal spinule rows and the pectinations of the outer spines on the swimming legs appeared different. Huys *et* *al.* (1996) also doubted the authenticity of the record because an as yet unnamed *Brianola* species was discovered on the other side of the English Channel in Percuil Creek in the Fal estuary, Cornwall. The English species differs from *B. stebleri* primarily in the different dimensions of the caudal ramus which appears to be longer in the Mediterranean species (Monard 1926a, 1937; Petkovski 1964b). Recently, Fiers (in Hendrickx & Fiers 2010) recorded *B. stebleri* as an associate of *Pagurus bernhardus* in the Roscoff area but it is likely that this record too should be attributed to *Brianola* sp. *sensu* Huys *et al.* (1996).

OD: Monard (1926a—as *Brianella stebleri*): 40, 45–48; Figs 1–12.
AD: Monard (1935a): 15–16. Monard (1935b): 9. Monard (1937): 28–30; Fig. 1a–c. Raibaut (1962b): 94–95; Figs 2–3. Bodin (1964): 120, 122; Plate I (Fig. 1). Petkovski (1964b): 4, 6; Figs 1–2. Por (1964): 61–62; Plate 3 (Figs 14–16). Raibaut (1967): 11, 13; Fig. 1. Marinov & Apostolov (1981): 24–25; Fig. 1(-3).
TL: France, Languedoc-Roussillon, Hérault, Sète (formerly Cette); Étang des Eaux Blanches, black mud, depth 2 m.
BL: 900 µm (♀/♂) [Monard 1926a, 1935b]; 1,050 µm (♀) [Monard 1935a]; 900 µm (♀), 800 µm (♂) [Raibaut 1962b, 1967]; 950–1,040 µm (♀), 750 µm (♂) [Por 1964].

Brianola elegans Hamond, 1973b

Hamond (1973b) observed slight sexual dimorphism in rostrum shape and spinulation around the posterior margins of the pedigerous somites, however, these differences require confirmation. Fiers (1982) observed several aberrant specimens with rami or entire legs (often leg 1) being replaced by a single, large blunt spine. No such variability was observed by Hamond (1973b).

The only other records of *B. elegans* are those of Fiers (1982) who found it in two intertidal localities in Papua New Guinea (Madang Province), *i.e.* on the north-east side of Laing Island and in Bogia Bay, Huys (1995) who recorded it in coralline sand samples from the Great Barrier Reef, and Chertoprud *et al.* (2009) who reported it from Nha Trang Bay in Vietnam. Given the benthic nature of these records, the symbiotic relationship with *Diogenes senex* reported by Hamond (1973b) may be accidental or at most facultative.

OD: Hamond (1973b): 192–198; Figs 61–83.
TL: Australia, New South Wales, Cronulla (southern metropolitan Sydney); swimming pool of former CSIRO Division of Fisheries and Oceanography (approx. 34º04’30”S, 151º08’53”E) which empties directly into Gunnamatta Bay during low tide; from washings of hermit crabs (*Diogenes senex* Heller, 1865) (Diogenidae) inhabiting empty gastropod shells of primarily *Pyrazus ebeninus* (Bruguière, 1792).
BL: 970 µm (♀), 800 µm (♂).

Brianola sydneyensis Hamond, 1973b

Wells & Rao (1987) provided a partial redescription and revealed the true nature of the hyaline frills and ornamentation of the abdominal somites, and spinular patterns on the caudal rami and protopods of legs 1–4. They also pointed out that the legends of Figs 26 and 28 in Hamond’s (1973b) original description need to be transposed. Besides the type locality, *B. sydneyensis* is also known from another three localities in the Indo-Pacific. Wells & Rao (1987) recorded it from Middle Andaman (Long Island, West Point; 12º22’48”N, 92º56’28”E) and Ritchie’s Archipelago (Neil Island, North Bay; 11º52’02”N, 93º04’30”E). Huys (1995) found it in coralline sand samples from the Great Barrier Reef.

OD: Hamond (1973b): 179–185; Figs 22–40.
AD: Wells & Rao (1987): 5–6; Figs 2a–c, 6b1–d1.
TL: Australia, New South Wales, Cronulla (southern metropolitan Sydney); swimming pool of former CSIRO Division of Fisheries and Oceanography (approx. 34º04’30”S, 151º08’53”E) which empties directly into Gunnamatta Bay during low tide; washings of hermit crabs (*Diogenes senex* Heller, 1865) (Diogenidae) inhabiting empty gastropod shells of primarily *Pyrazus ebeninus* (Bruguière, 1792).
BL: 1,430 µm (♀), 1,380 µm (♂) [Hamond 1973b]; 1,320 µm (♀) [Wells & Rao 1987].

Coullana Por, 1984b

Willey (1923) described *Canuella canadensis* from the surface plankton in the Shubenacadie River in Nova Scotia. His concise description was based solely on the female and included only two figures, illustrating leg 4, the anal somite and the caudal rami. Wilson (1932) subsequently described *Canuella elongata* from the upper Chesapeake Bay and also failed to obtain any males. Both authors compared their respective new species with the European members of the genus, *C. perplexa* and *C. furcigera*. Even though Wilson (1932) cited Willey's (1923) paper he did not compare *C. elongata* with *C. canadensis*. Lang (1948) considered both species names to be synonymous. Por (1967) ignored *C. canadensis* entirely in his review of the family on the ground that he was not sure if Willey's description was accurate (F.D. Por pers. commn, in Coull (1972)).

Coull (1972) re-examined both Wilson's (1932) syntypes and additional material from Maryland, New Jersey and North Carolina, and described the previously unknown male. He confirmed that *C. elongata* is a junior subjective synonym of *C. canadensis* and, based on Por's (1967) criteria, assigned the latter to the genus *Scottolana*.

Hamond (1973b) described the new species *Brianola pori* primarily from washings of hermit crabs. Por (1984b) suggested that *B. pori* did not belong to the genus *Brianola* and should probably be placed in a separate genus. Huys' (1995) observed close similarities between *B. pori* and *C. canadensis*, and transferred the former to the genus *Coullana*. This course of action was adopted by Wells (2007). Although no other species have been allocated to the genus, it is known that at least two other, as yet undescribed, species occur in the Gulf of Mexico (R. Huys, unpubl. data) and Queensland (Coull *et al.* 1995).

Coullana pori (Hamond, 1973b)

Only the female holotype was recorded at the type locality in Narrabeen Lagoon where hermit crabs were lacking. Hamond (1973b) found an additional 94 paratypes in washings of *Diogenes senex* at the shared type locality of *Sunaristes tranteri*, *Brianola elegans* and *B. sydneyensis* in Cronulla (southern metropolitan Sydney). Whether any of these four species effectively co-existed in the same gastropod shell (usually the Hercules club mud whelk, *Pyrazus ebeninus* (Bruguière, 1792), occasionally *Bellastraea* sp. or *Austrocochlea* sp.) is unknown since Hamond's (1973b) copepods were obtained from a collective washing of about 1,000 specimens of *D. senex* and no attempt had been made to prove the association by individual dissection of hermit crabs (R. Hamond *in litt.*). The absence of hermit crabs at the type locality made Hamond suggest that the association between *C. pori* and *D. senex* at Cronulla may either be accidental or facultative. The species has also been found in coralline sand samples from the Great Barrier Reef (Huys 1995). Hicks (1988d) recorded "*Brianola* cf. *pori*" from sediment rafts in Pauatahanui Inlet, an arm of the Porirua Harbour, New Zealand. The latter is probably conspecific with *Brianola* sp. reported from the same inlet by various workers (Coull & Wells 1981; Wells *et al.* 1982; Hicks 1986c; Iwasaki 1993, 1999).

Hamond (1973b) reported slight sexual dimorphism in the size and ornamentation of some setae on P3 and P4.

OD: Hamond (1973b): 186–191; Figs 41–60.
TL: Australia, New South Wales, Narrabeen (northern metropolitan Sydney), Narrabeen Lagoon (approx. 33°43'S, 151°17'E); among weeds at the border of the lagoon.
BL: 1,100 µm (♀), 830 µm (♂).

Intersunaristes Huys, 1995

Fiers (1982) proposed the genus *Parasunaristes* to accommodate four species that exhibited a 2-segmented P4 endopod: *Sunaristes curticaudata* Thompson & Scott, 1903, *Ellucana chelicerata* Por & Marcus, 1973, *Sunaristes dardani* Humes & Ho, 1969a and *Parasunaristes cucullaris* Fiers, 1982. Based on a suite of other characters (Table 19), Huys (1995) recognized a clear divide between the two species pairs *cucullaris-chelicerata* and *dardani-curticaudata* and proposed a new genus *Intersunaristes* for the latter.

Within the *Sunaristes* lineage, *Parasunaristes* and *Intersunaristes* share a sistergroup relationship on the basis of the 2-segmented condition of the P4 endopod. The immediate outgroup of this clade is formed by *Sunaristes* which has retained the 3-segmented condition. The monophyly of this group of three genera is supported by the absence of the inner seta on the P2 coxa, the presence of three elements on P3 enp-3 (*i.e.* outer spine absent), four elements on P4 exp-3 (*i.e.* only one outer spine), three elements on P4 enp-3 (or enp-2 when endopod 2-segmented), and the sexual dimorphism of the P2 endopod involving the formation of outer apophyses on enp-2 and enp-3 in the male.

TABLE 19. Differentiating characters between *Parasunaristes* Fiers, 1982 and *Intersunaristes* Huys, 1995.

	Parasunaristes	*Intersunaristes*
Cephalic pleural areas	backwardly extended into angular processes	rounded
Antennulary subchela ♂	extraordinarily large	moderately developed
Maxilla	sexually dimorphic	not sexually dimorphic
Maxillipedal syncoxa	without seta near proximal margin	with seta near proximal margin
P1 endopodal segments	elongated	not elongated
P2 enp-2 apophysis	not extending to insertion site of proximal inner seta of enp-3	extending to distal margin of enp-3
P6 ♂ armature	outer seta and 2 modified spines	outer seta and one modified spine

Intersunaristes curticaudata (Thompson & Scott, 1903)

Thompson & Scott's (1903) description was based on a single female. The only other record is that by Wells (1967) who found three females in a sandy beach on Inhaca Island (Mozambique). The male remains unknown. Although unconfirmed at present, the host is likely to be crustacean.

OD: Thompson & Scott (1903): 256–257; Plate III (figs 12–17) (♀ only).
TL: Sri Lanka; general washings of marine invertebrates.
BL: 1,600 µm (♀).

Intersunaristes dardani (Humes & Ho, 1969a)

The species is exclusively associated with diogenid hermit crab hosts and assumes an Indo-Pacific distribution with records from Kenya, Madagascar, Mauritius, New Caledonia and Eniwetok (= Enewetak) Atoll (Marshall Islands) (Table 20). *Dardanus lagopodes* (Forskål, 1775) serves as a host across the entire known distribution range of its copepod associate. *Clibanarius virescens* is a very infrequent host in New Caledonia; from the more than 700 individuals examined by Humes (1972) only two copepodids were recovered.

TABLE 20. Diogenid hermit crab hosts of *Intersunaristes dardani* (Humes & Ho, 1969a) in the Indo-Pacific [* type host].

Hermit crab host	Madagascar	Mauritius	Eniwetok Atoll	New Caledonia
Calcinus latens (Randall, 1840)			+	
Clibanarius virescens (Krauss, 1843)				+
Dardanus deformis (H. Milne Edwards, 1836)	+	+		
Dardanus guttatus (Olivier, 1812)	+		+	
Dardanus lagopodes (Forskål, 1775)	+	+	+	+
Dardanus megistos (Herbst, 1804) *	+		+	+
Dardanus scutellatus (H. Milne Edwards, 1848)			+	

TABLE 21. Hosts used by *Intersunaristes dardani* (Humes & Ho, 1969a) in the Nosy Bé area (Madagascar), including locality data and gastropod shells used [data from Humes & Ho (1969a)].

Host	Locality	Position relative to Nosy Bé	Gastropod shells used
Calcinus latens (Randall, 1840)	Nosy Tanga	W of Nosy Bé	*Cerithium*, *Conus*, *Strombus*
Dardanus deformis (H. Milne Edwards, 1836)	Ambariobe island	between Nosy Bé and Nosy Komba	———
Dardanus guttatus (Olivier, 1812)	Antsamantsara	on Nosy Bé	*Cassis*, *Conus*, *Lambis*
	Nosy Tanga	W of Nosy Bé	*Lambis*
	Sanitry	on Nosy Bé	*Lambis*
Dardanus lagopodes (Forskål, 1775)	Nosy Tanga	W of Nosy Bé	*Trochus*
	Pte. Lokobe	on Nosy Bé	*Cypraea*
Dardanus megistos (Herbst, 1804)	Ambariobe island	between Nosy Bé and Nosy Komba	——
	Ambatoloaka	on Nosy Bé	*Murex*
	Ankify	mainland Madagascar, opposite Nosy Komba	——
	Antafianambitry	on Nosy Bé	*Turbo*
	Antsakoabe	on Nosy Bé	*Tonna*
	Bamoko	on Nosy Bé	*Cassis*
	Bay of Ambanoro	on Nosy Bé	*Murex*
	Befifika	on Nosy Bé	*Lambis, Tonna*, *Turbo*
	Nosy Kisimany	S of Nosy Bé	———
	Nosy Tanga	W of Nosy Bé	*Tonna*, *Turbo*
	Pte. Andemby	Nosy Faly island, E of Nosy Bé	*Fasciolaria*
	Pte. à la Fièvre	on Nosy Bé	*Fasciolaria*
	Tany Kely island	S of Nosy Bé	*Bursa*

TABLE 22. Hosts used by *Intersunaristes dardani* (Humes & Ho, 1969a) in the Marshall Islands (Eniwetok Atoll), including locality data and gastropod shells used [data from Humes (1971)].

Host	Locality	Gastropod shells used
Calcinus latens (Randall, 1840)	Eniwetok Island	*Cerithium*, *Conus*, *Strombus*
	Muti (David) Island	*Strombus*
	Sand Island	*Conus*, *Strombus*
Dardanus guttatus (Olivier, 1812)	between Arambiru (Vera) Island and Rojoa (Ursula) Island	*Conus*
Dardanus lagopodes (Forskål, 1775)	Eniwetok Island	*Cerithium*, *Strombus*, *Terebra*
	Muti Island	*Cerithium*, *Terebra*
	Rigili (Leroy) Island	*Cypraea*
	Sand Island	*Cerithium*, *Terebra*
Dardanus megistos (Herbst, 1804)	Eniwetok Island	*Terebra*
Dardanus scutellatus (H. Milne Edwards, 1848)	Eniwetok Island	*Cerithium*
	Sand Island	*Terebra*

TABLE 23. Records of *Intersunaristes dardani* (Humes & Ho, 1969a) in New Caledonia, including hosts and locality data [data from Humes (1972)].

Host	Locality	Coordinates
Clibanarius virescens (Krauss, 1843)	Nouméa (Rocher à la Voile)	20°18’24”S, 166°25’50”E
Dardanus lagopodes (Forskål, 1775)	Îlot Maître (east coast)	22°20’35”S, 166°25’10”E
	5 km S of Yaté	22°11’00”S, 166°59’00”E
	W of Mando Island	20°18’59”S, 166°09’30”E
	Ricaudy reef	
	W of Isle N’Gou	22°13’44”S, 166°23’01”E
Dardanus megistos (Herbst, 1804)	Ricaudy reef	
	Îlot Maître (east coast)	22°20’35”S, 166°25’45”E

TABLE 24. Presence of outer groups of spinules on the rami of P1–P4 in *Intersunaristes dardani* (Humes & Ho, 1969a). Notations in parentheses indicate aberrant conditions.

	P1		P2		P3		P4		References
	exopod	endopod	exopod	endopod	exopod	endopod	exopod	endopod	
	1 2 3	1 2 3	1 2 3	1 2 3	1 2 3	1 2 3	1 2 3	1 2	
♀	+ – –	+ + –	+ + +	+ + –	+ + +	– + –	+ + –	– –	
								(– +)	(1), (2)
					(– – +)	(– – –)			(2)
♂	+ – –	+ + –	+ + +	– + –	+ + +	– + –	+ + –	– +	
								(– –)	(1)

(1): Humes & Ho (1969a); (2) Humes (1971)

Intersunaristes dardani appears to have low host specificity. For example, according to Humes & Ho (1969a) five species of diogenid hermit crab serve as hosts for *I. dardani* in the Nosy Bé area in north-western Madagascar. Their records are summarized in Table 21. The authors also recorded *I. dardani* from at least two diogenid hosts in Mauritius, *i.e. Dardanus deformis* (H. Milne Edwards, 1836) in Blue Bay near Mahébourg, and *Dardanus lagopodes* in the Baie du Tombeau. In addition, they obtained the species from washings of five hermit crabs mixed at the time of collection [*Dardanus setifer* (H. Milne Edwards, 1848), *D. lagopodes* and *Calcinus elegans* (H. Milne Edwards, 1836)], outside the reef at Flic en Flacq. The known hosts and records of *I. dardani* in the Marshall Islands and New Caledonia are tabulated in Tables 22 and 23, respectively. Innocenti (2009) recorded *I. dardani* from *D. lagopodes* in Kanamai, Kenya.

Widely separated populations of *I. dardani* appear to vary in certain intraspecific characters. For example, the Eniwetok population examined by Humes (1971) showed a smaller body size in both sexes, and had an acutely pointed (instead of bifid) process on the genital area of the female, caudal rami that are slightly wider proximally, and an outer spinule row on P4 enp-2 in most females (resembling the male condition: Table 24). Abberations were observed in the P4 endopod of both sexes, including the presence of an additional inner seta on enp-2 in some females and males. The outer spine on P4 enp-2 can occasionally be absent in the female (a similar aberration was observed in the Madagascar material by Humes & Ho (1969a)) and the female P5 can have five setae instead of four.

Humes & Ho (1969a) describe the colour of live females as follows: "the prosome is slightly amber, the urosome nearly colorless, the eye dark red, the intestine dark brown, the ovary lavender to violet, the egg sacs grayish lavender to bright blue". The heavily chitinized distal segment of the antennule and the scythe-like prolongation on P2 enp-1 are conspicuously brownish in the male. The large, elongated and oval egg sacs contain many eggs, often irregular in shape, and averaging about 57 µm in diameter. *Intersunaristes dardani* differs from *I. curticaudata* in the longer caudal rami (1.9 times as long as maximum width *vs* 1.25; length measured along inner margin) and shorter P4 endopod (distinctly shorter than exp-1 and -2 combined *vs* as long as).

OD: Humes & Ho (1969a): 2–12, 14; Figs 1–32; Tables I–II.
AD: Humes (1971): 529–531; Fig. 1(a–h). Huys & Boxshall (1991): 115–118, 120, 130–131, 135, 145–146; Figs 2.4.10A, 2.4.11A, 2.4.15E, 2.4.25C, 2.4.26C.
TL: Madagascar, Diana Region, Nosy Bé island, Antsakoabe; depth 10 m, washings of hermit crabs (*Dardanus megistos* (Herbst, 1804); Diogenidae) inhabiting empty gastropod shells.
BL: 1,900–2,370 µm (♀), 1,650–1,870 µm (♂) [Humes & Ho, 1969a]; 1,490–2,010 µm (♀), 1,430–1,780 µm (♂) [Humes, 1971].

Family Laophontidae

A new genus and species of Laophontidae was recently observed in washings of the sand crab *Blepharipoda liberata* collected in fisheries bycatches off the East Sea coast of South Korea (R. Huys, unpubl. data). The laophontids appeared to co-exist with a second harpacticoid, representing an as yet undescribed genus and species of Ameiridae (see above). The presence of large numbers at both Sacheong Port and Gajin Port suggest that both species are probably common symbionts of *B. liberata* throughout its distribution range in Korea and Japan, and possibly China.

Family Porcellidiidae

Members of the Porcellidiidae have shield-shaped and dorso-ventrally flattened bodies. The dorsal cephalic shield and epimeral plates of the free pedigerous somites are typically provided with a marginal hyaline membrane. Hence, during attachment the body is sealed around most of its perimeter by a membranous extension applied to the surface of the substratum, offering optimal suction efficiency. Attachment is achieved with the aid of a ventral sucker formed by the mandibular palps and first legs (Tiemann 1986).

The family Porcellidiidae contained only *Porcellidium* until Harris (1994) and Harris & Robertson (1994) proposed five new genera. A series of subsequent papers by Harris has raised the number of porcellidiid genera to 16 (Harris 2014b) but some of them have not gained universal acceptance (Huys *et al.* 1996; Walker-Smith 2001; Wells 2007). The great majority of the 71 currently valid species (Harris 2014b) are known as associates of macroalgae and often represent the dominant members in phytal communities (Hicks 1977a). Six described species, all belonging to *Kioloaria* Harris, 1994, have established symbiotic relationships with hermit crabs; a seventh is added here based on a reinterpretation of previously published illustrations. They are found crawling on the inside surface of the gastropod shells used by anomuran decapods and appear to be restricted to the Indo-West Pacific.

Ho (1986a) reported three species of Porcellidiidae from hermit crabs in Japan but only described one of them

(*Porcellidium paguri* Ho, 1986a = *Kioloaria paguri* (Ho, 1986a) **comb. nov.**). The remaining two were represented by only a few specimens collected from *Pagurus japonicus* (Stimpson, 1858) (Paguridae) and *Aniculus miyakei* Forest, 1984 (Diogenidae), respectively. Ho (1986a) collected hermit crabs from Sado Island (Niigata Prefecture) and Noto-ogi (Ishikawa Prefecture) on the west coast of Honshu and Shirahama (Wakayama Prefecture) on the east coast, but did not specify where the two undescribed species originated from. Williams & McDermott (2004) recorded an unidentified species of *Porcellidium* from the diogenid *Calcinus gaimardii* (H. Milne Edwards, 1848) in the Philippines.

Kioloaria Harris, 1994

Harris & Robertson (1994) proposed the genus *Acutiramus* to accommodate two new species, *A. quinquelineatus* Harris & Robertson, 1994 and *A. rufolineatus* Harris & Robertson, 1994, in addition to *Porcellidium acuticaudatum* Thompson & Scott, 1903, *P. brevicaudatum* and *P. ovatum* Haller, 1879 *sensu* Geddes (1968). Huys (2009b) pointed out that the genus was established without the mandatory type fixation, rendering the generic name *Acutiramus* Harris & Robertson, 1994 unavailable. Since the genus had been relegated to a junior subjective synonym of *Porcellidium* (Walker-Smith 2001) Huys (2009b) refrained from suggesting a new replacement name. He also revealed that Ruedemann (1935) had already proposed the name *Acutiramus* for a subgenus of pterygotid eurypterids (upgraded to generic level by Størmer (1974). The eurypterid generic name *Acutiramus* Ruedemann, 1935 (type species *Pterygotus buffaloensis* Pohlman, 1881, by original designation = *Pterygotus cummingsi* Grote & Pitt, 1875; *cf.* Tollerton (1997)) would therefore have made it available under a different authorship and date. In a recent paper, Harris (2014a: 138) reinstated *Acutiramus* by removing it from its synonymy with *Porcellidium*, fixing *A. rufolineatus* as the type species and providing a diagnosis which differentiates it from other genera in the family. Although the generic name was not explicitly indicated as intentionally new (ICZN Art. 16.1) it does satisfy the provisions of ICZN for new names published after 1999 (ICZN Arts 13.1.1 and 13.3). Since *Acutiramus* Harris, 2014a is a junior homonym of *Acutiramus* Ruedemann, 1935 it must be replaced by the next oldest available name from among its synonyms (ICZN Art. 23.3.5). Harris (2014a) recently relegated the monotypic *Kioloaria* Harris, 1994 (type species by original designation: *K. sesquimaculata* Harris, 1994) to a synonym of *Acutiramus*; it is here adopted as the valid replacement name.

Huys (2009b) noted that *Murramia* Harris, 1994—established for the new species *M. bicincta* Harris, 1994 and *M. magna* Harris, 1994—also lacks the mandatory type fixation and is therefore unavailable. Harris (2014b) removed the genus from its synonymy with *Porcellidium* (*cf.* Walker-Smith 2001) and included *Porcellidium poorei* Walker-Smith, 2001 in it but neglected to satisfy the provisions of ICZN Art. 13.3. *Murramia magna* is here fixed as the type of *Murramia* **gen. nov.**, which is expressly proposed as new under its original name (ICZN Art. 16.1), taking authorship and date of the present paper. The taxon can be differentiated from other genera in the Porcellidiidae by the characters outlined in Harris' (1994: 313) diagnosis, hence satisfying the provisions of ICZN Art. 13.1.2. The three species included are to be cited as new combinations, *Murramia magna* (Harris, 1994) **comb. nov.**, *M. bicincta* (Harris, 1994) **comb. nov.** and *M. poorei* (Walker-Smith, 2001) **comb. nov.** It must also be noted that the generic name *Tectacingulum* should be attributed to Huys (2009b) and not Harris (1994) who proposed it as an unavailable name and continued using it under his own authorship and date (Harris 2014b).

Harris (2014a) divided the genus in two groups based on the presence or absence of the inner seta on the proximal endopod segment of leg 3. Species lacking this seta are all associated with hermit crab hosts while those displaying it are typically associated with algae. Symbiotic members of *Kioloaria* occur commonly with diogenid and pagurid hermit crabs in the Indian Ocean and western Pacific Ocean but are notably absent from the Atlantic Ocean (Table 25). They typically produce small broods of large eggs (2–6 per brood), not enclosed by a common egg sac membrane but contained within the cup formed by the urosomites, caudal rami and fifth legs.

Kim & Kim's (1996) material of *Porcellidium brevicaudatum* from Jeju Island is here assigned to a new species, *K. jejuensis* **sp. nov.** The seven *Kioloaria* species that are associated with hermit crabs can be differentiated by the key below.

Key to species of *Kioloaria* Harris, 1994

Note. The terminology used for the caudal setae follows that proposed by Huys (1988b). Harris & Robertson (1994) who did not acknowledge the work of Huys (1988b) or Huys & Boxshall (1991) introduced their own numbering system. Huys (1988b) used Roman numerals while Harris & Robertson (1994) employed a combination of Arabic numerals and Greek letters. Both systems are referred to in the key below with Harris & Robertson's symbols being quoted in parentheses. Wells (2007: Fig. 120) accidentally denoted seta III (γ) by III (χ).

1. Proximal endopod segment of P3 without inner seta in both sexes; associated with hermit crab hosts. 2
Proximal endopod segment of P3 with inner seta in both sexes; associated with algae. . . . . .proceed to Harris (2014a: 140, couplet 6)

2. P3–P4 enp-3 with four and three elements, respectively (outer spine/seta absent) . . . . *K. paguri* (Ho, 1986a) **comb. nov.**
P3–P4 enp-3 with five and four elements, respectively (outer spine/seta present). . . . . 3.

3. P4 enp-1 without inner seta; female rostrum with trilobate anterior margin; male rostrum produced into pointed process . . . . *K. iwasakii* (Harris, 2014a) **comb. nov.**
P4 enp-1 with inner seta; anterior margin of female rostrum not trilobate; male rostrum typically not produced (but pyramidal in *K. tapui*). . . . . 4.

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4. Caudal ramus at least 2.2 times as long as maximum width; insertion site of seta II (T1) located at 75–80% of maximum caudal ramus length (measured from anterior margin); setae IV–VI (T2–T4) evenly spaced. . . . . 5.
Caudal ramus at most 1.9 times as long as maximum width; insertion site of seta II (T1) located at 50–65% of maximum caudal ramus length (measured from anterior margin); closely set setae IV–V (T2–T3) separated from seta VI (T4) by wide gap . . 6.

5. Caudal ramus about 2.7 times as long as maximum width, entire dorsal surface with distinct reticulation; setae IV–VI (T2–T4) closely set together on common prominence at inner distal corner and widely separated from seta III (γ); setae I (β) and VII (α) distinctly shorter than caudal ramus width . . . . *K. cumulus* (Harris, 2014a) **comb. nov.**
Caudal ramus about 2.2 times as long as maximum width, dorsal surface typically smooth, occasionally with inconspicuous reticulation in distal part; setae IV–VI (T2–T4) situated around distal margin; setae II–VI (T1–T4, γ) all about evenly spaced; setae I (β) and VII (α) at least as long as caudal ramus width . . . .*K. tapui* (Hicks & Webber, 1983) **comb. nov.**

6. Caudal ramus subrectangular (distal edge bevelled at outer corner making outer edge slightly shorter than inner one); anterior half of caudal ramus enclosed in arch of genital double-somite . . . . *K. similis* (Kim & Kim, 1996) **comb. nov.**
Caudal ramus distinctly rhomboidal (the long and approximately straight distal edge meeting inner edge at an acute angle with seta VI (T4) at its apex); caudal ramus almost entirely excluded from arch of genital double-somite . . . . 7.

7. Rostrum with rounded anterolateral corners; seta II (T1) 0.75 times as long as seta III (γ), the latter being about 25% of caudal ramus length; P5 exopod 2.2 times as long as wide . . . . *K. brevicaudata* (Thompson & Scott, 1903) **comb. nov.**
Rostrum with pointed anterolateral corners; seta II (T1) very short, about 0.15 times as long as seta III (γ), the latter being about 60% of caudal ramus length; P5 exopod 1.7 times as long as wide . . . .*K. jejuensis* **sp. nov.**

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4. Anterolateral corners ("shoulders") of cephalic shield prominent and protruding; caudal ramus with irregular pattern of round integumental pits on dorsal surface; seta VI (T4) small, shorter than setae II (T1) and IV (T2); seta VII (α) very short, about 20% of ramus length . . . . *K. cumulus* (Harris, 2014a) **comb. nov.**
Anterolateral corners ("shoulders") of cephalic shield rounded; caudal ramus with integumental surface pits; seta VI (T4) at least as long as setae II (T1) and IV (T2); seta VII (α) much longer, at least 45% of ramus length. . . . . 5.

5. Caudal ramus seta VI (T4) about 1/3 the ramus length; seta V (T3) reduced, only half the length of seta IV (T2). . . . . *K. brevicaudata* (Thompson & Scott, 1903) **comb. nov.**
Caudal ramus seta VI (T4) more than half the ramus length; setae IV–V (T2–T3) (sub)equal in length. . . . . 6.

6. Caudal ramus distinctly wider than long, about 0.6 times as long as wide; setae IV–V (T2–T3) half the length of seta VI (T4). . . . .*K. jejuensis* **sp. nov.**
Caudal ramus squarish, slightly wider than long (length about 80–90% of width); setae IV–V (T2–T3) only slightly shorter than seta VI (T4) . . . . 7.

7. Caudal setae I (β) and VII (α) shorter than ramus width and not extending beyond lateral or posterior margins of ramus; setophore (pedestal) bearing aesthetasc on fused antennulary segments 3–4 without a terminal process; anterior margin of rostrum convex . . . . *K. similis* (Kim & Kim, 1996) **comb. nov.**
Caudal setae I (β) and VII (α) at least as long as ramus width and extending well beyond ramus margins; setophore (pedestal) bearing aesthetasc on fused antennulary segments 3–4 with a terminal process; anterior margin of rostrum pyramidal . . . . . 8.

8. Aesthetasc-bearing setophore on third antennulary segment with very long acuminate process. . . . . *K. tapui* (Hicks & Webber, 1983) **comb. nov.**—morph 1.
Aesthetasc-bearing setophore on third antennulary segment with small blunt terminal process . . . . *K. tapui* (Hicks & Webber, 1983) **comb. nov.**—morph 2.

TABLE 25. Host and distributional records of Porcellidiidae associated with hermit crabs.

Host	Copepod species	Country	Locality	Reference
Family Diogenidae				
Aniculus miyakei Forest, 1984	Porcellidiidae sp.	Japan	Honshu (undisclosed locality)	Ho (1986a)
Calcinus gaimardii (H. Milne Edwards, 1848)	*Porcellidium* sp.	Philippines	—	Williams & McDermott (2004)
Calcinus latens (Randall, 1840)	*Kioloaria brevicaudata*	Indonesia	Banda, Goenoeng Api [10]	Humes (1981c)
		New Caledonia	Nouméa, Rocher à la Voile, Pte. Pontillion [11]	Humes (1972)
Calcinus minutus Buitendijk, 1937	*Kioloaria brevicaudata*	Indonesia	Banda, Goenoeng Api [10]	Humes (1981c)
			South of Obi, Pulau Gomumu [12]	Humes (1981c)
Ciliopagurus strigatus (Herbst, 1804) [1]	*Kioloaria brevicaudata*	Indonesia	Banda, Goenoeng Api [10]	Humes (1981c)
Clibanarius bimaculatus (De Haan, 1849)	*Kioloaria paguri*	Japan	Shirahama, Wakayama Prefecture	Ho (1986a)
Clibanarius virescens (Krauss, 1843)	*Kioloaria brevicaudata*	New Caledonia	near Nouméa, Ricaudy Reef	Humes (1972)
			Nouméa, Rocher à la Voile, Pte. Pontillion [11]	Humes (1972)
Dardanus deformis (H. Milne Edwards, 1836)	*Kioloaria brevicaudata*	New Caledonia	near Nouméa, Ricaudy Reef	Humes (1972)
Dardanus guttatus (Olivier, 1812)	*Kioloaria brevicaudata*	Indonesia	east central Halmahera, Karang Mie [13]	Humes (1981c)
			eastern Seram, Pulau Parang [14]	Humes (1981c)
		Madagascar	mainland opposite Nosy Komba, Ankifi	Humes & Ho (1969b) [37]
			Nosy Be (Nossi Bé), Antsamantsara	Humes & Ho (1969b) [38, 39]
			Nosy Be (Nossi Bé), Navetsy	Humes & Ho (1969b) [40]
			Nosy N'Tangam	Humes & Ho (1969b) [38]
		Mauritius	Batterie des Grenadiers, near Trou aux Biches	Humes & Ho (1969b)
		New Caledonia	Port Ngea, 2 km N of Ricaudy Reef [15]	Humes (1972)
Dardanus impressus (De Haan, 1849)	*Kioloaria jejuensis* **sp. nov.**	Korea	Jeju Island, Hanrim	Kim & Kim (1996)
Dardanus lagopodes (Forskål, 1775)	*Kioloaria brevicaudata*	Indonesia	Ambon, Natsepa [16]	Humes (1981c)
			Banda, Goenoeng Api [17]	Humes (1981c)
			east central Halmahera, Karang Mie [13]	Humes (1981c)
			eastern Seram, Pulau Parang [14]	Humes (1981c)
			western Seram, Pulau Marsegoe [18]	Humes (1981c)
		Madagascar	Nosy Be (Nossi Bé), Pte. Lokobe	Humes & Ho (1969b) [41]
		Mauritius	Blue Bay, near Mahébourg	Humes & Ho (1969b)
			Baie du Tombeau	Humes & Ho (1969b)
		New Caledonia	near Nouméa, western end of Ricaudy Reef [19]	Humes (1972)
			near Nouméa, eastern side of Ilot Maître [20]	Humes (1972)
			near Nouméa, Ricaudy Reef	Humes (1972)

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TABLE 25. (Continued)

Host	Copepod species	Country	Locality	Reference
			near Nouméa, W of Ilot Mando [21]	Humes (1972)
			near Nouméa, W of Ilot N'Gou [22]	Humes (1972)
			5 km S of Yaté [23]	Humes (1972)
Dardanus megistos (Herbst, 1804)	*Kioloaria brevicaudata*	Indonesia	western Seram, Pulau Marsegoe [18]	Humes (1981c)
		Kenya	Kanamai	Innocenti (2009)
		Madagascar	mainland opposite Nosy Komba, Ankifi	Humes & Ho (1969b)
			Nosy Be (Nossi Bé), Antsakoabe	Humes & Ho (1969b)
			Nosy Be (Nossi Bé), Bay of Ambanoro	Humes & Ho (1969b) [41]
			Nosy Be (Nossi Bé), Befifika	Humes & Ho (1969b) [42]
			Nosy Be (Nossi Bé), Navetsy	Humes & Ho (1969b) [42]
			Nosy Komba, Pte. Ambarionaomby	Humes & Ho (1969b)
			Nosy N'Tangam	Humes & Ho (1969b) [43]
			Nosy Tany Kely	Humes & Ho (1969b) [44]
		Mauritius	Baie du Tombeau	Humes & Ho (1969b)
		New Caledonia	near Nouméa, eastern side of Ilot Maître [24]	Humes (1972)
			near Nouméa, Ricaudy Reef	Humes (1972)
			near Nouméa, SW side of Port Ngea [15]	Humes (1972)
			near Nouméa, W of Paita [25]	Humes (1972)
Dardanus scutellatus (H. Milne Edwards, 1848)	*Kioloaria brevicaudata*	New Caledonia	near Bourail, Poe beach [26]	Humes (1972)
Paguristes barbatus (Heller, 1862)	*Kioloaria tapui*	New Zealand	Otago Shelf, 90 m [27]	Hicks & Webber (1983) [45, 46]
			Otago Shelf, 104 m [28]	Hicks & Webber (1983) [47]
			SE of Aldermen Islands, 202–207 m [29]	Hicks & Webber (1983) [48]
Areopaguristes pilosus (H. Milne Edwards, 1836) [2]	*Kioloaria tapui*	New Zealand	N of New Plymouth, 48 m [30]	Hicks & Webber (1983) [45]
"*Areopaguristes setosus*" (H. Milne Edwards, 1848) [3]	*Kioloaria tapui*	New Zealand	Whangaroa Harbour entrance, 25 m [31]	Hicks & Webber (1983) [49, 50]
Family Paguridae				
Diacanthurus rubricatus (Henderson, 1888) [4]	*Kioloaria tapui*	New Zealand	Plimmerton Beach, surf zone	Hicks & Webber (1983) [51]
			Otago Shelf, 90 m [27]	Hicks & Webber (1983) [45]
Diacanthurus spinulimanus (Miers, 1876) [5]	*Kioloaria tapui*	New Zealand	Otago Shelf, 90 m [27]	Hicks & Webber (1983) [45]
Lophopagurus cookii (Filhol, 1883) [6]	*Kioloaria tapui*	New Zealand	Otago Shelf, 58 m [32]	Hicks & Webber (1983) [46]

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TABLE 25. (Continued)

Host	Copepod species	Country	Locality	Reference
			Otago Shelf, 104 m [28]	Hicks & Webber (1983) [52, 53]
Lophopagurus stewarti (Filhol, 1883) [7]	*Kioloaria tapui*	New Zealand	SE Three Kings Islands [33]	Hicks & Webber (1983) [54]
Lophopagurus thompsoni (Filhol, 1885)	*Kioloaria tapui*	New Zealand	Otago Shelf, 58 m [32]	Hicks & Webber (1983) [46, 53, 55, 56]
			Otago Shelf, 104 m [28]	Hicks & Webber (1983) [46, 47, 57]
Pagurus filholi (De Man, 1887) [8]	*Kioloaria paguri*	Japan	Tassha Bay, Sado Island, Niigata Prefecture	Ho (1986a)
			Shirahama, Wakayama Prefecture	Ho (1986a)
Pagurus japonicus (Stimpson, 1858)	Porcellidiidae sp.	Japan	Honshu (undisclosed locality)	Ho (1986a)
	Kioloaria paguri	Japan	Tsukumo Bay, Noto-Ogi, Ishikawa Prefecture	Ho (1986a)
Pagurus novizealandiae (Dana, 1851b)	*Kioloaria tapui*	New Zealand	Kaikoura, Kean Point, intertidal	Hicks & Webber (1983) [43, 58, 59]
			Porirua Harbour, Pauatahanui Inlet, intertidal	Hicks & Webber (1983) [46, 60, 61]
Pagurus pectinatus (Stimpson, 1858)	*Kioloaria similis*	Korea	Ulleung Island	Kim & Kim (1996)
Pagurus similis (Ortmann, 1892)	*Kioloaria similis*	Korea	Munseom (Mun Island) off Jeju Island	Kim & Kim (1996)
			Chodong, Ulleung Island [34]	Kim & Kim (1996)
			Dokdo Island (Liancourt Rocks)	Kim & Kim (1996)
			Busan, Haeundae, Mip'o Port	Kim & Kim (1996)
			Chujado Island	Kim & Kim (1996)
Pagurus sinuatus (Stimpson, 1858)	*Kioloaria cumulus*	Australia	New South Wales, Kioloa, O'Hara Head [35]	Harris (2014a)
	Kioloaria iwasakii	Australia	New South Wales, Kioloa, O'Hara Head [35]	Harris (2014a)
Pagurus traversi (Filhol, 1885)	*Kioloaria tapui*	New Zealand	Kaikoura, Kean Point, intertidal	Hicks & Webber (1983) [43, 58]
			Kaikoura Peninsula, Baxter's Reef, 10–12 m [9]	Hicks & Webber (1983) [62, 63]
Pagurus sp. A	*Kioloaria tapui*	New Zealand	Banks Peninsula, Wainui Bay, surf zone	Hicks & Webber (1983) [64]
Pagurus sp.	*Kioloaria brevicaudata*	New Caledonia	Nouméa, Rocher à la Voile, Pte. Pontillion [11]	Humes (1972)
Pylopagurus sp.	*Kioloaria tapui*	New Zealand	Otago Shelf, 104 m [28]	Hicks & Webber (1983)
Unidentified Paguridae	*Kioloaria tapui*	New Zealand	Spirits Bay, 18m [36]	Hicks & Webber (1983) [59]

[1–9] Original host citations: [1] *Trizopagurus strigatus* (Herbst, 1804); [2] *Paguristes pilosus* (H. Milne Edwards, 1836; [3] "*Paguristes setosus*" (Filhol, 1885); [4] *Pagurus rubricatus* (Henderson, 1888); [5] *Pagurus spinulimanus* (Miers, 1876); [6] *Australeremus cooki* (Filhol, 1883); [7] *Pylopagurus stewarti* (Filhol, 1883), mixed with "*D. spinulimanus*" and "*Lophopagurus lacertosus*" (Henderson, 1888) [as "*Pylopagurus crenatus*" (Borradaile, 1916); [8] *Pagurus geminus* McLaughlin, 1976; [9] mixed with *Diacanthurus spinulimanus* (Miers, 1876) [as *Pagurus spinulimanus* (Miers, 1876)].

[10–36] Geographical coordinates: [10] 4°31'55"S, 129°52'12"E; [11] 22°18'24"S, 166°25'50"E; ; [12] 1°50'00"S, 127°30'54"E [13] 00°20'07"N, 128°25'00"E; [14] 03°17'00"S, 130°44'48"E; [15] 22°18'18"S, 166°26'47"E; [16] 3°27'0"S, 128°17'00"E; [17] 4°31'45"S, 129°51'55"E and 4°31'55"S, 129°52'12"E; [18] 02°59'30"S, 128°03'30"E; [19] 22°19'05"S, 166°26'28"E; [20] 22°20'35"S, 166°25'10"E; [21] 22°18'59"S, 166°09'30"E; [22] 22°13'44"S, 166°23'01"E; [23] 22°11'00"S, 166°59'00"E; [24] 22°20'35"S, 166°25'45"E; [25] 22°07'00"S, 166°12'00"E; [26] 21°40'00"S, 165°27'00"E; [27] 45°46.8'S, 170°55'E; [28] 45°52'S, 170°53.5'E; [29] 37°00.5'S, 176°12.7'E; [30] 38°55'S, 174°09.3'E; [31] 35°00.35'S, 173°45.7'E; [32] 45°49'S, 170°50'E; [33] 34°18.8'S, 172°18.5'E; [34] 35°05'N, 128°44'E; [35] 25°34'S, 150°25'E (estimated); [36] 34°25.9'S, 172°49.6'E.

[37–64] Gastropod and scaphopod shells utilized: [37] *Conus* sp.; [38] *Lambis* sp.; [39] *Cassis* sp.; [40] *Cypraea* sp.; [41] *Murex* sp.; [42] *Tonna* sp.; [43] *Turbo* sp.; [44] *Bursa* sp.; [45] *Austrofusus* sp.; [46] *Maoricolpus* sp.; [47] *Glaphyrina* sp.; [48] *Alcithoe* sp.; [49] *Xymene* sp.; [50] *Muricopsus* sp.; [51] *Semicassus* sp.; [52] *Astraea* sp.; [53] *Maurea* sp.; [54] *Dentalium* sp. (*P. stewarti* only); [55] *Trochus* sp.; [56] *Eucominia* sp.; [57] *Buccinulum* sp.; [58] *Melagraphia* sp.; [59] *Cominella* sp.; [60] *Diloma*; [61] *Amphibola* sp.; [62] *Cookia* sp.; [63] *Argobuccinum* sp.; [64] *Umbonium* sp..

Kioloaria brevicaudata (Thompson & Scott, 1903) comb. nov.

The species was originally described as *Porcellidium brevicaudatum* from six females obtained in washings of pearl oysters and other dredged invertebrates collected off Sri Lanka (Thompson & Scott 1903), however, Ho (1986a) assumed that the specimens were originally associated with a hermit crab host. A single female was subsequently found by Scott (1909) in similar washings of dredged invertebrates at 13 m depth near the anchorage off Pulu Jedan on the north-east coast of Tanahbesar Island (Indonesia, Maluku Province, Aru Islands; 05°24.0'S, 134°43.0'E). Humes & Ho (1969b) subsequently (re)described both sexes of *P. brevicaudatum* from material collected in Madagascar and Mauritius and confirmed its association with hermit crabs. Nauplii, copepodids and adults were found in washings of three diogenid hosts (*Dardanus guttatus*, *D. lagopodes* and *D. megistos*). Humes (1972, 1981c) recorded *P. brevicaudatum* from the same three *Dardanus* species in New Caledonia and the Maluku Islands (Moluccas), and added one new pagurid and six new diogenid hosts from the western Pacific (Table 25).

The various populations recorded across the Indo-Pacific are morphologically very similar except for the material reported from Korea (Kim & Kim 1996) which is assigned below to a new species. Specimens from the Moluccas are slightly smaller than those reported from Madagascar (Humes 1981c) but are otherwise identical.

Zaleha *et al.* (2013) reported *Porcellidium brevicaudatum* in washings of algae and seagrasses in Sungai Pulai, southern Peninsular Malaysia but the absence of an inner seta on the proximal endopodal segment of leg 3 indicates that their identification is incorrect. Provided the generic assignment of their material is correct (the authors presented only a concise text description without illustrations) it is likely that they were dealing with a member of the "algal group" of *Kioloaria* (*cf.* Harris 2014a: 139). This group comprises *K. quinquelineata* (Harris & Robertson, 1994) **comb. nov.**; *K. rufolineata* (Harris & Robertson, 1994) **comb. nov.**; *K. sesquimaculata* (Harris, 1994) **comb. nov.**; *K. bipunctata* (Harris, 2014a) **comb. nov.**; *K. edenensis* (Harris, 2014a) **comb. nov.** and *K. geddesi* (Harris, 2014a) **comb. nov.** [Note that Harris (2014a) proposed this name for *Porcellidium ovatum* Haller, 1879 *sensu* Geddes (1968) but erroneously attributed it to Geddes as *Acutiramus geddesi* (Geddes, 1968) comb. nov.].

The colour in life is slightly greenish amber and the nauplius eye red. The opaque grey egg sac contains 2–6 relatively large eggs, each about 100–130 µm in diameter (Humes & Ho 1969b). The number of copepods on an individual hermit crab may be very large. For example, Humes (1972) quoted the case of a single *D. megistos* from Port Ngea, New Caledonia, harbouring 623 specimens, including 253 females, 241 males and 129 copepodids. Humes (1981c) observed pairs in amplexus on *D. lagopodes*. In Madagascar *K. brevicaudata* occasionally cohabits with *Intersunaristes dardani* and *Paraidya occulta* on the same diogenid hosts (Humes & Ho 1969b).

OD: Thompson & Scott (1903—as *Porcellidium brevicaudatum*): 275; Plate XII (figs 11–14).
AD (all as *P. brevicaudatum*): Humes & Ho (1969b): 114–122; Figs 1–28. Humes (1981c): 6–7. Hicks & Webber (1983): 449; Table 2.
TL: Sri Lanka, washings of pearl oysters and other invertebrates (sponges, corals, ascidiaceans, etc.).
BL: 670 µm (♀) [Thompson & Scott 1903]; 770–780 µm (♀), 510–550 µm (♂) [Humes & Ho 1969b]; 610–660 [740] µm (♀), 420–450 µm (♂) [Humes 1981c].

Kioloaria tapui (Hicks & Webber, 1983) comb. nov.

Harris (2014a: 154) transferred the species from *Porcellidium* to *Acutiramus*. It is common and widespread throughout New Zealand from the intertidal to depths of 202–207 m southeast of the Aldermen Islands. Within such an extensive geographic and bathymetric distribution, it exhibits the greatest range of morphological variation yet recorded within the Porcellidiidae. Intra-, interpopulation, pathological, and even intra-individual variants were observed. Hicks & Webber (1983) assessed the magnitude of this variability with morphometric data and suggested that the high degree of variation is linked with the particular life style of *K. tapui*. Although algae-dwelling *Porcellidium* species presumably exhibit high gene flow, Hicks & Webber (1983) indicated that *P. tapui* and other species associated with hermit crabs are isolated from other such populations. This isolation could limit gene flow and lead to genetic drift, thereby explaining the observed variation in *Porcellidium* species associated with hermit crabs (Williams & McDermott 2004). Phenotypic traits imposed by different paguridean hosts, occupation of different gastropod shells with their attendant constraints on internal space, and different host habitats and depths, may all contribute to high variability (Hicks & Webber 1983).

Males are represented by two distinct morphs which can consistently be separated by size and the morphology of the antennule. Morph 1 displays a large conspicuous acuminate process arising laterally from the third antennulary segment and carrying an aesthetasc on the proximolateral margin. Morph 2 is significantly larger than morph 1 and its acuminate process is merely a rudiment of the former. The anterior border of the cephalothorax is slightly less concave, the rostrum and anterolateral comers of the cephalothorax are marginally more acute, and the setae along the rear margin of the caudal rami are often relatively shorter than in morph 1. There is no evidence that the morphs represent successive stages of development. Both can be found in a fully mature condition with well developed spermatophores visible inside and both were observed in amplexus with juvenile females. The adaptive value in alternative dominance by each morph and the precise function of the acuminate process remain enigmatic (Hicks & Webber 1983). Apart from exhibiting dimorphism, males are also variable (*i.e.* antennulary variability in morph 2).

The species appears to display low host specificity, being known from a wide range of hermit crab hosts, including three species of Diogenidae and ten species of Paguridae (Table 25).

OD: Hicks & Webber (1983—as *Porcellidium tapui*): 439–449; Figs 1–24; Tables 1–3.

TL: New Zealand, South Island, Canterbury Region, Kaikoura; Kean Point, intertidal zone; from inside gastropod shells containing *Pagurus novizealandiae* (Dana, 1851b) (Paguridae).

BL: 600–800 µm (♀), 510 ± 20 µm (♂ morph 1), 550 ± 20 µm (♂ morph 2).

Kioloaria paguri (Ho, 1986a) comb. nov.

The species has a radically divergent armature formula on the endopods of legs 3–4 in both sexes. Kim & Kim's (1996: Table 1) claim that Ho (1986a) had reported *Pagurus similis* (Ortmann, 1892) as a host in Tassha Bay, Sado Island (Niigata Prefecture) and Tsukumo Bay, Noto-ogi (Ishikawa Prefecture) is an inadvertent slip of the pen. *Kioloaria paguri* is so far endemic to Japan where it is associated with one diogenid and two pagurid hosts (Table 25).

OD: Ho (1986a—as *Porcellidium paguri*): 29, 31–37; Figs 25–46.

TL: Japan, Honshu island. Ho's (1986a) type material originated from three hermit crab hosts collected at three different localities, *i.e.* the pagurids *Pagurus filholi* (De Man, 1887) [as *Pagurus geminus* McLaughlin, 1976] from Tassha Bay, Sado Island (Niigata Prefecture) and *Pagurus japonicus* (Stimpson, 1858) from Tsukumo Bay, Noto-ogi (Ishikawa Prefecture), and the diogenid *Clibanarius bimaculatus* (De Haan, 1849) from Shirahama (Wakayama Prefecture). Since Ho neither fixed a holotype nor specified a type locality all the specimens of the type series are automatically syntypes and the type locality encompasses all of three places of origin (ICZN Art. 73.2.3).

BL: 540 µm (♀), 460 µm (♂) [Ho 1986a: based on Figs 25–26].

Kioloaria similis (Kim & Kim, 1996) comb. nov.

Kim & Kim (1996) observed slight variability in the length:width ratios of the female caudal ramus (1.67–2.00:1) and fifth legs 1.96–2.18:1). Additional variability was recorded in the shape of the genital double-somite. The egg sac contains four large eggs. The species is known from two pagurid hosts, *P. similis* and *P. pectinatus*, and is so far endemic to the Korean peninsula (Table 25).

OD: Kim & Kim (1996—as *Porcellidium similis*): 376–381, 384; Figs 1–3; Table 1.

AD: Kim (1998): 833–835; Fig. 412. Lee *et al.* (2012): 197–200; Figs 138–139 [reproduced from OD].

TL: Korea, East Sea (Sea of Japan), Ulleung Island, Chodong (35°05'N, 128°44'E); 35 m depth; washings of *Pagurus similis* (Ortmann, 1892) (Paguridae).

BL: 760 µm (♀), 500 ± 30 µm (♂) [Kim & Kim 1996; Kim 1998].

Kioloaria cumulus (Harris, 2014a) comb. nov.

Females and males are frequently covered with numerous naked and thecate protists such as suctorian ciliates (Harris 2014a). It was found to co-exist with *K. iwasakii* inside the same gastropod shell inhabited by *Pagurus sinuatus* (Stimpson, 1858) but not in empty shells or those occupied by the gastropod *Lunella torquata* (Gmelin, 1791).

OD: Harris (2014a—as *Acutiramus cumulus*): 151–155; Figs 27(A–G), 28(A, C, E), 29(B, E); Table 2.
TL: Australia, New South Wales, Kioloa; O'Hara Head (25°34'S 150°25'E, estimated); from inside shells of *Lunella torquata* (Gmelin, 1791) (as *Turbo torquatus* Gmelin, 1791) inhabited by *Pagurus sinuatus* (Stimpson, 1858) (Paguridae).
BL: 780 µm (♀), 550–580 µm (♂).

Kioloaria iwasakii (Harris, 2014a) comb. nov.

Individuals are often heavily burdened with suctorian ciliates around the perimeter of the body (Harris 2014a). The species cohabits with *K. cumulus* on the same host individual.

OD: Harris (2014a—as *Acutiramus iwasakii*): 149–150, 153–154; Figs 26(A–H), 28(B, D, F, G), 29(A, C, D).
TL: Australia, New South Wales, Kioloa; O'Hara Head (25°34'S 150°25'E, estimated); from inside shells of *Lunella torquata* (Gmelin, 1791) (as *Turbo torquatus* Gmelin, 1791) inhabited by *Pagurus sinuatus* (Stimpson, 1858) (Paguridae).
BL: 700–720 µm (♀), 540 µm (♂).

Kioloaria jejuensis sp. nov.

Kim & Kim (1996) noted some differences between their material of *Porcellidium brevicaudatum* from Jeju Island and the Madagascan specimens used by Humes & Ho (1969b) for their redescription, including the length and ornamentation of caudal seta III and body size in the female, and the shape of the caudal ramus and proportions of leg 5 in the male. Additional differences between females can be observed in the shape of the rostrum (pointed *vs* rounded anterolateral corners), the size of caudal seta seta II (T1) (0.15 *vs* 0.75 times as long as seta III (γ)), the length:width ratio of P5 exopod (1.7 *vs* 2.2) and the ratio between the length of the genital double-somite and the depth of its caudal arch (2.5 *vs* 3.5—as measured in Kim & Kim 1996: Fig. 1). Males can be further differentiated by additional caudal ramus characters such as the length of setae V (T3) (as long as *vs* only half the length of seta IV (T2)) and VI (T4) (almost as long as *vs* about 1/3 the ramus length). Having not been recorded before in other species it is unlikely that this suite of differences can be attributed to intraspecific variability. The Jeju Island population is here regarded as a new species, *K. jejuensis* **sp. nov.** which can be differentiated from its congeners by the characters described by Kim & Kim (1996: 381–384) and those listed above (ICZN Art. 13.1.2). In accordance with ICZN Arts 72.5.6 and 73.1.4 the female illustrated by Kim & Kim (1996: 382, Fig. 4A–F) is here fixed as the holotype.

The new species is known only from its type locality and its diogenid type host, *Dardanus impressus* (De Haan, 1849). The Korean material identified and illustrated by Lee *et al.* (2012) as *P. brevicaudatum* does not belong to *K. jejuensis* **sp. nov.** and not even to the genus *Kioloaria*.

OD: Kim & Kim (1996—as *Porcellidium brevicaudatum*): 381–384; Fig. 4; Table 1.
AD: Kim (1998): 831–833; Fig. 411.
TL: Korea, Jeju (Cheju) Island, Hanrim; associated with *Dardanus impressus* (De Haan, 1849) (Diogenidae).
BL: 680 ± 30 µm (♀), 500 ± 30 µm (♂) [Kim & Kim 1996; Kim 1998].

Family Pseudotachidiidae

Idomenella T. Scott, 1906a

Scott (1906a) proposed the genus *Idomenella* for two species initially described by him in the genus *Dactylopus* Claus, 1863, *D. rostratus* T. Scott, 1893 and *D. coronatus* T. Scott, 1894b, without explicitly fixing either of them as the type species. Both Lang (1934: 28) and Sars (1911: 375) erroneously claimed that only the latter species was originally included in *Idomenella*. According to ICZN Art. 69.4, elimination of all but one of the originally included species does not in itself constitute type fixation nor does Sars's statement "… the type species is in reality of considerably large size than either of the 2 known species belonging to the genus *Idomene*" qualify as a rigidly construed designation (ICZN Art. 67.5). Huys (2009b: 27), in discussing the synonymy of *Idomene* Philippi, 1843, subsequently fixed *D. coronatus* as the type of *Idomenella*. While Sars (1909a) redescribed the latter for no apparent reason under the name *Idomene coronata*, both Monard (1927) and Pesta (1927) maintained the distinction between *Idomene* and *Idomenella*, based on the segmentation and ornamentation of the antennule and the separation/fusion of the rami of leg 5. Lang (1934) considered his newly described *Idomene intermedia* from Campbell Island a transitionary form between *Idomenella* and *Idomene*, displaying the antennulary condition of the former and the leg 5 morphology of the latter. He consequently synonymized both genera and cited *Dactylopus coronatus* under its new combination *Idomene coronata* (T. Scott, 1894b). Huys (2009b) considered *Idomene sensu* Philippi (1843) a *genus incertae sedis* in the Clausidiidae (Cyclopoida) and replaced *Idomene sensu* Sars (1906a) by its oldest available synonym, *Xouthous* Thomson, 1883 (type: *X. novaezealandia* Thomson, 1883). The genus currently accommodates 15 valid species and four species of uncertain status (Table 26).

Sars (1905b, 1911) established *Dacylopodella* to accommodate *Dactylopus flavus* Claus, 1866 (type species by monotypy) and added a new species, *Dactylopodella clypeata* Sars, 1911, from southern Norway. Lang (1936a) subsequently included *Dactylopus rostratus* as well as *Dactylopusia ornata* Norman & Scott, 1905, the type species (by monotypy) of *Vallentinia* Norman & Scott, 1906, which he had relegated to a junior subjective synonym of *Dactylopodella*. The latter genus has since then seen the addition of *D. incerta* Vervoort, 1964, *D. vervoorti* Moore, 1976a (a new name proposed for *D. clypeata sensu* Vervoort (1962); *cf.* Moore 1976a) and *D. janetae* Hicks, 1989. Following the relegation of *D. ornata* (Norman & Scott, 1905) to a junior synonym of *D. flava* (Claus, 1866) by Hicks (1989) and the transfer of *D. incerta* to *Paradactylopodia* Lang, 1944 by Willen (1999) the genus currently accommodates five valid species (Wells 2007).

Vervoort (1964) described the distinction between *Xouthous* (as *Idomene*) and *Dactylopodella* in Lang's (1936a, 1948) sense as vague and in need of reconsideration while Willen (1999) casted doubt on the monophyly of the latter genus. Comparative analysis of the species currently assigned to *Xouthous* and *Dactylopodella* exposes the heterogeneity of both genera (Table 26). Four species (originally described as *Idomene australis* Brady, 1910, *I. pusilla* Brady, 1910, *Dactylopusia ferrieri* T. Scott, 1912 and *I. kabylica* Monard, 1936) are inadequately described and not considered here; pending re-examination of new material they should be ranked *species incertae sedis* in the Pseudotachidiidae. The remaining species can be divided in three groups based primarily on body shape, P1 endopodal armature and swimming leg segmentation. Species of Group I are characterized by a dorsoventrally depressed body, 3-segmented P2–P3 endopods in both sexes, a total of two claws and two setae on the distal segment of the P1 endopod, and the presence of 2–3 spines on the pleurotergites of the first three free pedigerous somites (bearing P2–P4). Although some of these characters cannot be verified for a number of species due to insufficient detail in the original descriptions it is clear that the members of Group I form a coherent cluster which is here considered to be equivalent to *Xouthous*. Future analysis will probably restrict the generic concept to a core group of species characterized by the discrete colour pattern (first three free somites red or brownish), the teardrop-shaped (guttiform) habitus, the presence of two enlarged spines on the mandibular exopod, and the 2-segmented P1 endopod with a distinctly trapezoidal-shaped proximal segment.

TABLE 26. Major characteristiscs of species previously assigned to *Xouthous* Thomson, 1883 and *Dactylopodella* Sars, 1905b. Body shape: guttiform = teardrop-shaped, clypeiform = shield-shaped, *i.e.* prosome dorsoventrally depressed and markedly wider than urosome. A1 ♀: number of segments. Md palp: presence/absence and number of enlarged spines on exopod. P1 endopod: segmentation (segm.) and armature of enp-2 (and enp- 3 when 3-segmented), cl = claw(s), s = seta(e). P5 ♀: exp = exopod, benp = baseoendopod, p = flat spines forming palisade, n = normal elements. [Group I = *Xouthous*; Group II = *Dactylopodella*; Group III = *Idomenella* T. Scott, 1906a].

	body shape	colour pattern	epimeral spines	A1 ♀	Md palp	P1 endopod		P2–P3 enp ♀	P2 enp ♂	P5 ♀	
						segm.	armature			exp	benp
Group I											
X. novaezealandiae Thomson, 1883	guttiform	opaque brown	?	7	yes-2	2-segm.	2 cl + ?	3-segm.	?	5	5/n
X. purpurocinctus (Norman & Scott, 1905)	guttiform	yes	?	7	yes-2	2-segm.	2 cl + 2 s	3-segm.	3-segm.	5	5/n
X. simulans (Brady, 1910)	guttiform	yes	+	7	yes-2	2-segm.	2 cl + 2 s	3-segm.	3-segm.	6	5/n
X. parasimulans (Médioni & Soyer, 1968)	guttiform	yes	+	7	yes-2	2-segm.	2 cl + 2 s	3-segm.	?	6	5/n
X. aemula (Thompson & Scott, 1903)	guttiform	yes	?	7	yes-2	2-segm.	2 cl + ?	3-segm.	?	5	5/p
X. wellsi **sp. nov.** [1]	guttiform	yes	+	7	yes-2	2-segm.	2 cl + 2 s	3-segm.	?	5	5/p
X. laticaudatus (Thompson & Scott, 1903)	guttiform	yes	+	6	yes-2	2-segm.	2 cl + 2 s	3-segm.	?	5	5/p
X. maldiviae Sewell, 1940	guttiform	yes	+	6	yes-2	2-segm.	2 cl + 2 s	3-segm.	?	6	5/p
X. andamanensis **sp. nov.**	guttiform	yes	+	6	yes-2	2-segm.	2 cl + 2 s	3-segm.	?	6	5/p
X. sarsi Huys, 2009b	clypeiform	yellowish	?	7	yes-3	3-segm.	1 s; 2 cl + 1 s	3-segm.	3-segm.	5	5/n
X. scotti (Lang, 1948) [2]	clypeiform	?	?	7	yes-3	3-segm.	? s; 2 cl + 1 s	3-segm.	3-segm.	5	5/n
X. cookensis (Pallares, 1975c)	clypeiform	yellowish	+	7	no	3-segm.	1 s; 2 cl + 1 s	3-segm.	3-segm.	5	5/n
X. borealis (Sars, 1911)	clypeiform	?	?	7	no	3-segm.	1 s; 2 cl + ? s	3-segm.	?	5	5/n
X. namibiensis **sp. nov.**	?	?	?	7	?	2-segm.	2 cl + 1 s	3-segm.	3-segm.	6	5/n
X. pectinatus (Scott & Scott, 1898)	clypeiform?	?	?	7	?	2-segm.	1 cl + 1 s	3-segm.	?	6	5
Group II											
D. flava (Claus, 1866)	elongate	no	no	6	no	2-segm.	1 cl + 1 s	2-segm.	2-segm.	5	5
D. clypeata Sars, 1911	clypeiform	no	no	6	no	2-segm.	1 cl + 1 s	2 segm.	2-segm.	5	5
D. vervoorti Moore, 1976a	elongate	no	no	6	?	2-segm.	1 cl + 1 s	2-segm.	2-segm.	5	5
Group III											
D. rostrata (T. Scott, 1893)	elongate	no	no	7	no	3-segm.	1 s; 2 cl + 2 s	3-segm.	3-segm.	5	4?
D. janetae Hicks, 1989	elongate	no	no	6	no	3-segm.	1 s; 2 cl + 2 s	3-segm.	?	5	5
X. coronatus (T. Scott, 1894b)	elongate	no	no	6	no	3-segm.	1 s; 2 cl + 2 s	3-segm.	?	5	5
Idomenella paracoronata **sp. nov.**	elongate	no	no	6	no	3-segm.	1 s; 2 cl + 2 s	3-segm.	?	5	5
X. antarcticus (Giesbrecht, 1902) [3]	elongate	no	no	6	no	3-segm.	1 s; 2 cl + 2 s	3-segm.	3-segm.	4	5
X. intermedius (Lang, 1934)	elongate	no	no	6	no	3-segm.	1 s; 2 cl + 1 s	3-segm.	?	5	5
Incertae sedis											
Idomene australis Brady, 1910	elongate	?	?	?	?	3-segm.	?	3-segm.	3-segm.	?	?
Idomene pusilla Brady, 1910	?	?	?	7	no	3-segm.	1 s; 2 cl + 1 s	3-segm.	?	5	5
Dactylopusia ferrieri T. Scott, 1912	elongate	?	?	7	?	3-segm.	0 + 2 cl	3-segm.	?	5	5
Idomene kabylica Monard, 1936	clypeiform	?	?	6	no	2-segm.	2 cl	3-segm.	?	6	5

[1]: based on re-examination of specimens of *Idomene laticaudata* (Thompson & Scott, 1903) *sensu* Wells (1967) (NHMUK reg. no 1967.8.4.155).

[2]: Pallares (1968) showed six elements on the endopodal lobe of ♀ P5 but this is probably an observational error.

[3]: based on data from Dahm & Schminke's (1992) redescription.

Key to species of *Xouthous* Thomson, 1883

1. Body guttiform (teardrop-shaped); somites bearing legs 2–4 red or brownish; P1 endopod 2-segmented . . . . 2.
Body clypeiform (shield-shaped); prosome without distinct colour pattern; P1 endopod 3-segmented . . . . 15.

2. Antennary exopod 2-segmented . . . . 3.
Antennary exopod 3-segmented . . . . *X. novaezealandiae* Thomson, 1883.

3. P5 baseoendopod ♀ truncate distally; with broad, spatulate, parallel-sided setae that are tapered or rounded only towards the extreme apex; setae set very close together and approximately equal in length, giving the appearance of a palisade. . . . . 4.
P5 baseoendopod ♀ with normal spines/setae . . . . 8.

4. Antennule ♀ 6-segmented. . . . . 5.
Antennule ♀ 7-segmented. . . . . 7.

5. P5 endopodal lobe ♀ extending at least to distal margin of exopod and palisade setae very short; outer corner with serrate extension . . . . *X. laticaudatus* (Thompson & Scott, 1903).
P5 endopodal lobe ♀ not extending to middle of exopod; palisade setae long, extending well beyond end of exopod; outer corner without serrate extension. . . . . 6.

6. P1 enp-1 1.3 times as long as exopod and 7.5 times as long as enp-1; P5 exopod ♀ with five elements, innermost (seta I) fused to segment; P5 ♀ endopodal spines about as long as exopod. . . . . *X. maldiviae* Sewell, 1940.
P1 enp-1 1.1 times as long as exopod and 4.5 times as long as enp-1; P5 exopod ♀ with six elements, innermost (seta I) discrete at base; P5 ♀ endopodal spines distinctly longer than exopod . . . . *X. andamanensis* **sp. nov.** [1]

7. P1 enp-1 about 2.4 times as long as wide; all elements of P5 exopod ♀ defined at base; P5 endopodal lobe ♀ 1.6 times as long (measured along inner margin) as wide, and about 3.2 times as wide as exopod, seta I longest . . . . *X. aemula* (Thompson & Scott, 1903).
P1 enp-1 about 2.2 times as long as wide; seta I of P5 exopod ♀ fused at base; P5 endopodal lobe ♀ 2.2 times as long (measured along inner margin) as wide, and about 2.6 times as wide as exopod, setae II–III longest. . . . . *X. wellsi* **sp. nov.** [2]

8. P2 enp-2 with one inner seta . . . . 9.
P2 enp-2 with two inner setae . . . . 10.

9. P5 exopod ♀ with five elements . . . . *X. purpurocinctus* (Norman & Scott, 1905) [3].
P5 exopod ♀ with six elements. . . . . *X. parasimulans* (Médioni & Soyer, 1968).

10. P5 exopod ♀ with five elements; seta II of endopodal lobe not markedly shorter than setae III–V . . . . 11.
P5 exopod ♀ with six elements; seta II of endopodal lobe less than half the length of setae III–V. . . . . 14.

11. Setae of P5 ♀ endopodal lobe evenly spaced, seta I longest and terminating in long flagellate portion; P5 exopod ♀ elongate, about three times as long as wide (width measured at insertion level of seta V) . . . . *X. simulans* (Brady, 1910) [4].
Gap between setae IV–V of P5 ♀ endopodal lobe wider than between other setae, seta I not longer than and of similar shape as other setae; P5 exopod ♀ at most twice as long as wide (width measured at insertion level of seta V) . . . . 12.

12. Antennule ♀ 6-segmented. . . . . *X. purpurocinctus* (Norman & Scott, 1905) *sensu* Vervoort (1964).
Antennule ♀ 7-segmented. . . . . 13.

13. P5 endopodal lobe ♀ extending to about insertion level of exopodal seta V; distal margin virtually straight . . . . *X. purpurocinctus* (Norman & Scott, 1905) *sensu* Sewell (1940).
P5 endopodal lobe ♀ extending to about insertion level of exopodal seta IV; distal margin rounded . . . . *X. purpurocinctus* (Norman & Scott, 1905) *sensu* Lang (1965).

14. Maxillipedal claw and apical claw of P1 enp-2 with large comb-like spinules; P1 enp-1 parallel-sided and about 1.6 times as long as exopod; P5 endopod ♀ extending approximately to end of exopod. . . . . *X. pectinatus* (Scott & Scott, 1898).
Maxillipedal claw and apical claw of P1 enp-2 without conspicuous spinular ornamentation; P1 enp-1 trapezoidal-shaped and about 1.3 times as long as exopod; P5 endopod ♀ barely reaching middle of exopod. . . . . *X. namibiensis* **sp. nov.** [5]

15. Inner margin of mandibular exopod with three stout modified spines; seta II of P5 ♀ endopodal lobe distinctly shorter than other setae . . . . 16.
Inner margin of mandibular exopod with setae only; seta II of P5 ♀ endopodal lobe not markedly shorter than other setae . 17.

16. P1 enp-1 twice as long as maximum width; P2 enp-2 ♂ with outer distal corner produced into small spinous process . . . . *X. sarsi* Huys, 2009b.
P1 enp-1 2.4 times as long as maximum width; P2 enp-2 ♂ with outer distal corner produced into large spinous process, extending to about middle of enp-3. . . . . *X. scotti* (Lang, 1948) [6].

17. P1 enp-1 2.3 times as long as maximum width; P2 enp-2 ♀ with outer distal corner produced into long spinous process, almost reaching to distal margin of enp-3; P5 exopod ♀ wider than long . . . . *X. cookensis* (Pallares, 1975c).
P1 enp-1 3.5 times as long as maximum width; P2 enp-2 ♀ with outer distal corner produced into small spinous process, not reaching to insertion point of proximal inner seta of enp-3; P5 exopod ♀ longer than wide. . . . . *X. borealis* (Sars, 1911).

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[1] New name proposed for *X. maldivae* [*sic*] Sewell, 1940 *sensu* Wells & Rao (1987). The species is known from two females; the specimen illustrated by Wells & Rao (1987: 275) in their Fig. 51a is here designated as the holotype of *X. andamanensis* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the key above and those mentioned and illustrated in Wells & Rao (1987: 59–61, 275–276; Figs 51–52) (ICZN Art. 13.1). The specific epithet refers to the Andaman Islands where the type locality is situated. Type locality: Andaman Island, Ritchie's Archipelago, Havelock Island, East point (11º58'32"N, 93º02'16"E); surface to 20 cm deep near half-tide level; algal sands rich in detritus.

[2] New name proposed for *X. laticaudatus* (Thompson & Scott, 1903) *sensu* Wells (1967). A female specimen preserved in ethanol has been selected from among the specimens deposited by J.B.J. Wells in The Natural History Museum (NHMUK reg. no. 1967.8.4.155) and designated as the holotype of *X. wellsi* **sp. nov.** (NHMUK reg. no. 2015.3280). Paratypes are one female and one male preserved in ethanol (NHMUK reg. nos 2015.3281–3282). The species can be differentiated by the characters listed in the key above and those mentioned and illustrated in Wells (1967: 263–265; Text-Fig. 39F–G) (ICZN Art. 13.1). The specific epithet refers to Prof. John B.J. Wells who first pointed out the discrepancies between the Mozambican and Sri Lankan "populations" of *X. laticaudatus*. Type locality: Mozambique, Maputo Bay, west coast of Inhaca Island, off Barriera Vermelha beach at 5 m depth; detritus sand.

[3] Wells's (2007: 689) score of two inner setae on P2 enp-2 was presumably based on the redescriptions by Sewell (1940, Vervoort (1964) and Lang (1965). However, Norman & Scott (1906: 175) clearly stated "The second to the fourth pairs of feet somewhat similar to the same pairs in *Dactylopusia*, in which both rami are distinctly three-jointed, but the middle joint of the inner ramus has only one seta on the inner margin". If this observation is correct the Pacific populations are likely to belong to a different species.

[4] Based on redescription by Kunz (1963).

[5] New name for *X. pectinatus* (Scott & Scott, 1898) *sensu* Kunz (1963). The female specimen whose leg 5 was illustrated by Kunz (1963: 38) in his Figs 14–22 is here designated as the holotype of *X. namibiensis* **sp. nov.** (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the key above and those mentioned and illustrated in Kunz (1963: 35–38; Figs 14–24) (ICZN Art. 13.1). The specific epithet refers to Namibia where the type locality is located. Type locality: Namibia, Lüderitz Bay, probably from *Vaucheria* mats.

[6] Based on redescription by Pallares (1968).

Group II is characterized by 2-segmented endopods in legs 1–3 in both sexes and a reduced armature pattern on the distal endopodal segment of leg 1, represented by one claw and one seta. This group includes the type species of *Dactylopodella* and is here considered as equivalent to the latter genus. The three species can be differentiated using the key below. Guille & Soyer (1966), Moore (1976a) and Wells (2007) had previously outlined characteristics separating *D. vervoorti* from *D. clypeata*. One of those characters, the presence of dorsal spinule rows on the free abdominal somites in *D. vervoorti*, is misleading since Vervoort (1962) clearly stated that the "… rows are interrupted on the dorsal surface", an observation clearly corroborated by his Fig. 12a.

Key to species of *Dactylopodella* Sars, 1905a

1. Cephalic shield wider than long; antennary exopod with two apical setae on distal segment . . . . *D. clypeata* Sars, 1911.
   Cephalic shield at most as long as wide; antennary exopod with three apical setae on distal segment . . . . 2.
2. P1 exp-2 distinctly longer than exp-1; P1 exopod moderately elongate, extending to about 4/5 the length of enp-1 and well beyond insertion site of its inner seta; P2 enp-2 ♀ with prominent notch about halfway along inner margin. . . . .*D. flava* (Claus, 1866).
   P1 exp-2 about as long as exp-1; P1 exopod short, extending to about halfway the length of enp-1 but not to insertion site of its inner seta; P2 enp-2 ♀ without prominent notch along inner margin. . . . . *D. vervoorti* Moore, 1976a.

Group III contains two species that were formerly placed in *Dactylopodella* and three species that were previously included in *Xouthous*. Since it also includes the type species of *Idomenella*, the latter name is formally reinstated here for this species group. All species display a normal, elongate body, 3-segmented P2–P3 endopods in both sexes, and a 3-segmented P1 endopod bearing one lateral seta on enp-2 and two lateral setae, one geniculate seta and a claw on enp-3 (Note that the proximal inner seta of enp-2 in *I. intermedia* was probably overlooked by Lang (1934)). While Sars's (1911) record of *I. coronata* from Norway agrees in most aspects with Scott's (1894b) material from the Firth of Forth, his previous record (Sars 1909a) from Ellesmere Island, northern Canada, shows several discrepancies with the original description. The Arctic female has a comparatively broader (almost clypeiform) habitus, a longer proximal endopodal segment in leg 1 and a 7-segmented antennule (*vs* 6-segmented in the type material). The outermost seta on the endopodal lobe of leg 5 is distinctly longer than seta IV whereas it is shorter or at most as long as this seta in the Scottish and Norwegian specimens (Scott 1894b; Sars 1911). Based on these differences *Idomene coronata sensu* Sars (1909a) is here renamed as a new species, *Idomenella paracoronata* **sp. nov.** and the single female described and illustrated by Sars (1909a: 26–27; Plate VI) is fixed as the holotype in accordance with ICZN Arts 16.4 and 72.5.6. Since males are known for only two species (*I. rostrata* (T. Scott, 1893) **comb. nov.**; *I. antarctica* (Giesbrecht, 1902) **comb. nov.**) the key below is based primarily on female characters.

Key to species of *Idomenella* T. Scott, 1906a

1. Antennary exopod 2-segmented; P3–P4 exp-3 with three outer spines; P2 enp-2 with two inner setae; inner setae of P1 enp-2 and -3 not reaching beyond tip of geniculate seta of enp-3; P5 exopod ♀ with five elements . . . . 2.
   Antennary exopod 3-segmented; P3–P4 exp-3 with two outer spines; P2 enp-2 with one inner seta; inner setae of P1 enp-2 and -3 reaching well beyond tip of geniculate seta of enp-3; P5 exopod ♀ with four elements . . . . *I. antarctica* (Giesbrecht, 1902) **comb. nov.** [1]
2. P5 exopod and baseoendopod separated in ♀ . . . . 3.
   P5 exopod and baseoendopod fused in ♀ . . . . 4.
3. Antennule ♀ 6-segmented; P1 enp-1 not extending to distal margin of exopod, and about 1.2 times as long as enp-2 and -3 combined (measured along outer margin); P5 ♀ endopodal seta V longer than seta IV . . . . *I. coronata* (T. Scott, 1894b) **comb. nov.**
   Antennule ♀ 7-segmented; P1 enp-1 slightly extending beyond distal margin of exopod, and about 1.7 times as long as enp-2 and -3 combined (measured along outer margin); P5 ♀ endopodal seta V at most as long as seta IV . . *I. paracoronata* **sp. nov.**
4. Antennule ♀ 6-segmented; P1 enp-1 about as long or only slightly shorter than exopod, and 1.7–2.0 times as long as enp-2 and -3 combined . . . . 5.
   Antennule ♀ 7-segmented; P1 enp-1 distinctly shorter than exopod, and about 1.3 times as long as enp-2 and -3 combined . . . . *I. rostrata* (T. Scott, 1893) **comb. nov.**
5. Segment 4 of ♀ antennule about as long as segment 5; pinnate spine on syncoxa of maxilliped as long as basis; proximal inner seta of P2 enp-2 ♀ more than half the length of distal inner seta . . . . *I. janetae* (Hicks, 1989) **comb. nov.**
   Segment 4 of ♀ antennule longer than segment 5; pinnate spine on syncoxa of maxilliped about half the length of basis; proximal inner seta of P2 enp-2 ♀ less than half the length of distal inner seta . . . . *I. intermedia* (Lang, 1934) **comb. nov.**

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[1] based on redescription by Dahms & Schminke (1992).

Idomenella rostrata (T. Scott, 1893)

The original description of *Dactylopus rostratus* was based on several specimens obtained in washings of gastropod shells inhabited by the common hermit crab *Pagurus bernhardus* but Scott (1893) assumed that the association may have been accidental. He also suggested that *D. rostratus* may just be a larger variety of *Dactyopus flavus* Claus, 1866 and consequently proposed the former only as a provisional name. According to Hicks (1989: 102), who re-examined the syntype material from the Firth of Forth, Scott subsequently found it also at Dundee and in the Moray Firth but no further sampling details are known. Thompson (1895) recorded a single specimen among dredged material from Port Erin on the Isle of Man. According to the late Dr Richard Hamond (*in litt.*) it is very common in shells occupied by *P. bernhardus* along the Norfolk coast, indicating that *I. rostrata* is a genuine hermit crab associate. Hicks (1989) provided new observations of the antennule, leg 1 and the exopod of leg 5. The record by Bonecker *et al.* (1991) from plankton samples taken off the northern coast of Espírito Santo in Brazil is probably an erroneous identification.

OD: Scott (1893—as *Dactylopus rostratus*): 205–206; Plate III (Figs 7–20).
AD: Hicks (1989—as *Dactylopodella rostrata*): 102–104; Fig. 3.
TL: Scotland, Fife, Firth of Forth, west of the island of Inchkeith; in gastropod shells inhabited by *Pagurus bernhardus* (Linnaeus, 1758) (Paguridae).
BL: 1,000 µm (♀), ♂ smaller.

Family Tisbidae

Paraidya Huys, 2009b

Sewell (1940) established the genus *Paraidya* Sewell, 1940 in the Tisbidae for two new species, *Paraidya major* Sewell, 1940 and *P. minor* Sewell, 1940, obtained in weed washings from Nancowry Island (Nankauri Harbour), Nicobar Islands. Humes & Ho (1969b) added a third species, *P. occulta*, associated with hermit crabs in Madagascar while Humes (1981c) confirmed the association of Sewell's species with the same host group. Huys (2009b) pointed out that the publication of *Paraidya* was not accompanied by the mandatory type fixation and the generic name must therefore be considered unavailable (ICZN Art. 13.3). He subsequently validated the name by fixing *P. major* as the type species and by making explicit reference to Humes & Ho's (1969b: 128) list of characters that differentiate *Paraidya* from the closely related genus *Tisbe*.

Members of *Paraidya* are restricted to the Indo-Pacific and exclusively associated with diogenid anomuran crabs of the genus *Dardanus* Paul'son, 1875, including the hairy red hermit crab, *D. lagopodes*, the white-spotted hermit crab, *D. megistos*, and the blue knee hermit crab, *D. guttatus* (Table 27). Humes (1972) reported small numbers of *Paraidya* spp. from several hermit crabs in New Caledonia but did not describe the species. Ovigerous females typically carry their eggs in a cluster instead of being enclosed in an egg sac. The three species can be separated by the key below.

Key to species of *Paraidya* Huys, 2009b

1. Antennary exopod 3-segmented, segment 2 unarmed; P5 exopod with three elements in both sexes .... *P. occulta* (Humes & Ho, 1969b).
   Antennary exopod 4-segmented, segments 2–3 each with one lateral seta; P5 exopod with four elements in both sexes..... 2.
2. Mandibular endopod at most 1.5 times length of exopod; maxilliped with two proximal conical processes on palmar margin of basis; P1 exp-3 with five elements; caudal ramus about 1.7 times as long as wide .... *P. minor* (Sewell, 1940).
   Mandibular endopod at least twice length of exopod; maxillipedal basis elongate, without processes on palmar margin; P1 exp-3 with six elements; caudal ramus about 2.4 times as long as wide .... *P. major* (Sewell, 1940).

Paraidya major (Sewell, 1940)

Being originally described from weed washings in the Nicobar Islands, Humes (1981c) suggested that Sewell's type specimens of *P. major* (and *P. minor*) may have been dislodged from shells inhabited by hermit crabs. In the Maluku Islands (Moluccas) it is known to utilize three different *Dardanus* hosts in shallow coastal waters (1–5 m depth) (Table 27). The eggs, usually four in a cluster, occasionally three, are elongate oval and measure 275–286 × 121–126 µm (Humes 1981c).

OD: Sewell (1940—combination with unavailable generic name): 164–167; Text-fig. 13.
AD: Humes (1981c): 11–16; Figs 19–33.
TL: Nicobar Islands, Nancowry (Nankauri) Island, Nankauri Harbour; weed washings.
BL: 1,070 µm (♀) [Sewell 1940]; 1,290–1,450 µm (♀), 940–1,180 µm (♂) [Humes 1981c].

Paraidya minor (Sewell, 1940)

Humes (1981c) remarked that Sewell's (1940) Text-fig. 14A of the labrum was mislabelled as the rostrum. Although *P. minor* utilizes the same hosts in the same localities as *P. major* (Table 27) it is not clear from Humes' (1981c) data whether both species also live together in association with the same hermit crab. Similarly, both *Sunaristes tranteri* and *Kioloaria brevicaudata* have been recorded from the same hermit crab hosts in the Moluccas (Humes 1981c) but whether or not they cohabit with the *Paraidya* species remains inconclusive. The eggs, usually three in a cluster, occasionally two or four, are oval and measure 169–185 × 96–101 µm. The colour in transmitted light is opaque light brown, the nauplius eye red, and the eggs black (Humes 1981c).

OD: Sewell (1940—combination with unavailable generic name): 167–169; Text-fig. 14.
AD: Humes (1981c): 7–11; Figs 6–18.
TL: Nicobar Islands, Nancowry (Nankauri) Island, Nankauri Harbour; weed washings.
BL: 700 µm (♀) [Sewell 1940]; 750–840 µm (♀), 690–730 µm (♂) [Humes 1981c].

TABLE 27. Host and distributional records of species of *Paraidya* Huys, 2009b (Tisbidae).

Species	Hermit crab host	Country	Archipelago	Island	Locality	Reference
P. major	*Dardanus guttatus*	Indonesia	Maluku Islands	Halmahera	Karang Mie [1]	Humes (1981c)
	Dardanus lagopodes	Indonesia	Maluku Islands	Halmahera	Karang Mie [1]	Humes (1981c)
				Seram (Ceram)	Pulau Marsegoe [2]	Humes (1981c)
				Seram (Ceram)	Pulau Parang [3]	Humes (1981c)
	Dardanus megistos	Indonesia	Maluku Islands	Seram (Ceram)	Pulau Marsegoe [2]	Humes (1981c)
	seaweed washings	India	Nicobar Islands	Nancowry Island	Nancowry Harbour	Sewell (1940)
P. minor	*Dardanus guttatus*	Indonesia	Maluku Islands	Halmahera	Karang Mie [1]	Humes (1981c)
				Seram (Ceram)	Pulau Parang [3]	Humes (1981c)
	Dardanus lagopodes	Indonesia	Maluku Islands	Ambon	Natsepa [4]	Humes (1981c)
				Halmahera	Karang Mie [1]	Humes (1981c)
				Seram (Ceram)	Pulau Parang [3]	Humes (1981c)
	Dardanus megistos	Indonesia	Maluku Islands	Seram (Ceram)	Pulau Marsegoe [2]	Humes (1981c)
	seaweed washings	India	Nicobar Islands	Nancowry Island	Nancowry Harbour	Sewell (1940)
P. occulta	*Dardanus guttatus*	Madagascar	—	Nosy Be (Nossi Bé)	Antsamantsara	Humes & Ho (1969b) [5]
					Navetsy	Humes & Ho (1969b) [6]
	Dardanus lagopodes	Kenya		—	Kanamai	Innocenti (2009)
	Dardanus megistos	Kenya		—	Kanamai	Innocenti (2009)
		Madagascar	—	Nosy Be (Nossi Bé)	Antsamantsara	Humes & Ho (1969b)
					Bay of Ambanoro	Humes & Ho (1969b)
				Nosy Kisimany	—	Humes & Ho (1969b)
				Nosy Komba	Pte. Ambarionaomby	Humes & Ho (1969b)
				Nosy N’Tangam	—	Humes & Ho (1969b)
				Nosy Tany Kely	—	Humes & Ho (1969b) [7]
Paraidya sp.	unidentified hermit crabs	New Caledonia	—	—	—	Humes (1972)

[1–4] Geographical coordinates: [1] 00°20’07”N, 128°25’00”E; [2] 02°59’30”S, 128°03’30”E; [3] 03°17’00”S, 130°44’48”E; [4] 3°27’0”S, 128°17’00”E.

[5–7] Gastropod shells utilized: [5] *Cassis* sp. and *Lambis* sp.; [6] *Cypraea* sp.; [7] *Bursa* sp.

Paraidya occulta (Humes & Ho, 1969b)

Except for a single outlier in the eastern Mediterranean, *P. occulta* appears to be endemic to northern Madagascar where it utilizes both *D. guttatus* and *D. megistos* in shallow coastal waters (0–7 m) (Table 27). Alper *et al.* (2010) recorded a single female from washings of the macroalgae *Cystoseira* sp. and *Corallina* sp. collected in the mediolittoral zone of the Datça Peninsula in the Aegean Sea, Turkey. Humes & Ho (1969b) observed that the association of *P. occulta* with a hermit crab does not preclude the presence also of *Kioloaria brevicaudata*, since these two copepods frequently occurred together. Furthermore, *P. occulta*, *K. brevicaudata* and *Intersunaristes dardani*, may live together in association with the same hermit crab, as observed in three instances (once in *D. megistos* and twice in *D. guttatus*).

OD: Humes & Ho (1969b): 121–128; figs 29–50.
TL: Madagascar, Tany Kely, south of island of Nosy Be (Nossi-bé) off west coast of Diana Region; associated with *Dardanus megistos* (Herbst, 1804) (Diogenidae) inside shell of a species of *Bursa* Röding, 1798 (Gastropoda, Bursidae); depth 0.5 m.
BL: 760–890 µm (♀), 730–840 µm (♂).

Tisbe sp. *sensu* Jansen *et al.* (1998)

Jansen *et al.* (1998) recorded an undescribed species of *Tisbe* from the gills of the red king crab, *Paralithodes camtschaticus* (Tilesius, 1815) (family Lithodidae). The crabs were caught in baited pots in the Varangerfjord, close to the border between Norway and Russia. Although the sample size was small ($n = 15$), prevalence of *Tisbe* sp. was relatively high (66.7%). Jansen *et al.* (1998) noted that turbellarian eggs, amphipods and copepods were not carried over from the old to the new set of gills during moulting. Haugen *et al.* (1998; pers. commn) examined a larger number of crabs ($n = 72$) from the same area and provided both prevalence (94% in spring, 100% in autumn) and mean intensity data [21.0 (range 1–146) in spring, 26.7 (range 1–88) in autumn] for *Tisbe* sp. Additionally, the species was also found on the egg clutches of the host, displaying a prevalence of 11% in spring and 30% in autumn (Haugen *et al.* 1998). In both studies of Varangerfjord crabs only one pair of gills was examined.

Dvoretsky & Dvoretsky (2013) recorded similar prevalence levels for *Tisbe furcata* (Baird, 1837) on *P. camtschaticus* from Dalnezelenetskaya Bay, a small gulf in the Barents Sea. Over 99% of the 7,587 specimens were found on the gills and only sporadically individuals were encountered on the carapace, abdomen, limbs or mouthparts. Provided their material is conspecific with *Tisbe* sp. from the Varangerfjord (an as yet undescribed species, Huys pers. obs.) it is highly unlikely that the authors were dealing with *T. furcata*. Principally owing to the fact that many *Tisbe* species conform to a common "*furcata*" habitus, this species has given rise to considerable confusion in the literature (Volkmann-Rocco 1971), not least because Sars's (1905a) redescription of *T. furcata* does not adequately present the details characterizing it (Bergmans 1979). Significant annual differences in the prevalence of "*Tisbe furcata*" on large Barent Sea crabs were observed, ranging from 71.6% to 95.4%. The mean intensity (based on examination of all 11 pairs of gills) of "*Tisbe furcata*" on crabs with new shells was 33.6 ± 3.5 individuals.host^{-1}, while on hosts with old shells (12–24 months post-ecdysis) it was distinctly higher (406.0 ± 176.5 individuals.host^{-1}) (Dvoretsky & Dvoretsky 2013). Prevalence and mean intensity of "*T. furcata*" thus tend to increase with crab carapace age, presumably because older crabs moult less frequently, offering symbionts more time (and space) to establish themselves. Based on amphipod gut contents analyses, Dvoretsky & Dvoretsky (2013) suggested that the recorded absence of copepods from crab gill chambers in their previous studies during August-September 2004–2008 (Dvoretsky & Dvoretsky 2009, 2010) may be explained by predation by, or competition with, the symbiotic amphipod, *Ischyrocerus commensalis* Chevreux, 1900, the most common associate of *P. camtschaticus*. The effect of "*Tisbe furcata*" on the anomuran host is unknown but Dvoretsky & Dvoretsky (2013) speculated that it may impart a physiological cost on *P. camtschaticus* individuals due to a decrease in respiratory function.

The red king crab is native to the Okhotsk and Japan seas, the Bering Sea and the northern Pacific Ocean. On the Asian side of the Pacific, crabs are found from Korea, along the eastern coast of Siberia and the coasts of the Kamchatka Peninsula. In the north-eastern Pacific they are distributed throughout the Aleutian Island chain, north to Norton Sound, Alaska, and south-east to Great Bay in Vancouver Island, Canada (Jørgensen 2014). During the 1960s, 1.5 million zoea I larvae, 10,000 1–3 year old juveniles and about 2,600 5–15 year old adult *P. camtschaticus* from West Kamchatka, were intentionally released by Russian scientists in the Kolafjord in the east Barents Sea (Russia) to create a new and valuable fishing resource in the region (Orlov & Ivanov 1978). Since then, it has spread northwards to Svalbard and westwards into Norwegian waters (Jørgensen 2014). The crab seems to have become a permanent inhabitant of the Barents Sea where it has thrived to the extent that a commercial fishery for it is now a viable proposition (Jansen *et al.* 1998). It has recently been recorded in the Ionian Sea (Faccia *et al.* 2009). It is not clear whether *Tisbe* sp. was transported as a hitchhiker on adult red king crabs from its native area during the large-scale translocation and implantation in the 1960s and late 1970s. Examination of native populations of *P. camtschaticus* would be crucial in resolving this issue. *Tisbe furcata* has been reported from the gills of the closely related golden king crab, *Lithodes aequispinus* Benedict, 1895 in the Sea of Okhotsk (Karmanova in Dvoretsky & Dvoretsky 2013). However, given that identification of *Tisbe* species is notoriously difficult, requiring extremely detailed observation and sometimes even cross-breeding experiments, it is debatable whether this record is reliable and refers to the same species as the one reported by Jansen *et al.* (1998), Haugen *et al.* (1998) and Dvoretsky & Dvoretsky (2013).

The mouthparts and swimming legs of most *Tisbe* specimens from Varangerfjord were heavily infested by chonotrich ciliates (Huys, pers. obs.). The protozoan epibionts were remarkably similar to *Isochonopsis kergueleni* Batisse & Crumeyrolle, 1988 (family Isochonopsidae), described from the pereiopods of another *Tisbe* species collected near Port-Bizet, Kerguelen Islands (Batisse & Crumeyrolle 1988).

(vi) Brachyuran hosts

Brachyura or "true crabs" are mostly marine, but freshwater, semi-terrestrial, and moist terrestrial species occur in the tropics. Harpacticoid copepods have developed associations with brachyuran hosts across the entire salinity spectrum. Twenty-nine species belonging to 15 genera and four families have so far been recorded but there is no doubt that the true incidence and diversity of harpacticoid symbionts in brachyuran decapods is far greater than previously thought.

Family Ameiridae

Although some species have at times been recorded from low salinity wells and cave pools (Fiers 1990; Petkovski 1973, 1978), demonstrating their ability to survive outside the host, members of the previously recognized family Cancrincolidae typically inhabit the gill chambers (rarely the egg masses) of grapsoidean land crabs belonging to the families Grapsidae, Sesarmidae, Varunidae and Gecarcinidae (classification according to De Grave *et al.* 2009) (Table 28). The family was proposed by Fiers (1990) to accommodate the Atlantic genera *Antillesia* Humes, 1958 and *Cancrincola* Wilson, 1913, which he had separated from the Ameiridae, and a third new genus, *Abscondicola* Fiers, 1990, from Papua New Guinea. Huys *et al.* (1996) added the previously overlooked genus *Neocancrincola* Mañé-Garzón & Sobota, 1974. Both maximum parsimony and Bayesian inference solutions based on SSU rDNA gene sequences showed topological congruence in placing the Cancrincolidae within the Ameiridae and in firmly resolving it as the sistergroup of taxa that have been reported as obligate or commensal associates of crayfish (Huys *et al.* 2009). This relationship was further supported by swimming leg sexual dimorphism and mandibular palp morphology. Morphological comparison with ameirid copepods revealed the majority of synapomorphies previously proposed in support of cancrincolid monophyly and familial distinctiveness could be attributed to heterochrony.

The cancrincolid lineage can be considered a freshwater incursion (invasion without significant subsequent speciation), being predominantly supratidal and estuarine in distribution but whose members are capable of moving into fresh water due to their basic euryhalinity without truly colonizing it. Mañé-Garzón & Sobota (1974) recorded *Neocancrincola platensis* from the gill chamber of *Neohelice granulata* (Dana, 1851a) in oligohaline habitats where salinity ranged between 0.10‰ and 6.70‰. Both *Cancrincola jamaicensis* Wilson, 1913 and *Antillesia cardisomae* Humes, 1958 have been found freely in coconut plantation wells where salinity approached 5‰

(chlorinity 2.804 mg/l) (Fiers 1990). The potential colonization of oligohaline habitats by cancrincolids could be classified as passive or indirect, as their transport to the habitat was via phoresis (*i.e.* carried by their hosts).

Nauplii appear to be free-living (Fiers 1990), being conceivably the infective stages, host specificity is relatively low, and no striking morphological adaptations are associated with the symbiotic mode of life. The progressive evolution of cancrincolid associates seems to be largely concordant with the sequential adaptation to terrestriality by their hosts (Huys *et al.* 2009). *Cancrincola longiseta* Humes, 1957a, considered the most primitive species within the cancrincolid lineage (Fiers 1990), is associated with mangrove inhabiting members of the Grapsidae (*Goniopsis* spp.), the sistergroup of the remaining Grapsoidea (Schubart *et al.* 2002). Species of the genus *Goniopsis* De Haan, 1833 usually live within 100 m of the seaward mangrove fringe, showing the lowest level of terrestrial adaptation. Two of the three crowngroup species of *Cancrincola* live exclusively in the gill chambers of members of the Sesarmidae, while *C. jamaicensis* has been recorded sporadically from *Sesarma huzardi* (Desmarest, 1825) (Humes 1957a) but appears to have secondarily switched to gecarcinid hosts (Huys *et al.* 2009). Sesarmids show limited terrestrial adaptation, remaining burrowed or sheltered under rocks during high tide, and becoming active only when exposed by the receding tide. The morphologically most reduced genera, *Antillesia* and *Abscondicola*, exclusively utilize Gecarcinidae generally referred to as true “land crabs”. Various species can be found several kilometres from the sea such as *Cardisoma guanhumi* Latreille, 1828 (*cf.* Hartnoll 1988), the host of *Antillesia cardisomae*, and *Discoplax hirtipes* (Dana, 1851a) (*cf.* Goshima *et al.* 1978), which acts as one of two hosts for *Abscondicola humesi*. Incomplete congruence between the cancrincolid phylogeny and the host phylogeny can be attributed to the apparently lower host specificity (and potential host switching) of two species, *C. longiseta* and *C. jamaicensis* (see below).

The current amphi-Atlantic distribution of the genus *Cancrincola* may suggest that its (possibly free-living) ancestor had already assumed an almost continuous distribution along the northern seaboard of Gondwana prior to the opening of the South Atlantic, implying symbiotic associations were established much later when grapsoidean crabs radiated and diversified. The alternative hypothesis, invoking transoceanic dispersal of grapsoidean crabs (and with them, their symbionts), is less conceivable but cannot be ruled out. For example, species of the grapsid genus *Planes* Bowdich, 1825 are often found living on a wide variety of floating substrata such as drifting *Sargassum*, scyphozoans, gastropods, shells of cephalopods and even loggerhead sea turtles (see references in Huys *et al.* 2009), and their dependence upon flotsam for survival may result in long distance dispersal beyond the limits of their area of origin.

Morphometric differences and anomalous setation patterns are commonly encountered in legs 1–5, hampering accurate species identification. Great care should therefore be exercised in interpreting the significance of setal variation in both number and length unless sufficient specimens are available for study. Observations based on a single specimen may not always reveal the usual (typical) condition. The species key given by Boxshall & Halsey (2004: 250) is deficient in couplet 1 (the male of *N. platensis* has two setae on the endopodal lobe of leg 5, not three) and is replaced by a new key below. As pointed out by Wells (2007), it is extremely difficult to distinguish between the males of *Cancrincola plumipes* and *C. abbreviata*.

Key to species of *Cancrincola* Wilson, 1913 and allied genera.

1\. P1 exp-2 without inner seta . . . . 2.
P1 exp-2 with inner seta . . . . 4.
2\. P1 exp-3 with four setae/spines; P2–P3 exp-2 without inner seta; P2–P4 exp-3 with four, four, five setae/spines, respectively; P5 exopod and baseoendopod ♀ with four and two elements, respectively . . . . *Abscondicola humesi* Fiers, 1990.
P1 exp-3 with five setae/spines; P2–P3 exp-2 with inner seta; P2–P4 exp-3 with six setae/spines; P5 exopod and baseoendopod ♀ each with five elements . . . . 3.
3\. Caudal ramus about three times as long as wide; P4 exp-2 and P2–P4 enp-2 with inner seta; P5 exopod ♂ with four elements, endopodal lobe unarmed . . . . *Antillesia cardisomae* Humes, 1958.
Caudal ramus about 1.5 times as long as wide; P4 exp-2 and P2–P4 enp-2 without inner seta; P5 exopod and baseoendopod ♂ with two and three elements, respectively . . . . *Neocancrincola platensis* Mañé-Garzón & Sobota, 1974.
4\. P2–P3 exp-3 with seven setae/spines; P4 exp-3 usually with six setae/spines; seta IV of P5 exopod ♀ more than twice as long as segment . . . . *Cancrincola longiseta* Humes, 1957a.
P2–P3 exp-3 with six setae/spines; P4 exp-3 usually with five setae/spines; seta IV of P5 exopod ♀ at most 1.5 times as long as segment . . . . 5.
5\. P1 enp-1 inner seta extending well beyond distal margin of enp-2; setae II and IV of ♀ P5 exopod equally long . . . .

. . . . *Cancrincola jamaicensis* Wilson, 1913.
P1 enp-1 inner seta shorter, reaching to about articulation between enp-1 and enp-2; setae II and IV of ♀ P5 exopod not equally long . . . . 6.

6. P5 exopod ♀ about twice as long as maximum width, seta II longer than seta IV; endopodal lobe without spinules along inner margin . . . . *Cancrincola abbreviata* Humes, 1957a.
P5 exopod ♀ about 1.5 times as long as maximum width, seta II shorter than seta IV; endopodal lobe with spinules along inner margin . . . . *Cancrincola plumipes* Humes, 1941.

Cancrincola Wilson, 1913

Cancrincola jamaicensis Wilson, 1913

The type host of *C. jamaicensis* is the blue land crab, *Cardisoma guanhumi*, which is found throughout estuarine and other coastal regions of the Caribbean, and along the Atlantic coast of Central and South America. In the United States it has been recorded from the Gulf of Mexico and coastal areas of Florida, and as far north as Vero Beach. It is likely that *C. jamaicensis* occurs throughout the range of its gecarcinid host (Humes 1958). Authenticated records include those from Bahamas, Barbados, Brazil, Cuba, Federation of Saint Kitts and Nevis, Haiti, Honduras, Jamaica and Florida, U.S.A. (Humes 1958; Table 28). The species is absent from the gill chambers of the co-occurring host crab *Gecarcinus lateralis* (Fréminville, 1835) in Bimini, Bahamas (Humes 1958). It has at times been recorded from low salinity wells and cave pools in Cuba and the Netherlands Antilles, demonstrating its ability to survive outside the host. Petkovski (1973, 1978) recorded a single female from a freshwater cave pool in western Cuba (Cueva de Jagüey, Pinar del Río Province). Fiers (1990) found several specimens in a well in a coconut plantation on Aruba (Daimari) and one female in an oligohaline cave pool on Bonaire (Boca Onima).

The Dry Tortugas (Florida) records from *Cardisoma guanhumi* and *Paguristes puncticeps* (Diogenidae) by Pearse (1934a) and from *Microphrys bicornutus* (Latreille, 1825) (Majidae) by Wilson (1935), as well as the Bahamian records (Bimini) from *C. guanhumi*, *Gecarcinus* sp. and *Panopeus herbstii* H. Milne Edwards, 1834 (Panopeidae) by Pearse (1951) are based on misidentifications or can no longer be authenticated (Humes 1958).

Humes (1957a) reported the species from the gill chamber of the rainbow land crab, *Cardisoma armatum* Herklots, 1851, in various localities along a 4,800 km stretch of the African west coast between Dakar and Pointe-Noire, including Senegal, Sierra Leone, Ivory Coast, Ghana, Nigeria and the Republic of the Congo (Brazzaville). He also found one individual among 100 specimens of *Cancrincola abbreviata* Humes, 1957a in the gill chambers of a male *Sesarma huzardi* collected on the shore of the Bunce River, near Freetown (Sierra Leone) but this is likely to be a contaminant. Within the West African range Humes (1957a) observed variation in setal lengths on the female P5 and the lengths of the P1 exopod, endopodal segments and inner seta on enp-1. He also reported variation in the armature of the female P3 endopod, the inner seta on enp-2 being occasionally absent. The latter anomaly was also observed by Fiers (1990) who added records from *C. armatum* collected in Banana in the Democratic Republic of the Congo (Zaire). He also noted that some males had three setae (instead of two) on the P5 baseoendopod. The amphi-Atlantic distribution of *C. jamaicensis* populations utilizing different hosts suggests the presence of two cryptic species and some morphological differences appear to support this assertion. In African specimens the proximal endopodal segment of leg 1 is relatively longer (enp-1:enp-2 4.0 *vs* 3.4) and the aesthetasc on the fourth antennulary segment is distinctly shorter (extending to distal margin of segment 7 *vs* beyond segment 8) than in the Jamaican topotype population (*cf.* Humes 1957a, 1958). Fiers' (1990) examined specimens from both sides of the Atlantic but did not explicitly state the origin of the material his redescription was based on. The short relative length of the P1 enp-1 and the list of dissected *vs* non-dissected specimens suggest Fiers' illustrations were based on the Congolese material, adding further support to the morphological distinctiveness between the West African populations and those along the American seaboard of the Atlantic. The position of *C. jamaicensis* within a sesarmid-utilizing clade indicates a genuine host switching event (Huys *et al.* 2009). Although the species occasionally utilizes *Sesarma huzardi* in West Africa, it is typically associated with the gecarcinid hosts along both American and African seaboards of the Atlantic. This switching is not necessarily at odds with the phylogenetic origin of the host groups, since among the four grapsoidean families utilized by cancrincolids, the Gecarcinidae may be most closely related to the Sesarmidae (Schubart *et al.* 2006).

Although both *C. jamaicensis* and *Antillesia cardisomae* are known to infest the same gecarcinid host in the same locality (Jamaica, Cuba, Swan Islands; Humes 1958) it is not known whether they co-exist in the same host individual or prefer crabs living under different environmental conditions (Fiers 1990).

Living specimens have a bright red nauplius eye and a generally colourless or opaque body. The multiseriate egg sac contains 8–15 eggs ($n = 22$; mean = 10) (Humes 1957a). According to Wilson (1913) and Bright & Hogue (1972) they cling to the gill filaments of the crab using their antennae and maxillipeds, and probably feed on the host's blood or secretions. Fiers (1990) described the five copepodid stages in detail. The presence of five setae on the antennary exopod of the first copepodid of this species and *C. longiseta* (instead of three as from copepodid II onwards) may be indicative of a multisegmented origin of the ramus (Fiers 1990).

OD: Wilson (1913): 264–268; Plate 50 (Fig. 281), Plate 51 (Figs 282–283), Plate 53 (Figs 289–302).
AD: Humes (1957a): 180–183; Plate I (Figs 1–13), Plate II (Figs 14–17). Humes (1958): 77–80; Figs 1–6. Petkovski (1978): 103–108; Figs 1–9 (♀ only). Fiers (1990): 72–80; Figs 1–6; Table II.
TL: Jamaica, Montego Bay; from the gill chambers of *Cardisoma guanhumi* Latreille, 1828 (Gecarcinidae).
BL: 800 µm (♀), 880 µm (♂) [Wilson 1913]; 692–832 µm (♀), 618–718 µm (♂) [Humes 1957a]; 624–815 µm (♀), 586–715 µm (♂) [Humes 1958]; 770 µm (♀) [Petkovski 1978]; 345 µm (CoI), 370 µm (CoII), 465 µm (CoIII), 445–455 µm (CoIV♀), 675–695 µm (CoV♀), 595–610 µm (CoV♂) [Fiers 1990].

Cancrincola plumipes Humes, 1941

Humes' (1941) type material was recovered from the gills of the purple marsh crab, *Sesarma reticulatum* (Say, 1817) on Grande Isle, Louisiana. Humes (1958) supplemented his original description and listed additional records from the same crab in northwest Florida and Rhode Island, suggesting the range of *C. plumipes* probably coincides with that of its grapsoidean host. Published distributional records for *S. reticulatum* suggest a range from Woods Hole, Massachusetts to Volusia County, Florida along the east coast of the United States, and from Sarasota County, Florida to Calhoun County, Texas within the Gulf of Mexico (Williams 1984). However, studies of reproductive biology (Zimmerman & Felder 1990, 1991), osmoregulatory ability (Staton & Felder 1992) and genetics (Felder & Staton 1994) uncovered evidence that populations endemic to the Gulf are distinctly different from the east coast *S. reticulatum* and should be considered a distinct species. Trans-Floridian allozyme divergence between Gulf and Atlantic populations of the *S. reticulatum* complex was found to be at levels previously reported for speciated populations and is compatible with models for periods of contact and subsequent isolation of both stocks during and since peak glacial advances in North America. The undescribed Gulf of Mexico form [referred to as *Sesarma* sp. (nr. *reticulatum*)] ranges from Sarasota County, Florida, to Barra del Tordo, Tamaulipas, Mexico, while genuine *S. reticulatum* ranges from Woods Hole, Massachusetts, to Volusia County, Florida (Zimmerman & Felder 1991). The type host of *C. plumipes* should therefore be referred to as *Sesarma* sp. (nr. *reticulatum*). Humes (1958) did not report any differences between *C. plumipes* from the Gulf and the material from Rhode Island and South Carolina. Zimmerman & Felder (1991) observed *C. plumipes* on the egg masses of *Sesarma* sp. (nr. *reticulatum*) from various coastal Louisianian habitats but made no mention of its presence in the gill chamber.

Humes (1958) reported the species also from the gill chambers of the squareback marsh crab, *Armases cinereum* (Bosc, 1802) [as *Sesarma cinereum*], at three different localities in South Carolina and Florida. The specimens from South Carolina are smaller in body size and certain appendages in the female (antennulary aesthetasc, P1 segments and inner seta on enp-1, P5 setae). Some variation in the swimming leg armature was noted in material from *A. cinereum* at Alligator Harbor. Presumably the species occurs throughout the range of *A. cinereum*, from Chesapeake Bay to Tampico, Mexico.

The egg sac contains 2–11 eggs, arranged in a single layer (Humes 1941).

OD: Humes (1941): 379–385; Fig. 18.
AD: Humes (1958): 80–82; Figs 7–17.
TL: U.S.A., Louisiana; Barataria Bay, Grand Isle, near Louisiana State University Marine Laboratory; from the gill chambers of *Sesarma* sp. (nr. *reticulatum* (Say, 1817)) (Sesarmidae).
BL: 586–659 µm (♀), 545–621 µm (♂) [Humes 1941]; 504–600 µm (♀), 504–576 µm (♂) [Humes 1958; South Carolina material from *A. cinereum*].

TABLE 28. Host and distributional records of *Cancrincola* Wilson, 1913 and allied genera associated with grapsoidean crabs. Type localities indicated by *.

Species	Grapsoidean host	Country	Locality	Reference
Cancrincola jamaicensis	*Cardisoma armatum*	DR Congo	Banana	Fiers (1990)
		Ghana	Accra and vicinity	Humes (1957a)
		Ivory Coast	near Abidjan	Humes (1957a)
		Nigeria	near Lagos	Humes (1957a)
		Republic of the Congo	Pointe-Noire and vicinity	Humes (1957a)
		Senegal	near Dakar and at Joal	Humes (1957a)
		Sierra Leone	near Freetown	Humes (1957a)
	Cardisoma guanhumi	Bahamas	Bimini	Humes (1958)
		Barbados	Saint James	Humes (1958)
		Brazil	Cannavieiras, State of Bahia	Humes (1958)
			State of Pernambuco, locality?	Humes (1958)
		Cuba	Bahia Honda	Humes (1958)
		Haiti	Grande Anse	Humes (1958)
		Honduras	Swan Islands	Humes (1958)
		Jamaica	Montego Bay *	Wilson (1913), Humes (1958)
			Saint Catherine	Humes (1958)
		Federation of St Kitts and Nevis	Saint Kitts, locality unspecified	Humes (1958)
		U.S.A., Florida	Vero Beach	Humes (1958)
	Sesarma huzardi	Sierra Leone	near Freetown	Humes (1957a)
	free-living	Cuba	Cueva del Jagüey	Petkovski (1973, 1978)
		Netherlands Antilles	Aruba and Bonaire	Fiers (1990)
Cancrincola plumipes	*Armases cinereum* [1]	U.S.A., Florida	Alligator Harbor	Humes (1958)
			Jacksonville	Humes (1958)
		U.S.A., South Carolina	Bears Bluff, Wadmalaw Island	Humes (1958)
	Sesarma reticulatum	U.S.A., Rhode Island	Tiverton	Humes (1958)
	Sesarma sp. (nr. *reticulatum*) [2]	U.S.A., Florida	Alligator Harbor	Humes (1958)
		U.S.A., Louisiana	Grande Isle *	Humes (1941)
			Cocodrie, Cypremort Point, Red-Fish Point, Rockefeller Wildlife Refuge, and Cameron	Zimmerman & Felder (1991)
Cancrincola abbreviata	*Metagrapsus curvatus* [3]	Republic of the Congo	near Pointe-Noire	Humes (1957a)
		Sierra Leone	near Freetown	Humes (1957a)
	Sesarma angolense	Republic of the Congo	near Pointe-Noire	Humes (1957a)
	Sesarma huzardi	Ivory Coast	Lagoon of Ébrié and Koumassi *	Humes (1957a)
		Nigeria	near Lagos	Humes (1957a)
		Republic of the Congo	Pointe-Noire and vicinity	Humes (1957a)
		Sierra Leone	near Freetown	Humes (1957a)

......*continued on the next page*

TABLE 28. (Continued)

Species	Grapsoidean host	Country	Locality	Reference
Cancrincola longiseta	*Goniopsis cruentata* [4]	Bermuda	locality unspecified	Humes (1958)
		Brazil	State of Bahia, Santa Clara	Humes (1958)
			State of Espírito Santo, Vitória	Humes (1958)
			State of Pará, Caruca	Humes (1958)
			State of Pernambuco, locality ?	Humes (1958)
			State of Rio de Janeiro, Rio de J.	Humes (1958)
		Haiti	Jeremie	Humes (1958)
		Panamá	Atlantic coast, locality unspecified	Humes (1958)
	Goniopsis pelii [5]	DR Congo	Banana	Fiers (1990)
		Ivory Coast	Lagoon of Ébrié	Humes (1957a)
		Nigeria	near Lagos	Humes (1957a)
		Republic of the Congo	near Pointe-Noire and vicinity	Humes (1957a)
		Sierra Leone	near Freetown *	Humes (1957a)
	Metagrapsus curvatus [4]	Republic of the Congo	near Pointe-Noire	Humes (1957a)
	Sesarma huzardi	Republic of the Congo	near Pointe-Noire	Humes (1957a)
Antillesia cardisomae	*Cardisoma guanhumi*	Bahamas	Bimini	Pearse (1951) [6], Humes (1958)
		Barbados	Saint James	Humes (1958)
		Cuba	Bahia Honda	Humes (1958)
		Haiti	Grande Anse	Humes (1958)
		Honduras	Swan Islands	Humes (1958)
		Jamaica	Montego Bay	Humes (1958)
			Saint Catherine *	Humes (1958)
		U.S.A., Florida	Key West	Humes (1958)
		Venezuela	Guanta	Humes (1958)
	free-living	Netherlands Antilles	Aruba and Bonaire	Fiers (1990)
		Venezuela	Tortuga Island	Fiers (1990)
Neocancrincola platensis	*Cyrtograpsus angulatus*	Argentina	Bahía Blanca estuary	Alda *et al.* (2011)
	Neohelice granulata [7]	Argentina	Bahía Blanca estuary	Alda *et al.* (2011)
			Mar Chiquita Lagoon	Silva *et al.* (2007) [8]
		Uruguay	Río de la Plata *	Mañé-Garzón & Sobota (1974)
Abscondicola humesi	*Discoplax hirtipes* [9]	Indonesia	Irian Jaya, Manokwari	Fiers (1990)
		Papua New Guinea	Madang Province, Laing Island *	Fiers (1990)
	Discoplax rotunda [10]	Papua New Guinea	Madang Province, Laing Island	Fiers (1990)

[1] as *Sesarma cinereum* Bosc, 1802; [2] records by Humes (1941, 1958) as *Sesarma reticulatum* (Say, 1817); [3] as *Sesarma* (or *Sarmatium*) *curvatum* H. Milne Edwards, 1837; [4] records from this host must be authenticated with molecular sequence data; [5] as *Goniopsis cruentata* (Latreille, 1803); [6] as *Cancrincola jamaicensis*; [7] as *Chasmagnathus granulata* Dana, 1851a; [8] as *Cancrincola* sp.; [9] as *Cardisoma hirtipes* Dana, 1851a; [10] as *Cardisoma rotundum* (Quoy & Gaimard, 1824).

Cancrincola abbreviata Humes, 1957a

This species is restricted to West Africa, being most commonly associated with the mangrove crab *Sesarma huzardi*. Humes (1957a) listed records from Sierra Leone, Ivory Coast, Nigeria and the Republic of the Congo (Table 28). Intensity is high, frequently reaching over 100 individuals.host^{-1}. *Sesarma huzardi* is a common species of muddy estuarine areas such as mangroves, salt marshes, tidal rice lands, and mouths of rivers. It inhabits the coast of West Africa from Senegal to Angola (Manning & Holthuis 1981) thus it is likely that future sampling will extend the range of *C. abbreviata* (the species has not been recorded again since its original description). Humes (1957a) also recorded high copepod numbers on the gills of another, co-occuring, sesarmid, *Metagrapsus curvatus* (H. Milne Edwards, 1837) [as *Sesarma* (or *Sarmatium*) *curvatum*)], in three estuarine localities in Sierra Leone and the Republic of the Congo. The host has a similar distributional range as *S. huzardi* (Manning & Holthuis 1981). A single specimen of a third host, *Sesarma angolense* Brito Capello, 1864, was found to be infested with *C. abbreviata* near the mouth of the Loeme River, about 18 km south of Pointe-Noire, Republic of the Congo (Humes 1957a).

The uniseriate egg sac contains 6–13 eggs. Live specimens have a generally colourless or opaque body except for the bright red nauplius eye. Some females display an inner seta on the middle endopodal segment of P3 and four instead of five setae on the P5 baseoendopod. Humes (1957a) noted slight variability between *C. abbreviata* females associated with *S. huzardi* and those found on *M. curvatus*, particularly in the proportional lengths of the antennulary aesthetasc, inner seta and first two segments of P1, and the setae of P5. No significant differences were observed between males inhabiting different hosts.

OD: Humes (1957a): 185–189; Plate III (Figs 30–38).
TL: Ivory Coast; on the embankment at Koumassi, between the entrance to the Abidjan airport and the village of Vridi; from the gill chambers of *Sesarma huzardi* (Desmarest, 1825) (Sesarmidae).
BL: 663–693 µm (♀), 641–691 µm (♂).

Cancrincola longiseta Humes, 1957a

This species is typically associated with members of *Goniopsis* (Grapsidae), however Humes (1957a) recorded single individuals from the gill chambers of *Metagrapsus curvata* and *Sesarma huzardi* in the Loeme River near Pointe-Noire, Republic of the Congo. Both sesarmids are common hosts of *C. abbreviata* (see above). Given the vast amount of host material examined by Humes, these records should be regarded as accidental or due to contamination during host processing and are by no means evidence for host switching. Based on published distributional records (Fiers 1990; Humes 1957a, 1958) *C. longiseta* assumes an amphi-Atlantic distribution and inhabits the same host, *Goniopsis cruentata* (Latreille, 1803), in West Africa and along the American seaboard from Bermuda to Brazil. Although this could imply that *C. longiseta* has dispersed from its area of origin into the other area, or may have failed to speciate in response to vicariance events, Huys *et al.* (2009) considered it more plausible that this ambiguity was based on erroneous identification of the host crab (and conceivably its associates). Most brachyuran workers had followed De Man (1879) in synonymizing the eastern Atlantic *Grapsus pelii* Herklots, 1851 with the western Atlantic *G. cruentata* until Manning & Holthuis (1981) compared West African material with specimens from the Caribbean and the north coast of South America. They concluded that the amphi-Atlantic populations represent two distinct species, the American *G. cruentata* and the African *Goniopsis pelii* (Herklots, 1851), which also proved to be genetically distinct (Schubart 2011). The records by Humes (1957a) from mangrove crabs in Sierra Leone, Ivory Coast, Nigeria and the Republic of the Congo (Table 28) and those from Banana in the Democratic Republic of Congo by Fiers (1990) must therefore be attributed to *G. pelii*. The host is known from the West African coast from Dakar, Senegal, in the north to Moçâmedes, Angola, in the south (Manning & Holthuis 1981); *C. longiseta* is likely to be distributed throughout this range.

While species differentiation within *Cancrincola* requires a substantial level of morphological detail, cryptic speciation in the genus has as yet not been documented. Unfortunately, Humes' (1958) western Atlantic records of *C. longiseta* from the closely related *Goniopsis cruentatum* were not accompanied by any morphological data that could have corroborated his identification. Given the different host and highly disjunct distribution of *C. longiseta*, Huys *et al.* (2009) questioned the authenticity of the American records and called for independent testing with molecular sequence data. Humes' (1957a) records from Brazil, Panamá, Haiti and Bermuda (Table 28) must therefore be treated as uncertain.

The uniseriate egg sac contains 8–16 eggs. Live specimens have a generally colourless or opaque body except for the bright red nauplius eye. Humes (1957a) noted abnormalities in some females (missing element on exp-3 of P2 or P4, P3 enp-2 with inner seta) and males (P1, P4) from Sierra Leone. Fiers (1990) described the five copepodid stages in detail.

OD: Humes (1957a): 183–185; Plate II (Figs 18–22), Plate III (Figs 23–29).
AD: Fiers (1990): 80–86; Figs 7–11; Table III.
TL: Sierra Leone, near Freetown; mangrove area at Rokupa; from the gill chambers of *Goniopsis pelii* (Herklots, 1851) (Grapsidae).
BL: 730–773 µm (♀), 650–716 µm (♂) [Humes, 1957a]; 250 µm (CoI), 385–395 µm (CoII), 420–435 µm (CoIII), 475–495 µm (CoIV♀), 460–475 µm (CoIV♂), 640–690 µm (CoV♀), 620–655 µm (CoV♂) [Fiers 1990].

***Antillesia* Humes, 1958**

***Antillesia cardisomae* Humes, 1958**

Pearse's (1951) material from *Cardisoma guanhumi* in Bimini (Bahamas) and identified as *Cancrincola jamaicensis* almost certainly belongs to this species. Humes (1958) recorded the species from the gill chambers of the same host in the Bahamas, Barbados, Cuba, Haiti, Jamaica, Honduras, Venezuela and U.S.A., Florida (Table 28). Fiers (1990) added additional records from Aruba (well at Daimara in coconut plantation), Bonaire (small cave close to Boca Onima) and Venezuela (Tortuga Island; coarse sandy sediment 0.5 m from high-tide mark), all of which were not associated with any hosts. Morales-Serna *et al.* (2012) claimed that Hendrickx & Fiers (2010) had reported *A. cardisomae* from the branchial cavity of *C. guanhumi* at an unspecified locality in Mexico but no evidence could be found for this record.

The egg sac usually contains eight eggs (range 6–9) arranged in a single layer (Humes 1958). Considerable variability has been noted in the ornamentation of the outer margin of the female P5 baseoendopod (spinules present/absent) and the length of the setae on P1 and P5 (and number; setae often retracted). The species is absent from the gill chambers of the co-occurring host crab *Gecarcinus lateralis* in Barbados and the Bahamas (Humes 1958). *Cancrincola jamaicensis* and *A. cardisomae* often infest *C. guanhumi* in the same locality but whether they co-exist in the same host individual has yet to be demonstrated (Fiers 1990).

Fiers (1990) published amended illustrations of the female urosome, genital field and male P1, gave additional notes on P2–P4, and confirmed the absence of sexual dimorphism on P1. He also provided the first ontogenetic data for the species (CoIII, CoIV♀, CoV♂).

OD: Humes (1958): 82–89; Figs 20–48.
AD: Fiers (1990): 86–90; Fig. 12.
TL: Jamaica, Saint Catherine, Port Henderson; mudflat, from the gill chambers of *Cardisoma guanhumi* Latreille, 1828 (Gecarcinidae).
BL: 900–1,272 µm (♀), 700–943 µm (♂) [Humes, 1958]; 500 µm (CoIII), 585 µm (CoIV♀), 770 µm (CoV♂) [Fiers 1990].

***Neocancrincola* Mañé-Garzón & Sobota, 1974**

***Neocancrincola platensis* Mañé-Garzón & Sobota, 1974**

Mañé-Garzón & Sobota (1974) recorded a new genus and species, *Neocancrincola platensis*, from the gill chamber of the varunid crab, *Chasmagnathus granulata* Dana, 1851a, in two localities in the Río de la Plata near

Montevideo, Uruguay. Following their revision of the *Chasmagnathus/Helice* complex, Sakai *et al.* (2006) recently designated the host species as the type of a new genus, *Neohelice* Sakai, Türkay & Yang, 2006. Prevalence approached 100% but intensity was generally low with 3–4 copepods per host. The egg sac contains 6–8 eggs, each about 78 µm in diameter. *Neohelice granulata* is an estuarine bimodal breathing crab which actively moves from subtidal to supratidal oligohaline areas, extracting oxygen directly from the air through branchiostegal lungs but relying on branchial exchange to eliminate carbon dioxide (Halperin *et al.* 2000). The absence of juvenile copepods and the known intolerance of *Neohelice* larvae to oligohaline conditions made Mañé-Garzón & Sobota (1974) speculate that naupliar eclosion in the copepod and spawning in the host are probably synchronized, when the latter migrates to coastal high salinity waters.

Silva *et al.* (2007) studied the impact of epibionts in *N. granulata* females from unvegetated mudflats and cordgrass (*Spartina densiflora*) salt marshes in Mar Chiquita Lagoon (Argentina) and occasionally recorded adult and larval harpacticoid copepods in the incubation chamber, brood mass and on the setae of the pleopods of both ovigerous and non-ovigerous hosts. Although the copepods appeared to be very similar to *N. platensis*, they were provisionally identified as *Cancrincola* sp. Copepod epibionts were never found among the embryos of *Cyrtograpsus angulatus* Dana, 1851a, which occurs in the same estuarine environment (Silva *et al.* 2003). The lower epibiosis observed in the brood pouch of *N. granulata* when compared with *C. angulatus* may be related to the presence of permanent populations of *Neocancrincola/Cancrincola* species. Silva *et al.* (2007) suggested the relation between the crab and the copepod could be mutualistic, since the host provides a suitable and protected habitat and the latter may control the potentially harmful epibiosis caused by bacteria, fungi and colonial ciliates. It is not clear whether the copepods also occurred on the gills. However, Alda *et al.* (2011) recorded *N. platensis* from the gill chambers of both varunid hosts at Puerto Cuatreros in the innermost part of the Bahía Blanca estuary, some 260 km southwest of Mar Chiquita Lagoon. Prevalence was higher in the type host, *N. granulata* (21%) compared to the co-occuring *Cyrtograpsus angulatus* (8%).

OD: Mañé-Garzón & Sobota (1974): 71–77; Figs 1–17.

TL: Uruguay, Montevideo, Río de la Plata, from the gill chambers of *Neohelice granulata* (Dana, 1851a) (Varunidae). Mañé-Garzón & Sobota (1974) collected the host crabs from two sites but did not designate a type locality: Barra del Río Santa Lucía (salinity 0.10–4.87‰) and Punta Carretas (salinity 1.15–6.70‰).

BL: 836 µm (♀), 972 µm (♂).

***Abscondicola* Fiers, 1990**

***Abscondicola humesi* Fiers, 1990**

The species is known from two gecarcinid hosts, *Discoplax hirtipes* (as *Cardisoma hirtipes* Dana, 1851a) and *D. rotunda* (Quoy & Gaimard, 1824) [as *Cardisoma rotundum* (Quoy & Gaimard, 1824)], inhabiting Laing Island, a small island along the northern coast of Papua New Guinea (Fiers 1990). Two other landcrab species, *Cardisoma carnifex* (Herbst, 1796) and *Gecarcoidea lalandii* H. Milne Edwards, 1837, which occupied the more elevated central parts of Laing Island, were also examined but never found to be infested by copepods. *Abscondicola humesi* was also recorded from *D. hirtipes* on the western (Indonesian) part of the island of New Guinea near Manokwari in West Papua (Irian Jaya). Given the range of its hosts it is likely that *A. humesi* assumes a much wider distribution. The type host, *D. hirtipes* is restricted to south-east Asia and the western Pacific as far east as Fiji (Ng & Shih 2014). *Discoplax rotunda* inhabits islands in the Indo-West Pacific oceans, from Aldabra and Mauritius to the Ryukyu Islands, Hawaii, and French Polynesia, and was recently sighted in Kenya (Innocenti & Vannini 2007). No variability was observed except for small differences in the proportional lengths of the endopodal setae on the female P5. The uniseriate egg string contains six eggs. Fiers (1990) described the complete series of copepodid stages. Based on their apparent scarcity in the gill chambers, he assumed that nauplii develop outside the host.

OD: Fiers (1990): 88–99; Figs 13–18; Table IV.

TL: Papua New Guinea, Madang Province, Laing Island; western shore of the island near the jetty; from the gill chambers of *Discoplax* (= *Cardisoma*) *hirtipes* (Dana, 1851a) (Gecarcinidae).

BL: 900–985 µm (♀), 838–895 µm (♂); 160 µm (CoI), 335–385 µm (CoII), 415–450 µm (CoIII), 635–650 µm (CoIV♀), 625–630 µm (CoIV♂), 760–785 µm (CoV♀), 760–795 µm (CoV♂) [Fiers 1990].

Family Canthocamptidae

Pholetiscus Humes, 1947

Pearse (1930) described a new species, *Cancrincola wilsoni*, from the gill chamber of two mudflat crab species in Japan but gave no justification for its generic assignment. Lang (1948) argued forcefully against its inclusion in *Cancrincola* Wilson, 1913, claiming that the species differed in almost every aspect from the type species, *C. jamaicensis* Wilson, 1913. He retained *C. wilsoni* as *species incertae sedis* in the genus but noted that a position in the Canthocamptidae (close to *Mesochra* Boeck, 1865), rather than in the Ameiridae, was more probable.

Unbeknown to Lang (1948), Humes (1947) had already proposed the genus *Pholetiscus* to accommodate *C. wilsoni*, which he fixed as the type by original designation, and a new species, *P. orientalis*, from Borneo. Adopting Monard's (1927) family classification, Humes (1947) explicitly placed the genus in the Canthocamptidae and not in the Ameiridae as erroneously stated by some authors (Lang 1965; Bodin 1979, 1988, 1997). Lang (1965) reiterated his earlier claim of a close relationship between *Pholetiscus* and *Mesochra*. A third species from Madagascar, *P. rectiseta*, was added by Humes (1956), extending the geographical range of the genus to the western Indian Ocean.

The three members of the genus are all gill symbionts of Indo-Pacific sesarmid mudflat crabs. A fourth, as yet undescribed, species from South Korea was communicated in a conference poster abstract (Song & Khim 2013) but is probably identical to *P. wilsoni*. The known species of *Pholetiscus* can be distinguished on the basis of antennulary segmentation, armature of the swimming legs and male P5, and morphology of caudal setae IV–V.

Key to species of *Pholetiscus* Humes, 1947

1. P1 exp-2, P2 exp-3 and P4 exp-2 with inner seta; P2–P4 enp-1 without inner seta; P5 ♂ with four elements; caudal ramus setae IV–V free at base. . . . . *P. wilsoni* (Pearse, 1930).
P1 exp-2, P2 exp-3 and P4 exp-2 without inner seta; P2–P4 enp-1 with inner seta; P5 ♂ with three elements; caudal ramus setae IV–V fused at base . . . . 2.
2. Antennule ♀ 6-segmented; P1 enp-1 and P2–P3 exp-2 without inner seta; P3–P4 enp-2 with four elements in ♀. . . . . *P. rectiseta* Humes, 1956.
Antennule ♀ 7-segmented; P1 enp-1 and P2–P3 exp-2 with inner seta; P3–P4 enp-2 with five elements in ♀ . . . . *P. orientalis* Humes, 1947.

Pholetiscus wilsoni (Pearse, 1930)

Pearse (1930) described this species (as *Cancrincola wilsoni*) from the gill chamber of the red-clawed crab, *Chiromantes haematocheir* (De Haan, 1833) [as *Sesarma haematocheir* (De Haan, 1833); erroneously cited *S. haematobium* by Humes (1956: 84)], at Aburatsubo, an inlet on the west side of the Miura Peninsula in Kanagawa, Japan, facing Sagami Bay on the Pacific Ocean. He also recorded *P. wilsoni* from the gills of a second mudflat crab host occurring at the type locality, *Parasesarma pictum* (De Haan, 1835) [as *Sesarma pictum* (De Haan, 1835)], but this material was—contrary to Humes' (1947: 170) claim—not considered part of the type series. The original description contained errors in the segmentation pattern of the male antennule, armature formula of the swimming legs, sexual dimorphism of P3 endopod and the dorsal subdivision of the female genital double-somite (Humes 1947). Unlike its congeners no sexual dimorphism was observed in the armature pattern of the P4 endopod. The single multiseriate egg sac contains 4–9 eggs (Pearse 1930).

The two sesarmid hosts are endemic to East Asia and typically inhabit mangrove swamps and the upper intertidal region of estuaries where they live in small crevices and abandoned holes made by other species. It is likely that the distribution of *C. wilsoni* mirrors that of its hosts. The as yet undescribed species, recorded from South Korea in a conference abstract (Song & Khim 2013) under the *nomen nudum* "*Pholetiscus dodukgei* sp. nov.", utilizes the same type host, *C. haematocheir*, and is probably conspecific with *P. wilsoni*.

OD: Pearse (1930—as *Cancrincola wilsoni*): 1–4; Figs 1–18.

AD: Humes (1947): 170–173; Figs 1–5; Table 1.

TL: Japan, Kanagawa Prefecture, west side of Miura Peninsula, Aburatsubo inlet, near Misaki (merged with Minami-Shitaura town in 1955 to form city of Miura); from the gills of the mudflat crab *Chiromantes haematocheir* (De Haan, 1833) (family Sesarmidae).

BL: 630–730 µm (♀); 580–660 µm (♂) [Pearse, 1930]; Humes (1947) did not give measurements.

Pholetiscus orientalis Humes, 1947

The species was recorded from the gills of three species of sesarmid mudflat crabs on Tarakan Island in Borneo, Indonesia: *Perisesarma eumolpe* (De Man, 1895) (as *Sesarma eumolpe* De Man, 1895), *Episesarma mederi* (H. Milne Edwards, 1853b) [as '*Sesarma taeniolatum* White, 1847' (*nomen nudum)*] and *E. palawanense* (Rathbun, 1914) (as *Sesarma palawanense* Rathbun, 1914). The identification of the latter host was considered somewhat uncertain. *Pholetiscus orientalis* appeared to be more common in *P. eumolpe* (prevalence 73%) than in *E. mederi* (42%); up to 34 specimens were found in a single host crab.

Humes (1947) noted slight variability in the spinular ornamentation of the swimming legs, particularly along the inner margin of the proximal endopodal segment of P1. The female antennule is here interpreted as 7-segmented; the thin, weakly chitinized zone between "segments" 7 and 8 in Humes' description is unlikely to be a genuine segment boundary. Males usually lack the two inner setae, rarely only one, on P4 enp-2. Occasionally the male P5 shows an additional seta, arising from a slightly projecting area, medially to the typical three setae. Humes (1947) observed blue-green algae and diatoms of the *Pinnularia* type in the alimentary tract of mounted specimens. Males clasp the caudal setae of the female during mate guarding. The egg sac contains 7–11 eggs, each about 50 µm in diameter.

OD: Humes (1947): 172–177; Figs 6–18; Tables 2–3.

TL: Indonesia, Borneo, North Kalimantan province, Tarakan Island, delta region formed by Sesayap River, marsh area 400 m west of Tarakan; from the gills of three sesarmid crab hosts, *Perisesarma eumolpe* (De Man, 1895), *Episesarma mederi* (H. Milne Edwards, 1853b) and *E. palawanense* (Rathbun, 1914) (the latter identification is provisional) (Sesarmidae).

BL: 588–705 µm (♀); 514–646 µm (♂).

Pholetiscus rectiseta Humes, 1956

Humes (1956) described *P. rectiseta* from the sesarmid crab *Neosarmatium meinerti* (De Man, 1887) (as *Sesarma meinerti* De Man, 1887) in Madagascar. The host has long been considered a widespread species throughout the Indo-West Pacific, however, Ragionieri *et al.* (2009, 2012) recently provided morphological, morphometric and genetic evidence that *N. meinerti* constitutes a species complex composed of four species, each with discrete ranges. The "populations" distributed along the East African coast from the middle of Somalia to Natal in South Africa, including north-western Madagascar, were assigned to a new species *N. africanum* Ragionieri, Fratini & Schubart, 2012.

According to Humes (1956) *P. rectiseta* showed a high prevalence (81%) at the type locality on the island of Nosy Be. *Neosarmatium africanum* also serves as the host on mainland Madagascar, near Anjiabe Ambony (Anjiabé) in the district of Ambilobe (Diana Region), about 65 km east of Nosy Be. Examination of the gills of the co-occurring gecarcinid *Cardisoma carnifex* failed to reveal any specimens. Males lack the inner seta on P4 enp-2. The egg sac contains 9–15 eggs (mean = 11). Humes (1956) provided some morphological details of the last copepodid of both sexes.

OD: Humes (1956): 79–84; Figs 1–32.

TL: Madagascar, island of Nosy Be (Nossi-bé) off west coast of Diana Region, Ambanoro (south coast); mangroves 2 km from the former Institut de Recherche Scientifique de Madagascar; from the gills of the mudflat crab, *Neosarmatium africanum* Ragionieri, Fratini & Schubart, 2012 (Sesarmidae).

BL: 605–700 µm (♀); 590–629 µm (♂); 595 µm (CoV♀); 600 µm (CoV♂).

Family Laophontidae

The Laophontidae is arguably the most successful family in utilizing brachyuran hosts. Seventeen species in eight genera have been recorded from spider crabs (Majidae), soldier crabs (Mictyridae) and especially xanthoidean crabs and allies (Xanthidae, Pilumnidae, Panopeidae, Eriphiidae, …). Several undescribed species of *Coullia* have also been obtained in washings of brachyuran hosts. The enigmatic *Raptolaophonte ardua* Cottarelli & Forniz, 1989 has been connected to a crab-associated symbiotic mode of life but is not considered here (see below—Unresolved cases).

Hemilaophonte Jakubisiak, 1932

The genus contains only the type species.

Hemilaophonte janinae Jakubisiak, 1932

Jakubisiak (1932) was the first to study harpacticoids associated, accidentally or obligatory, with the European spider crab which he identified as *Maja squinado* (Herbst, 1788). The crabs were mainly collected from Roscoff, Brittany except for one specimen that had been obtained from a fish market in Paris. Both Neumann's (1998) revision of the species complex around *M. squinado* and Sotelo *et al.*'s (2008) genetic identification demonstrated that the north-eastern Atlantic spider crab populations belong to a separate species, *M. brachydactyla* Balss, 1922 while genuine *M. squinado* is restricted to the Mediterranean basin. Interestingly, this separation is also mirrored in the copepod symbionts of both majid hosts. Fiers (1992a) based his redescription of *H. janinae* on material extracted from spider crabs collected in Dinard-St. Enogat (Brittany, France) and Nouadhibou (= Port Étienne) (Mauritania) and convincingly demonstrated that the species is absent from the Mediterranean. Neither Petkovski (1964a) nor Raibaut (1969), who studied the associated copepod fauna of mediterranean *Maja squinado*, found *H. janinae* in the gill chambers but discovered *Paralaophonte* species instead (see below).

Although Jakubisiak (1932) recovered no less than six species of Laophontidae in his washings of the spider crabs, he considered only *Hemilaophonte janinae* as a genuine commensal. Jakubisiak based his conviction on the dorsoventrally depressed body, reduced swimming legs and, not least, the strongly developed maxillipeds and prehensile P1, all of which he considered clear adaptations to a commensal life style, and on the fact that he found *H. janinae* on every spider crab he had examined. Of the seven laophontid genera known at that time he regarded *Harrietella* (also associated with a crustacean host—see above) as most closely related, primarily on account of the reduced swimming leg setal formula. This relationship was doubted by Lang (1948) because Jakubisiak's (1932) description was not only fragmentary but also deficient with regard to the male.

Fiers (1992a) redescribed *H. janinae* in great detail and showed that the fundamentally different sexual dimorphism in P3 endopod and P5 refutes any close affinity between *Hemilaophonte* and *Harrietella*. His dissenting view on relationships postulated a close link between *Hemilaophonte*, its alleged sistergroup *Coullia*, and *Phycolaophonte* Pallares, 1975b, based on the relative size of P2–P4 endopods (smallest in P2), the morphology of ♂ P3 endopod and setation of the fifth legs. Fiers (1992b) added his new genus *Robustunguis* to this lineage. It should be noted that even though Fiers' (1992a) setal formula (his Table I) is correct, he clearly reversed the P2 and P3 in the text and illustrations; his Fig. 3c, showing the diagnostic small endopod, refers to the P2, not the P3.

The few known records (Jakubisiak 1932, 1936; Fiers 1992a) suggest that *H. janinae* is probably associated with *M. brachydactyla* throughout its entire range in the eastern Atlantic, from Scotland to Ghana. It appears that *H. janinae* lives exclusively in the gill chamber of its host; despite several attempts Fiers (1992a) failed to find the species in superficial rinsings of the body and appendages of the spider crab.

OD: Jakubisiak (1932): 510–513; Fig. 2.
AD: Fiers (1992a): 214–221; Figs 1–3.
TL: France; locality unconfirmed. Jakubisiak (1932) found the species on several specimens of *Maja brachydactyla* Balss, 1922 (Majidae) collected near Roscoff, Brittany, and on a single specimen of unknown origin bought at a market in Paris.
BL: 640 µm (♀), ♂ slightly smaller [Jakubisiak 1932]; 565–605 µm (♀); 390–435 µm (♂) [Fiers 1992a].

Paralaophonte Lang, 1948

Vervoort (1964) remarked that *Paralaophonte* Lang, 1944 is an unavailable generic name which was subsequently validated by Lang (1948) by the indication of a type species (*Cleta brevirostris* Claus, 1863) and the provision of an accompanying generic diagnosis (Huys 2009b). The genus currently accommodates 41 valid species (Huys & Lee 2009; Gómez & Morales-Serna 2013) of which three are known to be associated with decapod hosts. According to Fiers (1992a) there are several indications suggesting that the three *Paralaophonte* species (*P. royi* (Jakubisiak, 1932), *P. majae* Petkovski, 1964a, *P. ormieresi* Raibaut, 1969), living in the gill chamber of spider crabs (*Maja* spp.), descended from a common ancestor. Identification is most easily achieved using Huys & Lee's (2009) key to species. The latter needs updating following the description of two new species (*P. pacificaemulator*, *P. pacificavicinum*) by Gómez & Morales-Serna (2013) by replacing couplet 28 as follows:

Antennule ♀ 6-segmented; P5 exopod ♀ with five elements . . . . 28bis.
Antennule ♀ 7-segmented; P5 exopod ♀ with four elements. . . . . *P. septemarticulata* Chislenko, 1978.
28bis. P1 enp-1 less than twice the length of exopod; P5 exopod ♀ longer than wide; endopodal seta of ♂ P5 shorter than exopod. . . . . *P. pacifica* Lang, 1965.
P1 enp-1 less than twice the length of exopod; P5 exopod ♀ longer than wide; endopodal seta of ♂ P5 noticeably longer than exopod . . . . *P. pacificaemulator* Gómez & Morales-Serna, 2013.
P1 enp-1 twice the length of exopod; P5 exopod ♀ wider than long; endopodal seta of ♂ P5 noticeably longer than exopod. . . . . *P. pacificavicinum* Gómez & Morales-Serna, 2013.

Paralaophonte royi (Jakubisiak, 1932)

Jakubisiak (1932) described the female of a new species, *Laophonte royi*, from washings of *Maja brachydactyla* (originally identified as *M. squinado*) from Roscoff. His text description is concise and only illustrations of leg 1, leg 5 and the caudal ramus were provided. Lang (1948) relegated *L. royi* to his repository "*Laophontinae incertae and incertae sedis*", a position it remained in until Fiers (1992a) transferred it to *Paralaophonte* Lang, 1948. Fiers did not explain his course of action and Wells (2007) continued classifying it as *species incertae sedis* in the family. Huys & Lee (2009) included *L. royi* as a valid species of *Paralaophonte*, considering it a very close relative of *P. majae*. Fiers' (1992a) record from the gill chamber of a male spider crab trawled off the coast of Ghana, extended considerably the known distribution of the species and identified the precise location on the host. Gheerardyn *et al.* (2006) referred to observations of "additional material" of *P. royi* but did not disclose its origin. The male is as yet undescribed.

OD: Jakubisiak (1932): 509–510; Fig. 1 [♀ only].
TL: France; locality not specified. Jakubisiak (1932) washed several specimens of *Maja brachydactyla* Balss, 1922 (Majidae) collected near Roscoff, Brittany (France), and a single specimen of unknown origin bought at a market in Paris.
BL: 680 µm (♀).

Paralaophonte majae Petkovski, 1964a

Petkovski (1964a) provided a full description of both sexes but did not disclose the type locality. The material the description was based on was donated by Zdravko Števčić and came from washings of the gill chamber of *Maja* *squinado*. Števčić (1965) recorded several unidentified harpacticoid species from the maxillipedal epipodites of *M. squinado* obtained in the northern Adriatic but did not specify whether *M. majae* was among them. Stiller & Števčić (1967) also reported the presence of harpacticoids in the branchial chamber and the abdominal cavity of *M. squinado* while Števčić (1968) observed them between the eggs of spider crabs collected in the vicinity of Rovinj. According to Petkovski (1964a) the species identified (but not illustrated) by Por (1964) as *Paralaophonte* aff. *taurina* (Monard, 1928) is potentially conspecific with *P. majae*. It is likely that Petkovski examined the original material before arriving at this conclusion (Bodin 1997). Por's (1964) record came from subtidal mud at 73 m off Cape Carmel along the Israeli mediterranean coast. Candás *et al.* (2012) recorded *P. majae* from sediment samples taken in the Ría de Ferrol in Galicia, north-western Spain.

OD: Petkovski (1964a): 156–160; Abb. 24–41.
TL: Adriatic Sea; coast of former Yugoslavia; locality unknown but probably northern Adriatic; in gill chamber of *Maja squinado* (Herbst, 1788) (Majidae).
BL: 730–800 µm (♀), 640–660 µm (♂).

Paralaophonte ormieresi Raibaut, 1969

Raibaut (1969) described *P. ormieresi* as an associate of spider crabs (*Maja squinado*) in the western Mediterranean. The species lives exclusively between the gill filaments but does not appear to have any noticeable effect on the host. Several hundreds of copepodids and adults can be found in the gill chamber of a single crab. No specimens were observed on the carapace of the host. Raibaut (1969) was unaware of Petkovski's (1964a) description of *P. majae* but recognized a certain affinity with "*Laophonte royi*".

OD: Raibaut (1969): 452–456; Plate I; Figs 1–3.
TL: France, Languedoc-Roussillon, Hérault; rocky littoral substratum east of Sète; in gill chamber of *Maja squinado* (Herbst, 1788) (Majidae).
BL: 460 µm (♀), 420 µm (♂).

Loureirophonte Jakobi, 1953a

The genus currently accommodates 12 valid species (Gómez & Boyko 2006) but only one of them is known to be associated with crustacean hosts (Fiers 1993). According to Huys & Lee (2009) it is highly probable that *Loureirophonte* is merely nested within the currently paraphyletic genus *Paralaophonte*. Gómez & Boyko (2006) provided an updated identification key to species and Huys & Lee (2009) compiled the armature formulae of legs 2–5 in both sexes for all species.

Loureirophonte majacola Fiers, 1993

Fiers (1993) obtained *L. majacola* from washings of the spider crab *Maja brachydactyla* (originally identified as *M. squinado*) collected off the south coast of Fuertaventura, Canary Islands. It was also recorded from the same host collected at 0–20 m in the western part of the harbour of Funchal in Madeira. It is not known whether *L. majacola* lives on the gills or on the external surface of the spider crab. Fiers (1993) considers the species an intimate associate of *M. brachydactyla* since analysis of eulittoral phytal samples from the same region failed to reveal its presence.

OD: Fiers (1993): 219–221, 233–235; figs 8h, 9a–d, l0a–d.
TL: Spain, Canary Islands, south coast of Fuertaventura near Punta de Gran Tarajal; washings of *Maja brachydactyla* Balss, 1922 (Majidae).
BL: 400 µm (♀), 370 µm (♂).

Mictyricola Nicholls, 1957

Nicholls (1957) proposed a new genus *Mictyricola* (misspelled *Myctyricola* in the heading of the generic diagnosis: p. 897) for two new species found on soldier crabs (family Mictyridae) in Australia. *Mictyricola typica* (the type species) was associated with *Mictyris platycheles* H. Milne Edwards, 1852 while *M. proxima* was commonly encountered on the light-blue soldier crab, *Mictyris longicarpus* Latreille, 1806. Both species live on the ventral surface of the host in the space enclosed between the thorax and the reflexed abdomen. This region is abundantly provided with bristles, both on the median surface of the body segments and marginally on the pleura. In female crabs they are also found on the pleopods. Copepods tend to be most densely congregated in the region just posterior to the host's maxillipeds, and can occasionally be found on the bristles of these appendages. The strongly developed maxilipeds are the major appendages involved in temporary attachment to the host's bristles. It is likely that they feed on the abundant material adhering to or growing on these setae. The copepods are active while on the host, moving rapidly among the bristles, using their first legs and maxillipeds, but swim poorly and sink rapidly when dislodged from the host. The nauplius eye is present.

Nicholls (1957) obtained all stages, from the first nauplius to the adult, suggesting that the entire life cycle is completed on the hosts. Ovigerous females carrying a single egg sac with 9–18 eggs were also observed. A total of five dorsoventrally flattend naupliar stages were recognized in the material of which Nicholls illustrated the third and fifth ones. In October (Spring) the population of all stages of *M. typica* carried by each of five *M. platycheles* averaged over 50, varying from 35 to 82.

According to Poore (2004) *M. longicarpus* is found from Singapore and the Bay of Bengal to New Caledonia and Australia, reaching as far south as Perth, Western Australia in the west, and around the coast of Queensland and New South Wales to Wilsons Promontory, Victoria. However, recent revisionary work has shown its range to be confined to the eastern coast of Australia (Davie *et al.* 2013). *Mictyris platycheles* is found along the east coast of Australia from northern Tasmania and Victoria, extending north along the east coast as far as Moreton Bay, Queensland (Poore 2004). Nicholls (1957) assumed that both *Mictyricola* species were probably as widely distributed as their hosts but Fiers (1991) showed that the distribution of the genus is limited since washings of *Mictyris* specimens from Japan, China and Indonesia revealed only *Xanthilaophonte trispinosa* (Sewell, 1940). No copepods have been reported from the other six species currently recognised in the genus *Mictyris*.

Records of *Mictyricola* spp. are extremely rare, with only one published record since Nicholls (1957). Warwick *et al.* (1990) found *M. typica* associated with *M. platycheles* on a sheltered intertidal sandflat at Eaglehawk Neck, Tasman Peninsula, south-eastern Tasmania. They also found the species in sediment samples taken in intensely disturbed areas of the sandflat; however, since the soldier crabs were preserved along with the sand, they had clearly become dislodged in the samples. This is in agreement with Nicholls' (1957) observation that *Mictyricola* spp. were absent from the sand surrounding the crab burrows.

Fiers (1992b) regarded *Mictyricola* most closely related to *Heterolaophonte* (a claim also made by Nicholls) on the basis of the reduced antennary exopod and the sexually dimorphic seta on the P2 endopod. Leg 4 appears to be absent in all stages and its modification in the female copepodids IV–V (displayed by the great majority of *Heterolaophonte* spp.; *cf.* Fiers 1998) is therefore probably secondarily lost. Nicholls (1957) observed pairs *in amplexus* in which the male grasps the female by the caudal rami; this offers a functional explanation for the sexual dimorphism displayed in the caudal rami. Both species can be differentiated by the key below.

Key to species of *Mictyricola* Nicholls, 1957

1. Caudal ramus ♀ with straight outer margin; outer seta of P3 enp-2 ♀ shorter than endopod; P2 enp-1 ♂ about as long as enp-2; P3 enp-1 ♂ as long as wide. . . . . *M. typica* Nicholls, 1957.
- Caudal ramus ♀ with concave outer margin; outer seta of P3 enp-2 ♀ much longer than endopod; P2 enp-1 ♂ distinctly longer than enp-2; P3 enp-1 ♂ twice as long as wide . . . . *M. proxima* Nicholls, 1957.

Mictyricola typica Nicholls, 1957

OD: Nicholls (1957): 898–900, 904; Figs 1–2.

TL: Australia, southern Tasmania; from the ventral surface of *Mictyris platycheles* H. Milne Edwards, 1852

(Mictyridae). Nicholls (1957) recorded the species from Howrah Beach and Pipe Clay Lagoon but did not designate a type locality; the label on the jar containing the spirit preserved syntypes in The Natural History Museum (NHMUK reg. no. 1959.1.2.1) confirms the latter as the type locality.

BL: 760–860 µm (♀), 760–830 µm (♂).

Mictyricola proxima Nicholls, 1957

OD: Nicholls (1957): 900–904; Figs 3–4 (adults), 6 (nauplius stages).

TL: Australia; from the ventral surface of *Mictyris longicarpus* Latreille, 1806 (Mictyridae). Nicholls (1957) reported the species from Gunnamatta Bay, Cronulla, New South Wales, and from Dunwich on Stradbroke Island, Queensland, but neither was specified as the type locality. The collections of The Natural History Museum contain two jars of spirit preserved syntypes, one from each locality (NHMUK reg. nos 1959.1.2.5 and 1959.1.2.6, respectively). The type locality therefore encompasses both places of origin (ICZN Art. 73.2.3).

BL: 950–1,090 µm (♀), 990–1,130 µm (♂).

Coullia Hamond, 1973a

Huys (2009a) relegated *Phycolaophonte* and *Eolaophonte* Apostolov, 1990 to junior subjective synonyms of *Coullia* and provided a key to the six valid species. Other, as yet undescribed, species of *Coullia* have been reported in washings of *Maja squinado* from the Mediterranean and of unidentified decapods from the Eastern Pacific (Fiers 1991, 1992a).

Xanthilaophonte Fiers, 1991

Sewell (1940) described *Laophonte trispinosa* from a single female obtained in weed-washings in the Maldives. He regarded the species to be close to *L. mirabilis* Gurney, 1927 in the shape and general proportions of the body and to *L. armiger* Gurney, 1927 in the absence of any conspicuous spiny projections on the body. Sewell (1940) further recognized a similarity in the female P5 morphology with *Laophonte horrida* (Norman, 1876), *L. brevispinosa* Sars, 1908a and *L. armiger* (all subsequently assigned to the genus *Echinolaophonte* by Nicholls (1941) and the *Onychocamptus horridus*-group by Lang (1948)). Both Noodt (1958) and Lang (1965) suspected that *L. trispinosa* should be placed in the "*Onychocamptus*-*Klieonychocamptus* complex" (possibly because of the presence of three setae on the female P5 exopod), however neither author defined this taxon unambiguously or made a strong recommendation for its generic assignment.

Fiers (1991) showed that *L. trispinosa* is a very common and abundant associate of various marine brachyuran crabs in the Indian and western Pacific Ocean. His excellent redescription of the adults and study of copepodids demonstrated its close relationship with *Echinolaophonte* as Sewell (1940) had originally assumed. Based on the absence of dorsal cephalic processes, Fiers (1991) believed that *L. trispinosa* could not be accommodated in *Echinolaophonte*, and consequently fixed it as the type of a new genus, *Xanthilaophonte*. The close relationship between both genera is not only apparent by the remarkably long basis in the P1 but also by the morphology of the cephalothorax. In adult *X. trispinosa* the cephalothorax shows a mediodorsal rounded process exactly in the same position where the dorsal spinous thorn is found in members of *Echinolaophonte*. Based on unpublished ontogenetic data Fiers (1991) demonstrated that a similar rounded process is found in the copepodid V of *Echinolaophonte*, being the precursor of the cephalic thorn in the adult. This feature in conjunction with the more derived armature and lack of sexual dimorphism on the swimming legs made Fiers (1991) conclude that the development of *X. trispinosa* is post-displaced in comparison to that of *Echinolaophonte*.

A second species, *X. carcinicola*, associated with an Indonesian pilumnid, was added by Fiers (1991). He regarded the genus as a typical Indo-West Pacific faunal element, apparently having been replaced in the Eastern Pacific by members of the genus *Coullia*, which independently entered into association with xanthoidean crab hosts. Both *Xanthilaophonte* species occur between the carapace bristles of their xanthoidean hosts. Individuals that utilize soldier crabs (Mictyridae) probably attach to the hirsute mouthparts and/or the rigid bristles in the ventral space enclosed between the thorax and the reflexed abdomen. Cottarelli *et al.* (2006) announced the description of a third species, which co-exists with *X. trispinosa* on the same xanthid hosts on Cebu Island (Philippines), but to my knowledge this has remained unpublished. The two described species can be separated by the key below.

Key to species of *Xanthilaophonte* Fiers, 1991

1. P1 exopod 1-segmented; P2 exopod 3-segmented with four elements on distal segment; P3 exp-3 with five elements; P5 exopod of female twice as long as wide; P5 exopod of male discrete . . . . *X. trispinosa* (Sewell, 1940).

\- P1 exopod 2-segmented; P2 exopod 2-segmented with three elements on distal segment; P3 exp-3 with four elements; P5 exopod of female as long as wide; P5 of male with fused rami . . . .*X. carcinicola* Fiers, 1991.

Xanthilaophonte carcinicola is distinctly more slender than *X. trispinosa*. Additional discriminants are the size of the female endopodal lobe of leg 5 (much shorter in *X. carcinicola*), the ornamentation of the body somites (dorsal posterior margins spinulose in *X. trispinosa*, smooth in *X. carcinicola*), and the morphology of the cephalothorax (posterodorsal margin forming rounded plate bearing spinules ventrally in *X. trispinosa*; obsolete in *X. carcinicola*) and penultimate somite (dorsal posterior margin forming pseudoperculum in *X. trispinosa*, consisting of four incised lobate extensions; absent in *X. carcinicola*). The loss of the outer basal seta of the male P5 is unique to *X. carcinicola*.

Xanthilaophonte trispinosa (Sewell, 1940)

Fiers (1991) described the complete copepodid development and reported variability in the armature of the P4 exopod (exp-3 with/without inner seta) and endopod (enp-2 with one or two inner setae). The normal armature patterns for these segments are 0.0.122 and 0.120, respectively. Adult males display precocious mate guarding, clasping leg 2 in copepodid I, leg 3 in copepodid II and probably leg 4 from copepodid III onwards. Sexual dimorphism is expressed from copepodid III onwards (in size, antennule and length of P2–P4 armature elements).

Cottarelli *et al.* (2006) recorded specimens from the Philippines (Cebu Island, Mindoro Island) with longer caudal rami and slight differences in the maxilliped (longer basis and endopodal claw; outer spinules on basis absent; syncoxal setae unequal in length with longest arising from a socle). They also described the female genital field for the first time. On Mindoro Island *X. trispinosa* and *Carcinocaris serrichelata* share and even co-exist on the same (unidentified) xanthid host. The species is distributed throughout the Indo-Western Pacific as far east as Auckland, New Zealand (174°E) and utilizes intertidal brachyuran crab hosts belonging to four families. Known hosts and distributional records are summarized in Table 29.

OD: Sewell (1940—as *Laophonte trispinosa*): 326–327; Text-Fig. 76 [♀ only].
AD: Fiers (1991): 290–295; Figs 1–10; Tables 1–2 [both sexes and copepodids]. Cottarelli *et al.* (2006): 7, 11; Figs 25–28.
TL: Maldives, Addu Atoll; weed-washings.
BL: 800 µm (♀) [Sewell 1940]; 590 µm (♀), 400–480 µm (♂) [Fiers 1991].

Xanthilaophonte carcinicola Fiers, 1991

The species is known from two females and one male and has not been discovered again since its original description. It co-occured with *X. trispinosa* on the same host specimen but is easily distinguishable by its slender habitus (Fiers 1991). The female genital field and male P6 remain to be confirmed.

OD: Fiers (1991): 295–296; Figs 11–12; Table 1.
TL: Indonesia, Sula Islands, Sula Besi; washings of *Pilumnus vespertilio* (J.C. Fabricius, 1793) (Pilumnidae).
BL: 600 µm (♀), 475 µm (♂).

TABLE 29. Records of *Xanthilaophonte trispinosa* (Sewell, 1940) from intertidal decapod hosts. All records from Fiers (1991) except for * (Cottarelli *et al.* 2006).

(SUPER)family	Decapod host	Country	Locality
OCYPODOIDEA			
Mictyridae	*Mictyris longicarpus* Latreille, 1806	Indonesia	West Papua (Irian Jaya Barat), Boeti nea Mezauke beach
	Mictyris spec.	China	Unknown localities
		Japan	Unkwown localities
		Indonesia	Maluku Province, Aru Islands, Manoembrai beach
			Maluku Province, Ambon Island southwest of Seram
PARTHENOPOIDEA			
Parthenopidae	*Daldorfia horrida* (Linnaeus, 1758) [1]	Madagascar	Nosy Be (Nossi Bé)
PILUMNOIDEA			
Pilumnidae	*Pilumnopeus makianus* (Rathbun, 1931)	Japan	Kyushu, Ariaka Wan beach near Mizuho
	Pilumnus hirtellus (Linnaeus, 1761)	Madagascar	Nosy Be (Nosi Bé), Pointe Luboké
	Pilumnus tomentosus Latreille, 1825 [2]	Australia	New South Wales, Port Jackson (Sydney Harbour)
		New Zealand	North Island, Auckland
	Pilumnus vespertilio (J.C. Fabricius, 1793)	Eritrea	Dahlak Archipelago, Entedebir, Goliath Bay
		Indonesia	North Maluku, Sula Islands, Sula Besi
		Japan	Honshu, Wakayama Prefecture, Shirahama
		Philippines	Luzon, Camarines Sur Province, Pasacao Semper [3]
		Red Sea	unknown locality
		Thailand	Laem Singh, Ban Laem Pong
			South coast of Phuket Island
XANTHOIDEA			
Xanthidae	*Phymodius monticulosus* (Dana, 1852b) [4]	Indonesia	Postilyon Islands, Sepoeka Besar
	Unidentified species	Australia	Great Barrier Reef, Yonge Reef
		Maldives	South Malé Atoll, Biyadhoo Island
		New Caledonia	Nouméa
		New Zealand	Auckland, Omana beach
		Papua New Guinea	Madang Province
		Philippines *	Cebu Island, beach near Moalboal
			Mindoro Island, Puerto Galera, Big La Laguna beach

[1] as *Parthenope horrida* (Linnaeus, 1758); [2] host name misspelled as *Pilumnus tormentosus*; [3] as *Pilumnus ursulus* Adams & White, 1848; [4] Although the genus *Phymodius* A. Milne-Edwards, 1863 does not feature in De Grave *et al.*'s (2009) classification of living and fossil decapod genera it is here provisionally listed under de family Xanthidae following the *World Register of Marine Species*.

Robustunguis Fiers, 1992b

Fiers (1992b) established this genus to accommodate two new species, *Robustunguis ungulatus* and *R. minor*, recovered from washings of xanthid crabs from the Gulf of Mexico and Kenya, respectively. The marked discrepancy between both species in swimming leg segmentation and setation made Fiers consider placing *R. minor* in a separate genus, however, since a similar variation occurs within the closely related genus *Coullia* he refrained from taking that course of action.

The most conspicuous characteristic of *Robustunguis* is the disproportionately enlarged prehensile leg 1, which reaches to the posterior end of the caudal rami. Its size is equivalent to about two-thirds of the body length and is—except for members of *Carcinocaris*—unrivalled in the family. The arched claw appears to interlock with the proximal rounded process on the proximal endopod segment, enabling the copepod to grasp around the carapace bristles of the host decapod with great efficiency and tenacity. Even on crabs preserved for many years, copepods can be seen attached as if they had not been affected by the sudden impact of the fixative (Hendricks & Fiers 2010). Both species have a smooth integument, lack distinct pleural extensions on the urosomites and have a relatively long cephalothorax, equalling about one third of the body length. Fiers (1992b) did not report copepodid stages but his later study on the female leg 4 development in Laophontidae showed adult males clasping legs 1–2 of a second copepodid. Fiers (1998) speculated that adult males hold on to both developing females as well as future males until their primary attachment device (leg 1) is fully developed and has acquired its maximum grasping efficiency. This adaptation would avoid that the young stages become separated from their host and lose contact with their founding population. This would imply that in species associated with decapod hosts the original roles of clasping behaviour and modification of the juvenile female leg 4 must have shifted during their evolutionary history. Such a case of exaptation, in which securing contact with the host environment has become the secondary function, obviously only applies to species that are associated with the carapaces of their hosts (see also *Carcinocaris* below). Hendricks & Fiers (2010) illustrated the first ovigerous female (*Robustunguis* sp. 2).

Fiers (1992b) placed *Robustunguis* in a lineage comprising the genera *Coullia*, *Phycolaophonte* and *Hemilaophonte*. The close relationship between these four genera is portrayed by the reduced P2 endopod (smaller than P3 endopod), the sexual dimorphism on the swimming legs and the ovate shape of the female P5 exopod. Lee & Huys (1999) also recognized this clade and placed *Psammoplatypus* Lee & Huys, 1999 at the base of it. The more recent literature (Gómez & Boyko 2006; McCormack 2006; Huys 2009a; Back & Lee 2014) recognizes a closely knit cluster of six genera: *Hemilaophonte*, *Coullia* (syn. *Phycolaophonte*, *Eolaophonte*), *Robustunguis*, *Psammoplatypus*, *Carraroenia* McCormack, 2006 and *Jejulaophonte* Back & Lee, 2014. Members of *Robustunguis* are not related to other decapod associated Laophontidae such as *Xanthilaophonte* spp., *Carcinocaris* spp. or *Raibautius commensalis* (Raibaut, 1962a) **comb. nov.**

The two described species differ in many aspects, including body size and the segmentation and setation of legs 2–5 in both sexes, which are summarized in Table 30. Male *R. ungulatus* possess two setae on the P6 and display sexual dimorphism in the exopods of legs 2–4. In male *R. minor* the P6 is unarmed and the exopods of legs 2–4 are not modified. Hendrickx & Fiers (2010) figure the habitus of two undescribed species from the Pacific coast of Mexico.

TABLE 30. Armature formulae of legs 2–5 in species of *Robustunguis* Fiers, 1992b.

		P2		P3		P4		P5	
		exp	enp	exp	enp	exp	enp	exp	enp
R. ungulatus	♀	0.0.022	010	0.0.022	020	0.0.022	020	6	4
	♂	0.1.022	0.010	0.0.022	0.020	0.0.022	0.021	5	2
R. minor	♀	0.022	010	0.022	0.020	0.022	1	5	1
	♂	0.022	010	0.022	0.020	0.022	1	bisetose plate	

Robustunguis ungulatus Fiers, 1992b

The exopods of legs 2–4 are distinctly shorter in the male than in the female due to shortening of exp-1. The outer spines of P2 exp-3 and P3 exp-(2 and 3) are bipinnate in the female but smooth in the male. Males of this species can display substantial variability in the exopodal armature of leg 2 and in the exopodal segmentation of legs 3–4 (Fiers 1992b: 403–404). *Robustunguis ungulatus* was also found in washings of unidentified small xanthids collected on the reef of Majahual (Mahahual) on the Costa Maya, Quintana Roo, Mexico (Fiers 1992b). It has not been recorded from other localities within the range of its type host, the spineback hairy crab, *Pilumnus sayi* Rathbun, 1897, which extends from North Carolina through the Gulf of Mexico and West Indies to Curaçao. Fiers (1992b) found 63 individuals on just two specimens of *P. sayi*.

OD: Fiers (1992b): 402–404; Figs 1–4.
AD: Fiers (1998): 49; Fig. 3a–b.
TL: U.S.A., Florida; in washings of two specimens of *Pilumnus sayi* Rathbun, 1897 (Pilumnidae); depth 40 m.
BL: 650 µm (♀), 565 µm (♂).

***Robustunguis minor* Fiers, 1992b**

The paedomorphic body morphology of *R. minor* is illustrated by the smaller body size, the 2-segmented P2–P4 exopods, the reduced P2–P4 endopods (particularly P4, represented by a single seta), the strongly reduced P5 in both sexes, the unarmed male P6 and the lack of distinct sexual dimorphism on the swimming legs (except ♂ P3 endopod). Most of these paedomorphic features can be viewed as the result of progenesis (early offset; *e.g.* reductions in P2–P5; lack of sexual dimorphism) or post-displacement (late onset; *e.g.* ♂ P6). Kim (2013) added a second record from Ulreungdo Island east of the Korean peninsula. His specimens were obtained in washings of the pilumnid *Pilumnus minutus* De Haan, 1835.

OD: Fiers (1992b): 404–405; Figs 5–6.
TL: Kenya, Shimoni (south-east coast near the border with Tanzania); in washings of unidentified xanthid crab collected on unspecified species of *Pocillopora* Lamarck, 1816a (Scleractinia). Hendricks & Fiers (2010) list the host as "(?) *Pilumnus* sp.".
AD: Kim (2013): 44–46; Figs 17–18.
BL: 320 µm (♀), 210 µm (♂) [Fiers 1992b]; 380 µm (♀), 320 µm (♂) [Kim 2013].

***Robustunguis* sp. 1 *sensu* Hendrickx & Fiers (2010)**

OD: Hendrickx & Fiers (2010): 20; Figs 7C–D, 8B (erroneously labelled 8A).
TL: Mexico, eastern Pacific coast; on carapace of *Pilumnus townsendi* Rathbun, 1923 (Pilumnidae).
BL: 400 µm (♀), 325 µm (♂) (based on figures).

***Robustunguis* sp. 2 *sensu* Hendrickx & Fiers (2010)**

OD: Hendrickx & Fiers (2010): 20; Figs 7E–G.
TL: Mexico, eastern Pacific coast; on carapace of *Daira americana* Stimpson, 1860 (Dairidae).
BL: 440 µm (♀), 365 µm (♂) (based on figures).

***Carcinocaris* Cottarelli, Bruno & Berera, 2006**

Cottarelli *et al.* (2006) established the genus for a new species discovered in carapace washings of unidentified xanthid crabs in the Philippines. Two more species were added from panopeid and xanthid hosts in the Gulf of Thailand, Florida and southeastern Brazil (Björnberg & Santos 2009; Cottarelli & Bruno 2011). Members of *Carcinocaris* have a characteristic maxilliped displaying a series of strong spinules along the palmar margin which seem to interlock with three or four teeth-like processes on the endopodal claw. The maxilliped and the excessively elongate leg 1 endopod are the key appendages that secure a firm grasp around the carapace bristles of the host. According to Cottarelli *et al.* (2006) the genus is probably most closely related to *Raptolaophonte* because of the morphology of the maxilliped, the loss of leg 3 endopod in both sexes and the reduction of legs 4–6.

Cottarelli & Bruno (2011) used several characters to differentiate the three species but some of them are of limited usefulness, including the segmentation pattern (male) and armature formula (both sexes) of the antennule, the number of setae on the caudal ramus (seta I is often difficult to observe), the number of lateral pores and sensilla on the cephalothorax, and the number of endites on the maxillary syncoxa. All these characters have not been documented correctly in at least one description and should not be employed in species discrimination. For example, Björnberg & Santos (2009) claimed that *C. serrichelata* has one less maxillary endite than in *C. minipedia*. However, their illustration of the maxilla (Fig. 12) is problematic since the syncoxa is figured with three well developed cylindrical endites. This condition has not been observed in the family Laophontidae before, not even in members of the primitive subfamily Esolinae (Huys & Lee 2000). Both *C. serrichelata* and *C. dussarti* have three syncoxal endites, the proximal one being represented by a small seta, and the middle and distal one being cylindrical with two or three elements. This condition corresponds with the groundpattern of the Laophontoidea (Huys 1990b). Comparison with Cottarelli & Bruno's (2011: Fig. 2I) description shows that the proximal cylindrical endite in *C. minipedia* is in fact homologous with the middle endite in its two congeners, implying that either the middle or distal endite was inadvertently duplicated in Björnberg & Santos' (2009) illustration; the real proximal endite (represented by a single seta) was probably overlooked.

Carcinocaris minipedia can readily be distinguished from its two Indo-Pacific congeners by differences in the segmentation and armature of the swimming legs. Cottarelli & Bruno (2011) pointed out several morphometric differences between *C. serrichelata* and *C. dussarti* (*e.g.* relative length of some setae on legs 1–5 and the caudal rami; proportional lengths of coxa, basis and endopod in leg 1; length/width ratio of the female genital double-somite) but these have been omitted from the key below.

Key to species of *Carcinocaris* Cottarelli, Bruno & Berera, 2006

1. P2 exopod 1-segmented, bearing three setae; distal outer element of P3 exp-2 a well developed spine in both sexes; P4 exopod 2-segmented and endopod absent in both sexes . . . . *C. minipedia* Björnberg & Santos, 2009.
P2 protopod and exopod fused forming single segment with outer basal seta and two apical (exopodal) setae; distal outer element of P3 exp-2 setiform in female and spiniform in male; P4 exopod 1-segmented in female and 1- or 2-segmented in male, endopod represented by a single long seta in female and completely absent in male . . . . 2.

2. Maxillipedal claw with four teeth-like processes; in female, P3 exp-1 with both outer spines of about equal length; P4 exopod 1-segmented in both sexes; P6 of female represented by two small setae . . . . *C. serrichelata* Cottarelli, Bruno & Berera, 2006.
Maxillipedal claw with three teeth-like processes; in female, P3 exp-1 with distal outer spine about twice as long as proximal one; P4 exopod 1-segmented in female, 2-segmented in male; P6 of female represented by one small seta. . . . . *C. dussarti* Cottarelli & Bruno, 2011.

Carcinocaris serrichelata Cottarelli, Bruno & Berera, 2006

The species is only known from the Philippines. In addition to the type locality on Verde Island, Cottarelli *et al.* (2006) also collected it from two intertidal localities in the Oriental Mindoro Province on Mindoro Island. A new population of *C. serrichelata* from unidentified xanthid crabs was obtained from a beach on North Pandan Island in the Occidental Mindoro Province, thus further extending westwards the geographical range of the species (Cottarelli & Bruno 2011). Ovigerous females carry 4–6 large eggs in a single egg sac. Males typically grasp the modified leg 4 of female copepodids (CoIV–V) but occasionally attach to even younger copepodids (CoII–III) (as in *Robustunguis*—see above). Exceptionally, males were also found attached to the caudal rami of an ovigerous female and in one instance two males were grasping the same female (Cottarelli *et al.* 2006). In the Philippines, *C. serrichelata*, *Xanthilaophonte trispinosa* and other, as yet undescribed, laophontids frequently co-exist on the same host xanthid.

OD: Cottarelli *et al.* (2006): 4–10; Figs 1–24, 29–45.

TL: Philippines, Oriental Mindoro Province, Verde Island (north of Puerto Galera); north beach along east coast (13°32’45.6”N, 121°03’94.2”E); associated with unidentified xanthid crabs collected in intertidal zone at low tide.

BL: 342–435 µm (♀), 288–319 µm (♂).

Carcinocaris minipedia Björnberg & Santos, 2009

The species has been recorded from three panopeid hosts in two geographically disjunct localities, *i.e.* from the narrowback mud crab, *Panopeus americanus* Saussure, 1858, and the black-fingered mud crab, *P. herbstii* H. Milne Edwards, 1834, in the mangroves of Araçá Bay in São Sebastião, Brazil, and from the flatback mud crab, *Eurypanopeus depressus* (Smith, 1869), near Fort Pierce, Florida. Adults are commonly found among the setae of the carapace and on the eggs of their hosts although adults can also occur in rock pools. Nauplii and copepodids were only found on the eggs of the host. Björnberg & Santos (2009) illustrated the fifth nauplius and all copepodid stages. The female copepodid V (and to a lesser extent copepodid IV) has a conspicuously modified leg 5, consisting of two lobes with digitiform processes. Considerable variability was observed in the male leg 5 which forms a lobate expansion bearing the outer basal seta and 2–4 exopodal setae; additional variability can occur in the segmentation of the female antennules (5–6 segments). Ovigerous females carry a single egg sac containing up to 12 eggs.

OD: Björnberg & Santos (2009): 116–123; Figs 1–56.

TL: Brazil, São Paulo State, São Sebastião, Araçá Bay; from carapace and eggs of panopeid crabs collected in mangroves; the type host was not specified.

BL: 571–685 µm (♀), 380–410 µm (♂), 175 µm (NV), 200–211 µm (CoI), 245 µm (CoII), 260–270 µm (CoIII), 301–360 µm (CoIV), 300–330 µm (CoV♂).

Carcinocaris dussarti Cottarelli & Bruno, 2011

Cottarelli & Bruno (2011) observed slight variability in the number of teeth (three or four) on the maxillipedal claw. Unlike its congeners, which show four teeth in the adult, *C. dussarti* typically have only three although younger developmental stages (CoIII) have four. Males were frequently observed clasping copepodid females with their antennules. In one exceptional case an adult male was found holding onto a late naupliar instar. The significance of this behaviour is unknown. Ovigerous females carry 8–10 large eggs in a single egg sac.

The host was originally identified as *Leptodius exaratus* (H. Milne Edwards, 1834) which has been widely reported from the Indo-West Pacific, where it is a ubiquitous component of the intertidal and shallow subtidal fauna. A close examination of material throughout its range recently demonstrated that *L. exaratus* in reality represents an amalgam of two species (Lee *et al.* 2013). *Leptodius exaratus* s. str. is restricted to the Western Indian Ocean, ranging from the eastern and southern coasts of Africa, including Madagascar, to the western coast of India, including the Red Sea and the Persian Gulf. *Leptodius affinis* (De Haan, 1835) is found in the Eastern Indian Ocean and in the Western and Central Pacific Ocean, ranging from the eastern coast of India all the way to the oceanic islands of French Polynesia in the west, and from central Japan in the north to Australia in the south. The specimens examined by Cottarelli & Bruno (2011) almost certainly belong to *L. affinis*. Given the extensive range of its host it is conceivable that *C. dussarti* will also be encountered outside of the Gulf of Thailand.

OD: Cottarelli & Bruno (2011): 107–114; Figs 1–4.

TL: Thailand, Gulf of Thailand, eastern side of Samed Island (Ko Samet), Ao Thian beach (12°50’22’N, 120°45’24”E); on carapace of *Leptodius affinis* (De Haan, 1835) (Xanthidae) collected beneath coral fragments in intertidal zone at low tide.

BL: 395–483 µm (♀), 358–386 µm (♂).

Raibautius gen. nov.

Raibaut (1962a, 1967), accepting Nicholls' (1941) classification of the family Laophontidae and its type genus *Laophonte*, placed his new species *L. commensalis* in the subgenus *Mesolaophonte* Nicholls, 1941, rather than creating a new monotypic genus for it. Nicholls' (1941) subgeneric division was based solely on the endopodal armature of the female leg 3 and his system has been criticised for its artificiality by both Lang (1948) and Vervoort (1964) who abolished it. Fiers (1992b, 1998) stated that *L. commensalis* has many features in common with the *Laophonte setosa* group but does not elaborate on this claim. There appears to be a general consensus that the genus *Laophonte* should be restricted to a close-knit group of species, commonly referred to as the *cornuta* group (Fiers 1986b; Huys & Lee 2000; Gómez & Boyko 2006; Gómez & Morales-Serna 2013). *Laophonte commensalis* cannot be accommodated in this group since it differs radically in antennulary segmentation and shape, swimming leg armature, and leg 5 morphology. Unlike *L. commensalis* members of the *cornuta* group do not display a modified leg 4 in copepodids IV–V (Fiers 1988). The species is here fixed as the type of a new genus on account of its unique armature pattern on the swimming legs, including the presence of five elements on P2–P4 exp-3 and only two setae on P4 enp-2, and the 2-segmented P3 endopod in the male.

Diagnosis. Laophontidae. Body cylindrical and linear; cephalic shield conical. Posterior margins of cephalothorax and body somites with spinule rows dorsally and laterally; urosomites without marginal spinules midventrally. Rostrum small, fused at base. Genital double-somite ♀ without dorsal internal/external chitinous ribs marking original segmentation. Pleural extensions of ♀ abdominal somites rudimentary. Caudal ramus cylindrical, subrectangular, about as long as wide; with six setae (seta I possibly absent); seta V well developed, pinnate; setae IV about ¼ the length of seta V.

Sexual dimorphism in antennule, P3 endopod, P5, P6 and in genital segmentation.

Antennule short and 6-segmented in ♀; 7-segmented and subchirocer with two segments distal to geniculation in ♂; segments without conspicuous ornamentation along anterior margin except for few spinules on segment 1; segments 1–2 without processes; with aesthetasc on segment 4 (♀) or 5 (♂). Antenna with four setae on exopod; allobasis with abexopodal seta. Mandibular palp relatively short, 1-segmented; with four setae. Maxillule with defined exopod bearing two setae. Maxilla with two endites on syncoxa; endopod unconfirmed. Maxilliped robust; syncoxa with two setae; basis without spinules along palmar margin; endopodal claw long and curved, with one accessory seta.

P1 long, with 3-segmented exopod, exp-3 with two normal and two geniculate setae; endopod stout, enp-1 without inner seta, enp-2 with minute seta and long pinnate claw. P2–P4 exopods 3-segmented; endopods 2-segmented. P3 endopod ♂ 2-segmented with enp-2 extending into apophysis. Armature formula as follows:

	Exopod	Endopod
Leg 2	0.0.023	0.220
Leg 3	0.0.023	0.221 (♀) or 0.22apo (♂)
Leg 4	0.0.023	0.110

Leg 5 ♀ with separate rami; exopod elongate, subrectangular, reaching far beyond endopodal lobe, with five setae; endopodal lobe small, with four setae. Fifth pair of legs in ♂ minute, not fused medially; baseoendopod free at base; endopodal lobe obsolete, unarmed; exopod small, slightly longer than wide, with three setae. Leg 6 and genital field of ♀ unconfirmed; leg 6 ♂ with two setae. Leg 4 of ♀ copepodids IV–V modified.

Marine; associated with xanthid and eriphiid decapods.

Type species. *Laophonte commensalis* Raibaut, 1962a (by original designation).

Etymology. The genus is named after the late Prof. André Raibaut (Université de Montpellier II) in recognition of his contributions to the taxonomy of commensal Harpacticoida.

Raibautius commensalis (Raibaut, 1962a) comb. nov.

Raibaut (1962a, 1967) discovered *L. commensalis*, while inspecting the external surface of *Xantho poressa* (Olivi, 1792) [as *Xantho rivulosus* Risso, 1827] (family Xanthidae) collected along the French mediterranean coast near

Banyuls and Sète. It was commonly found on the hirsute areas of the ventral side of the cephalothorax, particularly near the last pair of pereiopods, and occasionally in between the pleopods of female crabs. Adults and copepodids typically clasp the host bristles by means of the prehensile leg 1 and maxillipeds; nauplii use the terminal claw on the antennary endopod. The incidence of infection in *X. poressa* was 100% with an intensity of infection of up to 50 copepods.host^{-1}. Raibaut (1962a, 1967) recorded *L. commensalis* also from two other xanthid decapods, *Xantho pilipes* A. Milne-Edwards, 1867 and *X. hydrophilus* (Herbst, 1790) [as *X. floridus* (Montagu, 1808)], both collected from Roscoff. The copepod was not found in the gill chamber or in the sediment substrata inhabited by the hosts in their natural environment. Except for Fiers (1998) who found adults and copepodids in washings of another decapod host, *Eriphia verrucosa* (Forskål, 1775) (family Eriphiidae), collected off Sardinia, no other published records of *L. commensalis* exist.

Ovigerous females carry a single egg sac containing on average eight eggs (around 50 µm in diameter). Raibaut (1963b) described the developmental stages, including five naupliar instars and six copepodid stages; the sixth nauplius stage was not observed. Rearing experiments in isolation of the host, *X. poressa*, appeared unsuccessful, suggesting the association with xanthid crabs is obligatory. Raibaut did not observe any marked differences in the legs between male and female copepodids, except for the presence of an apophysis on the male P3 endopod of CoIV; however, based on examination of his Sardinian material, Fiers (1998) showed that leg 4 in juvenile females follows a different developmental pathway than in males. At CoIV and CoV the exopod is represented by a long, flat ramus (distinctly 2-segmented at CoV), bearing an outer spinulose element and five short setae along the distal border. Fiers (1998) observed this pattern also in *Laophonte elongata* Boeck, 1873 (a member of the *L. setosa* species group) and in an as yet undescribed species that is closely related to *L. commensalis* and lives in association with *Maja brachydactyla* (originally identified as *M. squinado*) along the African Atlantic coast. The modification of leg 4 facilitates precopulatory mate guarding during which the adult male grasps the exopod of female CoIV–V, *i.e.* prior to changing posture at the final moult when the adult P5 exopod is grasped (postcopulatory posture).

OD: Raibaut (1962a—as *Laophonte* (*Mesolaophonte*) *commensalis*): 624–627; Figs 1–2 (adults).

AD: Raibaut (1963b): 112–118; Figs 1–3 (nauplii, copepodids). Raibaut (1967): 29–36; Figs 7–8. Fiers (1998): 45.

TL: France, Languedoc-Roussillon region; on carapace of *Xantho poressa* (Olivi, 1792) [as *Xantho rivulosus* Risso, 1827] (Xanthidae). Raibaut (1962a) recorded the species from the vicinity of Banyuls-sur-Mer (Pyrénées-Orientales) and Sète (Hérault) but did not specify the type locality.

BL: 390 µm (♀), 260 µm (♂) [Raibaut 1962a]; 65–75 µm (NI), 75–80 µm (NII), 85–90 µm (NIII), 100 µm (NIV), 130 µm (NV), 180 µm (CoI), 210 µm (CoII), 250 µm (CoIII), 280 µm (CoIV), 320 µm (CoV) [Raibaut 1963b].

Family Miraciidae

Amphiascus Sars, 1905c

See p. 486 for a key to species.

Amphiascus paromolae (Soyer, 1973)

Soyer (1973) obtained about 700 individuals of *Paramphiascopsis paromolae* from the gill lamellae of a single adult female of the box crab, *Paromola cuvieri* (Risso, 1816) (family Homolidae). Both sexes and all developmental stages were represented in the washings. No information is available on the biology of the species. Huys (2009b) transferred the species to *Amphiascus* but erroneously cited the new combination as *Amphiascopsis paromolae* (Soyer, 1973). The host occurs in the eastern Atlantic Ocean and the Mediterranean, from Angola to Norway, the Northern Isles and Iceland. It has occasionally been reported from coastal waters but is predominantly a deep water species, occurring most frequently at depths of 150–1,331 metres (Ingle 1996).

OD: Soyer (1973—as *Paramphiascopsis paromolae* Soyer, 1973): 90–95; Figs 1–2.

TL: France, Roussillon-Languedoc region, Pyrénées-Orientales, Banyuls-sur-Mer; on the gill filaments of *Paromola cuvieri* (Risso, 1816) (Homolidae).

BL: 2,300 µm (♀); 2,000 µm (♂).

***Sarsamphiascus* Huys, 2009b**

Sarsamphiascus elongatus (Itô, 1972)

Itô (1972) described a new species, *Amphiascus elongatus*, from the gills of the helmet crab *Telmessus cheiragonus* (Tilesius, 1815) (family Cheiragonidae) along the Pacific coast of Hokkaido, Japan. Although it is found in the intertidal zone and to a depth of 110 m, the host crab is mostly shallow subtidal in zonation. It occurs in the coastal areas of Siberia, Japan and Korea while its North American range stretches from the Bering Sea to Monterey, California. Itô (1972) observed both ovigerous females and copepodid stages in the gill chamber, suggesting that the postmetamorphic phase of the life cycle is largely completed on the host.

Substantial variability was recorded in the shape and number of armature elements on the female P5 baseoendopod, including asymmetrical individuals that have five setae on the right endopodal lobe and six on the left. The species is a member of the *varians*-group of *Sarsamphiascus* (previously *Amphiascus*; *cf.* Huys 2009b) which currently circumscribes a complex of 12 valid species (Hicks 1989); see above for an identification key to species of the *varians*-group. Uncertainties about the limits of intraspecific variation hamper species identification and add to the difficulty in separating males in this complex. Although the ornamentation pattern of the urosome will prove to be a most crucial character in this process, it has as yet not been properly documented for most species and its intrapopulation variability has not been thoroughly investigated (Wells 2007). For example, it is not clear from Itô's (1972) description (no illustrations were given) whether the male abdominal ornamentation quoted in the text replaces the female pattern or is additional to it. *Sarsamphiascus elongatus* is much larger (> 1.1 mm) than other members (600–700 µm) of the *varians*-group and can readily be distinguished by the reductrion of the mandibular exopod, the very slender maxilliped and the elongate P1 endopod (particularly the proximal segment).

The species has not been recorded again except for two doubtful records from Livingston Island, South Shetland Islands, Western Antarctica (Apostolov & Pandourski 1999, 2002). The single female recorded from the marine interstitial in a littoral sand bank south of Cape Hesperides in the South Bay (Apostolov & Pandourski 1999) agrees in size with Itô's (1972) type population but differs in the morphology of the caudal ramus (setae I–II more slender and less spiniform), maxilliped (more robust and endopod shorter), P1 endopod (enp-1 and -3 distinctly shorter) and P5 (shape of exopod and length of setae). In addition, the authors' claim that the presence of only two inner setae (instead of three) on the distal endopodal segment of P3 is due to interspecific variability is unlikely since this character was also observed in Argentinian specimens of *S. gauthieri* (Monard, 1936) *sensu* Pallares (1968). Apostolov & Pandourski's (1999) illustrations of the habitus, mandible, maxillule and maxilla are almost certainly reproduced from Itô's (1972) description. In a second report on the marine copepods from Livingston Island, Apostolov & Pandourski (2002) recorded *S. elongatus* from the coastal plankton and coarse sediments in Marine Lion Bay. The significant variability observed in the male P5 precludes judgement on conspecificity of these specimens and *S. elongatus* until the Antarctic material can be redescribed more adequately.

OD: Itô (1972—as *Amphiascus elongatus*): 312–320; Figs 5–10; Table 1.
TL: Japan, Hokkaido, Kushiro Subprefecture, Akkeshi; from the gills of *Telmessus cheiragonus* (Tilesius, 1815) (Cheiragonidae).
BL: 1,300 µm (♀); 1,140 µm (♂); 940 µm (CoV♀).

Unidentified records

Hobbs & Villalobos (1958) recorded an unidentified harpacticoid copepod from the freshwater crab *Tehuana lamellifrons* (Rathbun, 1893) [as *Pseudothelphusa lamellifrons*] (family Pseudothelphusidae) collected in the Arroyo Tapalapan, Santiago Tuxtla, southern Veracruz, Mexico. The copepod was present in numbers such as to suggest that the association was not accidental.

McDermott (2005) studied the ectosymbionts of the pinnotherid crab *Pinnixa chaetopterana* Stimpson, 1860 which inhabits marine polychaete tubes (*e.g. Amphitrite ornata* (Leidy, 1855), *Chaetopterus variopedatus* (Renier, 1804)) along the Atlantic and Gulf of Mexico coasts of the United States. An unidentified harpacticoid copepod (*ca.* 600 µm long), usually found in abundance around the bases of the legs of the host, was recorded in nearly all mature crabs in New Jersey (136 males and 158 females). The immature crabs collected in September and October 1964, which represented new host-tube invasions, did not have any copepods. Ovigerous females appeared in the field in July and August and periodically became ovigerous in the laboratory. In all of the numerous crab moults that occurred in the laboratory, the populations of these copepods moved off of the moulted exoskeleton and relocated on the new instar. About 41% of the mature crabs collected in North Carolina were infested by the same harpacticoid copepod which showed a similar synchronization with moulting of *P. chaetopterana* as seen in the animals from New Jersey. The synchronization of reproduction and behaviour with host-moulting suggests a strong facultative or obligate dependence of the copepod on its host. The copepod was classified as a non-parasitic hypersymbiont by McDermott (2009).

(vii) Palinurid hosts (Achelata)

Shields (2011) and Shields *et al.* (2006) reported an unidentified *Sunaristes*-like copepod (Canuellidae) from the gills of *Panulirus* spp. from the Great Barrier Reef. An unidentified species of *Amphiascus* (as *Paramphiascopsis*; *cf.* Huys 2009b) has been reported from the gills of both females and males of the spiny lobsters *Jasus edwardsii* (Hutton, 1875) and *Sagmariasus verreauxi* (H. Milne Edwards, 1851) (J.D. Booth in Shields (2011) and Shields *et al.* (2006); Jeffs *et al.* 2013). No locality data were given but both palinurid hosts are native to Australia and New Zealand.

(viii) Axiidean hosts

Family Canuellidae

Scottolana **Huys, 2009b**

Scottolana scotti **(Sewell, 1940)**

Scott (1909) assumed that Thompson & Scott's (1903) original description of *Sunaristes curticaudata* was based on an immature specimen and that he himself had found the adults but Sewell (1940) rejected this claim and confirmed that Scott's (1909) material belonged to a different species which he named *Canuella* (*Canuella*) *scotti* Sewell, 1940. Scott (1909) found the species in washings of dredged invertebrates near Indonesian New Guinea (Raja Ampat Islands, between Salawati and Misool; 01°42.5'S, 130°47.5'E; depth 32 m) and near the anchorage off Pulu Jedan on the north-east coast of Tanahbesar Island (Indonesia, Maluku Province, Aru Islands; 05°24.0'S, 134°43.0'E; depth 13 m). Por (1967) proposed the genus *Scottolana* to accommodate three species that had originally been placed in the genus *Sunaristes*: *Sunaristes inopinata*, *S. longipes* and *S. bulbosus* Por, 1964. He also considered *Canuella scotti* and *Sunaristes curticaudata* Thompson & Scott, 1903 as potential candidate members of the genus. Por (1967) did not designate a type species for the genus *Scottolana*, making the genus-group name unavailable. In the interest of nomenclatural stability Huys (2009b) re-established the generic name *Scottolana* as intentionally new, taking the authorship and date of his paper, and included *C. scotti* as a valid species.

Hamond (1973b) rejected the conspecificity between Sewell's (1940) *C.* (*C.*) *scotti* and Scott's (1909) *C. curticaudata* based on the presence of an additional small element on P1 enp-3 in the former and a long inner seta on P1 enp-1 in the latter. He considered Scott's material as possibly identical with *S. bulbosa* and effectively listed it as a synonym of the latter but this course of action was dismissed by Fiers (1982). The absence of the latter seta in *S. scotti* is doubtful since all canuellids possess it and hence one can assume that Sewell either overlooked it or examined a damaged specimen. Sewell's (1940: Text-fig. 2E) illustration of the P1 shows the correct number of elements on the distal endopodal segment but gives the misleading impression that there are four inner setae and two outer spines. The small inner seta is in reality the short apical spine which is typically directed inwards and often crossing over the distal inner seta in some species of *Scottolana* (*cf.* Wells & Rao 1987: Figs 14e, 16b; Mu & Huys 2004: Fig. 19A) which makes it less noticeable under low magnification. Since the P1 armature is extremely conservative within the genus it is likely that Scott (1909) overlooked this sixth element. Bodin (1997) claimed that

Lang (1948: 1615) did not accept *S. scotti* as a valid species but this must be a slip of the pen as he stated the contrary. Being unaware of Ummerkutty's (1968) description of the male, which had been recorded before (but not illustrated) by Scott (1909), Por (1984b) considered its systematic status uncertain because "… the male is unknown …".

Ummerkutty (1968) recorded forty females and five males of this species from washings of the axiidean shrimp, *Upogebia darwinii* (Miers, 1884) (family Upogebiidae), collected in Palk Bay, Tamil Nadu, India. The shrimps inhabited holes inside large submerged coral stones.

OD: Sewell (1940—as *Canuella* (*Canuella*) *scotti*): 135–136; Text-fig. 2(A–H) (♀ only).
AD: Scott (1909—as *Sunaristes curticauda* Thompson & Scott, 1903): 197–198; Plate LXIV (figs 1–6). Ummerkutty (1968—as *Canuella* (*Canuella*) *scotti*): 305–307; Figs 4–6.
TL: India, Nicobar Islands, Nancowry (= Nankauri); Nancowry Harbour, weed-washings.
BL: not given by Sewell (1940); 1,270 µm (♀), 940 µm (♂) [Scott 1909]; 1,300 µm (♀), 1,280 µm (♂) [Ummerkutty 1968].

(ix) Barnacle hosts

Two families, Harpacticidae and Laophontidae, contain a single representative that is known to live associated with a thoracican host. A potentially symbiotic relationship has been suggested for a third species but the isolated observation requires confirmation.

Family Balaenophilidae

Balaenophilus Aurivillius, 1879a

Balaenophilus manatorum (Ortíz, Lalana & Torres Fundora, 1992)

Lazo-Wasem *et al.* (2007) reported on a distinct correlation between the presence of the turtle barnacle, *Stomatolepas elegans* (Costa, 1838) (as *S. praegustator* Pilsbry, 1916), and the symbiotic copepod, *Balaenophilus manatorum* (Ortíz, Lalana & Torres Fundora, 1992) (as *B. umigamecolus* Ogawa, Matsuzaki & Misaki, 1997), on the olive ridley sea turtle, *Lepidochelys olivacea* (Eschscholtz, 1829) in western Mexico. Usually occurring in the soft skin at the base of the limbs, neck, and tail, *S. elegans* penetrates the epidermal and dermal layers of the turtle skin, residing with its wide aperture positioned nearly flush with the surface of its host and its test fully embedded. The test typically bears horizontal imbricating ranks of short spikes which serve to hold the barnacle in place by becoming enmeshed in host connective tissue (Zardus & Balazs 2007). Although Lazo-Wasem *et al.* (2007) speculated that *B. manatorum* may feed on irritated skin patches surrounding the embedded barnacles they also suggested a more direct association between the two epibionts. In a detailed examination of over 70 preserved specimens of *S. elegans*, they found a single individual of *B. manatorum* inside the barnacle, seemingly attached to its mantle tissue. Whether *B. manatorum* feeds on barnacle tissue is as yet unkown but examination of live *S. elegans in situ* will be essential for evaluating this potentially parasitic relationship (Lazo-Wasem *et al.* 2007).

Family Harpacticidae

Paratigriopus Itô, 1969

Paratigriopus hoshidei Itô, 1969

Itô (1969) proposed the genus *Paratigriopus* for a new species *P. hoshidei* Itô, 1969 which he observed inside the shells of the barnacle *Chthamalus challengeri* Hoek, 1883 *sensu stricto* (*cf.* Southward & Newman 2003) (family

Chthamalidae) on a rocky shore in southern Hokkaido, Japan. More than 100 non-ovigerous females and males were obtained on two different sampling dates (February, October). In a later study Itô (1976a) claimed that the species occurred inside the barnacles all year round in Oshoro, citing one particular case of 113 *P. hoshidei* obtained from examination of 200 *C. challengeri*. Copepods actively creep in and out of the barnacle shells when disturbed under the light microscope and appear to be positively phototactic. No precocious mate guarding or mating was observed *in situ* (Itô 1976a). *Paratigriopus hoshidei* differs from members of the genus *Tigriopus* Norman, 1869 primarily by the reduced antennary exopod, maxillule and maxilla, and the absence of a strongly modified leg 2 endopod in the male. These characteristics are all autapomorphic states and thus it is probable that *P. hoshidei* evolved within *Tigriopus* when it made the transition from rock pools to a commensal mode of life.

Adults are dark orange in colour and particularly females exhibit a dorsoventrally depressed body. Itô (1976a) described the fourth and fifth copepodids of both sexes. No nauplii or early copepodid instars were found inside the barnacles, possibly suggesting that these stages develop outside the host. Breeding takes place during the warmer months of the year. Ovigerous females possess a dorsoventrally flattened egg sac containing 7–9 eggs. Eggs at an early stage of development are blue in colour while older ones turn reddish. Attempts to culture *P. hoshidei* in isolation of the barnacle host failed.

Chthamalus challengeri is a common high-shore barnacle occurring in the north-western Pacific from southern Hokkaido in the north to the East China Sea, including Taiwan and the Ryukyu Islands, in the south (Cheang *et al.* 2012). Despite its ubiquitous presence in this region, *P. hoshidei* has not been recorded again since Itô's (1969, 1976a) studies in southern Hokkaido.

OD: Itô (1969): 64–68; Figs 3–5.
AD: Itô (1976a): 221–228; Figs 10–14; Table 1.
TL: Japan, southern Hokkaido, Shiribeshi Province, Oshoro (now part of Otaru City) on Sea of Japan coast; inside *Chthamalus challengeri* Hoek, 1883 (Chthamalidae) on rocks in upper intertidal zone.
BL: 720 µm (♀), 550 µm (♂) [Itô 1969]; 540 µm (CoIV♀), 500 µm (CoIV♂), 620 µm (CoV♀), 600 µm (CoIV♂) [Itô 1976a].

Family Laophontidae

Heterolaophonte Lang, 1948

Heterolaophonte brevipes Roe, 1958

Ventham (1990) first discovered *Heterolaophonte brevipes* on intertidal barnacles encrusting concrete groynes (and other artificial structures) at Roedean and Kemp Town, Brighton during 1983–1985. Its continued presence on *Semibalanus balanoides* (Linnaeus, 1767) and (sparse) *Austrominius modestus* (Darwin, 1854) was confirmed at Kemp Town in 1992 (Ventham 2011), indicating the association with its barnacle hosts is genuine. On average 7–18 adult *H. brevipes* were found per sample of *ca.* 20–30 adult barnacles.

Roe (1958) described *H. brevipes* from various intertidal habitats in the Dalkey area (Co. Dublin), ranging from the laminarian zone to pools in the *Pelvetia* zone. Greatest numbers were recorded in the upper shore, particularly in washings of the black lichen *Lichina pygmaea* (O.F. Müller) C. Agardh, 1820. The latter forms extensive patchy mats at or just below high water level of neap tides on wave exposed rocky shores which commonly coincides with the upper limit of barnacles (which were not examined by Roe). In a subsequent paper Roe (1960) reported two females in stone washings from the southern shore of Lough Ine, Co. Cork.

OD: Roe (1958): 240, 242–243; Figs 65–81.
TL: Ireland, Co. Dublin. Roe (1958) collected the species from three intertidal localities on Dalkey Island and one site on the neighbouring rocky outcrop to the east, The Muglins. Since Roe neither fixed a holotype nor specified a type locality all the specimens of the type series are automatically syntypes and the type locality encompasses all of the places of origin (ICZN Art. 73.2.3).
BL: 480 µm (♀), smaller (♂).

Echinodermata

All four classes (Asteroidea, Echinoidea, Holothuroidea, Ophiuroidea) of the Eleutherozoa serve as hosts to harpacticoid copepods. Although being common hosts to other copepod orders no harpacticoid symbionts are known from sea lilies or feather stars.

(i) Asteroidean hosts

Only a single species is known to utilize starfishes.

Family Tisbidae

Tisbe Lilljeborg, 1853

Tisbe japonica Ho, 1982

Ho (1982) obtained several hundreds of adults and copepodids of *T. japonica* in washings of the blue bat star *Patiria pectinifera* (Müller & Troschel, 1842) [as *Asterina pectinifera* (Müller & Troschel, 1842)] collected off Sado Island, Sea of Japan. The species can readily be distinguished by the morphology of the endopod of leg 1, including (1) the unique armature of the distal segment, consisting of one very stout, short, recurved, naked spine and one stout, spinulose spine, in addition to a short, unguiform projection of the medial distal margin, and (2) the very prominent convex swelling along the inner edge of the proximal segment. Ho's (1982) assignment of *T. japonica* to Volkmann's (1979b) *Tisbe gracilis*-group is debatable. Males of this species complex typically have the inner basal spine of leg 1 modified into a slender, flexible seta, and possess one spine and two long setae on leg 6. In *T. japonica* the inner basal spine of leg 1 does not display sexual dimorphism and the male leg 6 bears three slender setae. Note that Ho (1982) mislabelled the female maxilla and maxilliped.

Kim (2013) recorded *T. japonica* in washings of the hermit crab *Pagurus rubrior* Komai, 2003 (Paguridae) in Ulreungdo and Jeju Island, Korea. Dahms *et al.* (2004) recorded *T. japonica* from macroalgae in Hong Kong but their specimens differed from the type population in a number of aspects, including the shape of the female caudal rami (more elongate), the length of the caudal setae (more stout in both sexes), and the length of the antennulary aesthetascs (shorter in both sexes). Contemporary thought would probably reject this polymorphic concept in favour of a set of sibling species.

OD: Ho (1982): 34–39; Figs 1–3.
AD: Kim (2013): 73–75; Fig. 23.
TL: Japan, Niigata Prefecture, west coast of Sado Island (Sea of Japan); off Tassha Bay, depth 25–30 m; washings of *Patiria pectinifera* (Müller & Troschel, 1842) (Asteroidea, Asterinidae).
BL: 1,080–1,380 µm (♀), 799–884 µm (♂) [Ho 1982]; 980 µm (♀), 840 µm (♂) [Kim 2013].

(ii) Echinoidean hosts

Two monotypic genera in the families Canuellidae and Harpacticidae, respectively, and a single species in the Porcellidiidae have been reported as symbionts of sea urchins belonging to the infraclasses Irregularia and Carinacea. Other published records (Willey 1930; Noodt 1954a; Bresciani & Lützen 1962; Volkmann 1979b) from echinoid hosts are to be treated as accidental (see below).

Family Canuellidae

See p. 519 for an updated key to genera.

Echinosunaristes Huys, 1995

Echinosunaristes bathyalis Huys, 1995

Both sexes of this species were discovered during dissection of several specimens of an unidentified deepwater member of the irregular sea urchin genus *Paleopneustes* Agassiz, 1873 (family Paleopneustidae) collected off San Salvador Island, Bahamas (Huys 1995). It lives exclusively in the rectum of its echinoid host and can readily be distinguished from other canuellids by the unusual body shape of the female, several atypical reductions in the mouthparts, the unusual swimming legs and the remarkable sexual dimorphism in body form, size and caudal ramus structure. Gross disparity in size between the sexes clearly imposes certain constraints on the body posture that is assumed during mate guarding. Male *E. bathyalis* have evolved a unique antennulary geniculation mechanism in response to this size disparity (Huys 1995). The swimming leg morphology of *E. bathyalis* is unique in two aspects, *i.e.* (a) the segments of both rami of legs 1–4 are unusually flattened and transversely expanded, and legs 2–3 lack the distinct attenuations of the proximal and middle endopodal segments typically found in other Canuellidae, and (b) the inner setae lack the typical plumosity found in other members of the family, the ornamentation being replaced by multiple longitudinal rows of fine spinules.

Huys (1995) speculated that the habitat shift towards a sheltered environment inside the echinoid host, and consequently the change in food availability, impacted the feeding mode of the harpacticoid. In contrast to the related genera *Sunaristes* and *Intersunaristes*, which are associated with hermit crabs and also inhabit a protected microhabitat, this habitat shift had significant implications for the morphology of the feeding appendages. With the exception of the antenna which has retained its primitive morphology, all other postantennulary appendages of the cephalosome have undergone strong reductions, in particular the endites but also the maxillulary epipodite. Huys (1995) assumed that the antenna (as demonstrated for *Canuella perplexa*; *cf.* Kohlhage 1993) is involved in grooming since it is the only cephalic appendage that has retained the ancestral complement of segments and armature.

There is no evidence to suggest that *E. bathyalis* temporarily leaves the host to feed on or in the sediment. Its integument is clearly thinner and less chitinized than in free-living Canuellidae, probably because concealment inside the host protects it from external mechanical stress. In addition, since the copepods were found to be restricted to the part of the alimentary tract where enzymatic activity is virtually non-existent, they probably do not require special cuticular adaptations to prevent digestion by the host. The presence of numerous ovigerous females and several pairs *in amplexus* suggests that both mating and reproduction take place inside the host. Nauplii seemed to be entirely absent from the rectum content which is reminiscent of the life cycle observed in hermit crab associated *Sunaristes* species where the nauplius stages represent the infective dispersal phase (Ho 1988). Ovigerous females carry paired, elongate egg sacs, each containing 25–30 eggs. The colour of live specimens is a bright orange. Huys (1995) placed *Echinosunaristes* in the *Sunaristes*-lineage on the basis of the morphology of the genital field in both sexes and considered it the most primitive taxon of this clade.

OD: Huys (1995): 226–236, 240–241; Figs 1–10.
TL: North Atlantic, Bahamas archipelago, French Bay off San Salvador Island; about 530 m depth; in rectum of *Paleopneustes* sp. (Paleopneustidae).
BL: 1,800–1,950 µm (♀), 1,120–1,210 µm (♂).

Family Harpacticidae

Discoharpacticus Noodt, 1954a

Discoharpacticus mirabilis Noodt, 1954a

Noodt (1954a) described a new genus and species, *Discoharpacticus mirabilis*, from washings of the Chilean edible sea urchin, *Loxechinus albus* (Molina, 1782) (family Parechinidae). It is not known where Noodt's material originated from other than that it was collected by the late Prof. Riveros-Zuñiga from the University of Viña del

Mar, Valparaíso Region, central Chile. The host is native to the coasts of Chile and Peru, distributed from Isla Lobos de Afuera, Peru (6°53'S) to the southern tip of South America (*ca.* Cape Horn, Chile, 56°70'S), from rock pools with permanent water circulation through the low intertidal zone to as deep as 340 m (Vásquez 2007).

Females, males and at least late copepodids (see Noodt 1954a: Fig. 3) possess a ventral suction disc or cup which assists in securing temporary attachment to the host at different stages in the life cycle. The attachment organ is situated between the maxillipeds and the first pair of legs, and is operated by strong dorsoventral muscles which probably originate on the dorsal cephalothoracic shield and insert on the internal sclerites near the suction cup surface. The ventral concavity of the suction cup is sealed around most of its perimeter by a membranous extension applied to the surface of the host (interpreted by Noodt as a "hyaline, gelatinösen Masse"), offering optimal suction efficiency. The well developed maxillipeds and the first legs do not appear to be functionally integrated in the suction cup but probably play a secondary role in helping to prevent the symbiont from being detached from its host. Noodt (1954a) observed precocious mate guarding with adult males grasping late copepodid females around the posterior margin of the cephalothoracic shield.

The species has not been recorded again since its original description. It was erroneously cited as *Discoharpacticus hoshidei* Itô, 1969 in Bodin's (1997: 53) catalogue (and previous versions).

OD: Noodt (1954a): 248–250; Plates 34–35 (Figs 1–18).
TL: Chile, locality unknown but probably central Chile; between the spines of *Loxechinus albus* (Molina, 1782) (Parechinidae).
BL: 920–1,100 µm (♀), 830–950 µm (♂).

Family Porcellidiidae

Clavigofera Harris & Iwasaki, 1996

Humes & Gelerman (1962) recognized a close relationship between their newly described species, *Porcellidium echinophilum*, associated with sea urchins, and the free-living *P. clavigerum* Pesta, 1935. They did not exclude the possibility that the latter may have been accidentally dislodged from an echinoderm host. Hicks (1982) re-examined the material of both species and dismissed two of the three characters used by Humes & Gelerman to differentiate them (body size and extent of the P5 exopod), but maintained the validity of *P. echinophilum* based on differences in the caudal rami (position of dorsal seta VII; form and ornamentation of terminal setae). Both species were assigned to his "*clavigerum* complex" which further included two new species collected from marine algae of St. Croix Island, Algoa Bay, South Africa: *P. laurencium* Hicks, 1982 and *P. ulvum* Hicks, 1982. Specimens collected from Inhaca Island, Mozambique (Wells 1967) and Saint Helena (Marques 1977) which had previously been identified as *P. clavigerum* were found to be conspecific with *P. laurencium* (Hicks 1982). Harris & Iwasaki (1996) attributed generic rank to the *clavigerum* complex by proposing a new genus *Clavigofera* for it in which they included a fifth species, *C. pacifica* Harris & Iwasaki, 1996, described from Japan and subsequently recorded from New South Wales, Australia (Harris 2014a). Members of *Clavigofera* share the same form and spacing of the caudal ramus setae, a patch of striated chitin anterolaterally on the second urosomite of the female and the presence of only three setae on the distal endopod segment of the male P2. Species discrimination in the genus is notoriously difficult, primarily relying on morphometric characters, and keys constructed for females are also not applicable to males (*cf.* Harris 2014a). Harris & Iwasaki (1996) noted only minute differences between *C. echinophila* and *C. pacifica*, stating that the most compelling reason for regarding them as separate species is their preferred ecological niche (sea urchins *vs* brown algae). The male of *C. clavigera* is as yet unknown.

Key to species of *Clavigofera* Harris & Iwasaki, 1996

FEMALES

1. Posterior extensions of penultimate somite reaching beyond hind margin of caudal rami......... *C. clavigera* (Pesta, 1935).
   Posterior extensions of penultimate somite not reaching to end of caudal rami...................................... 2.
2. Hicks' index*for caudal ramus seta VII 65%; body length 760–800 µm.......................... *C. ulva* (Hicks, 1982).

Hicks' index for caudal ramus seta VII less than 60%; body length at most 600 µm . . . . 3.
3. Hicks' index for caudal ramus setae I and VII, 21% and 51%, respectively . . . . . . *C. echinophila* (Humes & Gelerman, 1962).
4. Hicks' index for caudal ramus setae I and VII, 22% and 56%, respectively . . . . *C. laurencia* (Hicks, 1982).
5. Hicks' index for caudal ramus setae I and VII, 24% and 51%, respectively . . . . *C. pacifica* Harris & Iwasaki, 1996.

* Hicks (1982: Table 3 and Fig. 45) codified the position of caudal ramus setae II and VII (coded β and α, respectively, by Harris & Robertson (1994)) by expressing the distance between their origin and the distal margin of the ramus as a percentage of the maximum length of the ramus. Harris (2002: 3–4) named this statistic "Hicks' index". Care must be taken to measure the caudal ramus length from the base of the ramus, which frequently is concealed by the distal margin of the anal somite. The male of *C. clavigera* is as yet unknown.

MALES

1. Proximal segment of P1 endopod with patch of minute spinules on anterior surface (on outer side immediately proximal to beginning of fimbriate crescent) . . . . *C. pacifica* Harris & Iwasaki, 1996.
Proximal segment of P1 endopod without spinular patches on anterior surface . . . . 2.
2. δ seta* on segment 3 of antennule "whip-like" (> length of antennule); body length 520–540 µm. . . . . .*C. ulva* (Hicks, 1982).
δ seta on segment 3 of antennule not long (< length of antennule); body length 410–450 µm . . . . 3.
3. Caudal ramus setae II, III and VII (coded β, γ and α, respectively by Harris & Robertson (1994)) about 3/4 of ramus length; associated with sea urchins . . . .*C. echinophila* (Humes & Gelerman, 1962).
Caudal ramus setae II, III and VII about 2/3 of ramus length; associated with algae. . . . . *C. laurencia* (Hicks, 1982).

* See Harris (2014a) for terminology and coding of male antennulary setae.

Clavigofera echinophila (Humes & Gelerman, 1962)

Humes & Gelerman (1962) collected *Porcellidium echinophilum* from washings of the regular sea urchin, *Echinometra mathaei* (Blainville, 1825), in Madagascar. Both adults and immature stages (nauplii and copepodids) occurred in great numbers on the body surface of the host. Humes & Gelerman (1962) recovered 971 copepods from the washings of 60 urchins, an average of about 16 on each host. Ovigerous females carry a median egg sac containing 6–7 eggs, each about 50–60 µm in diameter. Several adult males were seen clasping immature females, with their geniculate antennules embracing the fifth legs of the female. The cyclopoid *Mecomerinx notabilis* (Humes & Cressey, 1961) also utilizes *E. mathaei* as host but does not seem to co-exist with the porcellidiid.

OD: Humes & Gelerman (1962): 311–; figs 1–31.
TL: Madagascar, near Nosy Be (Nossi Bé); west side of Pointe Ambarionaomby on Nosy (Nossi) Komba; on body surface of *Echinometra mathaei* (Echinometridae) collected in 1 m at low tide from among branches of staghorn coral.
BL: 554–582 µm (♀), 414–448 µm (♂).

(iii) Holothuroidean hosts

At least two species of the laophontid genus *Microchelonia* Brady, 1918 and a single species of *Sacodiscus* are known to live in association with sea cucumbers of the families Stichopodidae and/or Holothuriidae. *Tisbe cucumariae* Humes, 1957b and *T. holothuriae* Humes, 1957b were named after their respective hosts when discovered in their washings (Humes 1957b) but subsequently turned out to be free-living (see below).

Family Laophontidae

Microchelonia Brady, 1918

Ho & Perkins (1977) proposed the genus *Namakosiramia* for a remarkable ectoparasitic copepod found on the body surface of the holothurian *Apostichopus* [as *Stichopus*] *parvimensis* (Clark, 1813) in southern California (Ho & Perkins 1977). *Namakosiramia californiensis* was originally designated as the type of a new family, Namakosiramiidae, which was placed in the "siphonostome" Cyclopoida. Despite the absence of an oral cone, the ventral position of the female gonopores and the presence of a tetrasetose antennary exopod (referred to as "compound seta"), Ho & Perkins (1977) indicated a possible relationship with the siphonostomatoid families Micropontiidae, Stellicomitidae and Nanaspididae, all of which have a reduced oral cone and are associated with echinoderm hosts. Gotto (1979) also allied *Namakosiramia* with the Siphonostomatoida but Bowman & Abele (1982) continued placing the Namakosiramiidae in the Cyclopoida.

In his analysis of the phylogenetic relationships between the various cyclopoid families, Ho (1986b) concluded that the Namakosiramiidae should have been placed in the Harpacticoida because of a number of non-cyclopoid features: (1) genital apertures located midventrally on the genital double-somite, (2) antenna with rudimentary exopod, and (3) modification of P1–P2 into prehensile appendages involved in grasping the host. Huys (1988a) redescribed *N. californiensis* and demonstrated that it should be assigned to the Laophontidae, rendering the Namakosiramiidae a junior synonym of the latter. He also redescribed the well developed paired paragnaths (not medially fused forming a labium) and confirmed the presence of six armature elements on the distal tip of the antenna, both characters ruling out a position in the Siphonostomatoida. Kim (1991) pointed out the striking resemblance in mouthpart structure between *Namakosiramia* and most poecilostomatoid copepods but rightly attributed this to convergent adaptation to a parasitic mode of life. He added *N. koreensis* Kim, 1991 from two holothurian hosts obtained at Korean fish markets and provided the first description of the male.

Brady (1918), in a brief supplementary note to his report on the Copepoda collected during the Australasian Antarctic Expedition 1911–1914, proposed the genus *Microchelonia* for a single species, *M. glacialis* Brady, 1918, found in a gathering from Macquarie Island. The genus was not mentioned in Lang's (1948) monograph but was listed as a *genus inquirendum* without ordinal or familial assignment by Boxshall & Halsey (2004). Brady (1918) himself was of the opinion that it represented an "entirely new division of the Copepoda". Huys (2009b) identified *M. glacialis* as a member of the genus *Namakosiramia* and consequently sank the latter as a junior objective synonym of *Microchelonia*. The description of *M. glacialis* is grossly inadequate and its host is as yet unknown. Females of *M. californiensis* and *M. koreensis* can be differentiated by the key below.

Key to species of *Microchelonia* Brady, 1918

1\. Body length:width ratio 1.55; lateral lobes of cephalic shield unilobate; distal setae of antennary endopod all distinctly shorter than claw; P3 exopod fused to protopod . . . . *M. californiensis* (Ho & Perkins, 1977).
Body length:width ratio 1.74–1.85; lateral lobes of cephalic shield bilobate; at least two distal setae of antennary endopod as long as claw; P3 exopod a free segment with two setae . . . . *M. koreensis* (Kim, 1991).

Kim (1991) also used other characters such as the degree of separation between the cephalothorax and P2-bearing somite, and the contour of the anterolateral margin of the cephalic shield but such differences may be artefacts caused by squashing during the mounting process; they are omitted here as discriminating features.

The genus can readily be identified by its body shape and prehensile P2, however, the absence of clear sexual dimorphism on the swimming legs hampers any analysis of its relationships with other Laophontidae. *Microchelonia* is the only genus in the family that is associated with echinoderm hosts. Adherence to the host is facilitated by the dorsoventral depression of the body, the powerful prehensile or subchelate antennae, maxillipeds and legs 1–2, and by the presence of spinulose pads along the pleural margins of the body somites. No information is available about the life cycle and copepodid stages are as yet unknown.

Microchelonia glacialis Brady, 1918

Brady (1918) found a single male in a sample from Macquarie Island in the southwest Pacific Ocean. Although he suggested that it would probably be found again by "… washing the fronds and roots of sea-weeds—especially Laminariæ" it is more than likely that it was associated with a holothurian host. Brady (1918) admitted that his dissection was imperfect because of the excessively tough, pachydermatous and opaque nature of the specimen; these are also typical attributes of the two Northern Hemisphere *Microchelonia* species. Some of the illustrated appendages were misinterpreted, *i.e.* the supposed antennule in Fig. 4 is in reality the prehensile leg 1, and the limb labelled as the maxilliped in Fig. 6 is the maxilla. Brady's Fig. 5 is more puzzling since it refers to the antenna but is more likely to represent parts of the rudimentary legs 3–5.

OD: Brady (1918): 34, 44; Plate 15.
TL: Australia, Macquarie Island. Host unknown.
BL: 460 µm (♂).

Microchelonia californiensis (Ho & Perkins, 1977)

Huys (1988a) remarked that the maxillule and maxilla had been reversed in the original description. Other minor amendments include the correct setal number for the mandible (two rather than three) and P5 (four rather than two). Ho & Perkins (1977) also mistakenly interpreted the prehensile P1 endopod as a 3-segmented exopod (counting the claw as a distinct segment), and the 1-segmented exopod as a rudimentary endopod. Subsequent attempts to collect males of *N. californiensis* were unsuccessful (Ho in Huys 1988a). The egg sac contains 9–13 small, oval eggs, about 66 µm in diameter.

OD: Ho & Perkins (1977—as *Namakosiramia californiensis*): 368–370; Figs 1–13 (♀ only).
AD: Huys (1988a): 1519–1527; Figs 1–7 (♀ only).
TL: U.S.A., southern California, off Palos Verdes, 600 m north of Pt. Vincente; washings of *Apostichopus parvimensis* (Clark, 1913) (Stichopodidae).
BL: 235–523 µm (♀) [Ho & Perkins 1977]; 490 µm (♀) [Huys 1988a].

Microchelonia koreensis (Kim, 1991)

The species was found to be associated with *Holothuria* (*Mertensiothuria*) *hilla* Lesson, 1830 [as *Holothuria monacaria* (Lesson, 1830)] (family Holothuriidae) in Pusan (Korea Strait), and with *Apostichopus japonicus* (Selenka, 1867) [as *Stichopus japonicus* (Selenka, 1867)] (family Stichopodidae) in Gangneung (East Sea coast) and Mokpo (Yellow Sea coast) (Kim 1991). All these specimens were obtained from holothurians kept in aquaria at fish markets. Kim (2013) recorded it in washings of the latter host collected at 15 m depth in Uljin (East Sea coast). Kim (1991) observed variability in the number of setae on the male P6 (one or two; left-right asymmetry), and in the size and ornamentation of the exopodal setae of P3 and inner setae of the vestigial P4–P5.

OD: Kim (1991—as *Namakosiramia koreensis*): 429–434; Figs 1–3.
AD: Kim (1998): 827–831; Figs 409–410; Plate 58. Kim (2013): 48–50.
TL: South Korea, East Sea (Sea of Japan) coast, Gangneung (37°44'N, 128°56'E); washings of *Apostichopus japonicus* (Selenka, 1867) (Stichopodidae) kept in aquarium of fish market.
BL: 502 µm (♀), 379 µm (♂) [Kim 1991]; 480 µm (♀), 340 µm (♂) [Kim 2013].

Family Tisbidae

Sacodiscus Wilson, 1924

See p. 546 for a key to species.

Sacodiscus humesi Stock, 1960

Stock (1960) based his description of *Sacodiscus humesi* on two females recovered from washings of *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1791 collected in *Posidonia* seagrass beds in the Bay of Banyuls. The species has not been recorded again since its original description. Further confirmation whether its association with the holothurian host is specific would be needed.

OD: Stock (1960): 219–221; Figs 1–2 (♀ only).

TL: France, Languedoc-Roussillon, Pyrénées-Orientales, Bay of Banyuls-sur-Mer; 1–4 m depth, *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows; washings of *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1791 (Holothuriidae).

BL: 730–800 µm (♀).

(iv) Ophiuroidean hosts

Although brittle stars and basket stars commonly serve as hosts to cyclopoid and siphonostomatoid copepods (Boxshall & Halsey 2004) no published accounts exist on harpacticoids living in symbiosis with ophiuroids.

Family Canuellidae

Canuellidae gen. et sp. nov.

Recent examination of washings of brittle stars collected from Daecheon Beach (36°18.09'N, 164°30.56'E) on the Yellow Sea coast of South Korea revealed numerous copepodids and adults of an as yet unknown genus and species of Canuellidae (R. Huys, unpubl. data). The new species shares the same armature formula on legs 1–4 with members of the genus *Coullana* but differs radically in the morphology of leg 2, the genital field in both sexes and caudal ramus sexual dimorphism and ornamentation. The association appears to be genuine since the canuellid was not found in the surrounding sediment but consistently obtained in ophiuroid washings on three different sampling dates (February, September and October 2015). The brittle star hosts were burrowing members of the Amphiuridae (probably *Amphiura* sp.) and living intertidally near the low-water mark. Amphiurids are specialized deposit feeders which typically obtain their food from within the substratum although some species extend their arms from the burrow and sweep them over the surrounding sediment, gathering particles with the tube-feet and transferring them from one tube-foot to the next towards the mouth. The copepods probably live in the channels connecting the amphiurid burrow with the surface where they may benefit from the stream of material passing across the oral side of the disc. Other copepods associated with the brittle stars at Daecheon Beach included members of the Synaptiphilidae (*Presynaptiphilus* Bocquet & Stock, 1960) which had previously been recorded from amphiurid hosts in the Yellow Sea (Kim 2000; Shin & Kim 2003).

Tunicata

On grounds of priority the current and formally correct trend is to abandon the name Urochordata Balfour, 1881 in favour of the senior name Tunicata Lamarck, 1816b, which is almost invariably used in modern scientific works and accepted as valid by the World Register of Marine Species (WoRMS Editorial Board 2016). The Tunicata comprises three classes and harpacticoid copepods have been reported from two of them, *i.e.* the pelagic, free-swimming Appendicularia (larvaceans) and the sessile Ascidiacea (sea squirts). Although some copepods are assumed to be specialized predators of salps (Heron 1973) and are sometimes found lodged inside their prey (Gasca *et al.* 2015), no copepods are known to live in symbiotic relationships with the third class, Thaliacea.

(i) Appendicularia (Larvacea)

Marine snow originates from two general pathways, *i.e.* from mucus discarded by gelatinous and mucus-producing organisms such as larvaceans and pteropods, and from the biologically enhanced physical aggregation of smaller component particles such as diatoms or faecal pellets (Alldredge & Silver 1988; Green & Dagg 1997). Larvaceans (Appendicularia) produce mucus structures or "houses" that act as filters to remove particulate food from the water and are abandoned when the house filters become clogged or when the larvacean is disturbed (Alldredge 1976). Some larvaceans may discard 4–16 houses per day (Fenaux 1985) which provide benthic-like habitats for midwater zooplankton and serve as feeding centers (Steinberg *et al.* 1994). On average, copepods may constitute as much as

96% of the assemblage on houses, and many of the species are considered genuine detrital associates, including calanoids, oncaeids, corycaeids and some harpacticoids (Steinberg *et al.* 1994, 1998). Copepods utilize phytoplankters and protozoans remaining on larvacean house membranes, incurrent and food-concentrating filters of the houses themselves, and larvacean faecal pellets within the houses, making both discarded and occupied larvacean houses one of the most important food sources for some associated pelagic copepods (Ohtsuka *et al.* 1993). They may also use marine snow as nursery sites for their eggs and nauplii, as refuges from predation, and as vertical transport vehicles. Members of the genera *Oithona* Baird, 1843, *Oncaea* Philippi, 1843 and *Microsetella* may at times be several orders of magnitude more concentrated on marine snow aggregates than in the surrounding water (*e.g.* Steinberg *et al.* 1994; Green & Dagg 1997). Based on compiled published observations, Kiørboe (2000) concluded that some invertebrates are closer associates of aggregates than others. Harpacticoid copepods, for example, are more than one order of magnitude relatively more abundant than the mixed group of cyclopoid (including poecilostomatoids) and calanoid copepods.

Family Ectinosomatidae

Microsetella Brady & Robertson, 1873

Both species of the holoplanktonic genus *Microsetella* are known to attach and feed on discarded and occupied larvacean houses and may in fact be dependent on such benthic-like surfaces to obtain food and shelter in the pelagic environment. Alldredge (1972) observed *M. norvegica* resting on abandoned houses of three oikopleurid appendicularians collected at 10–15 m depth in the Florida Current west of Bimini, *i.e.*, *Megalocercus abyssorum* Chun, 1887, *Oikopleura* (*Coecaria*) *fusiformis* Fol, 1872 and *O.* (*C.*) *longicauda* (Vogt, 1854). *Microsetella rosea* was found to be periodically numerous on the houses and filtering apparatuses of giant midwater larvaceans, *Bathochordaeus* spp., between 100–500 m at the seaward edge of Monterey Bay (Steinberg *et al.* 1994) and further down in water deeper than 1,000 m in the submarine canyon (Ferrari & Steinberg 1993). Green & Dagg (1997) noted that up to 57% of the population of *M. norvegica* in the Gulf of Mexico was associated with snow aggregates. Copepods were rarely observed on the snow surface, but were typically burrowed or embedded in the gelatinous matrix of appendicularian house aggregates. Direct observations with SCUBA diving in Honmura Bay, Kuchinoerabu Island revealed that adult *M. norvegica* attached to the outer membranes of discarded larvacean houses or were creeping into the houses (Ohtsuka & Kubo 1991). Gut content analysis of the saprophagous calanoid *Scolecithrix danae* (Lubbock, 1856) in this area showed that attached *M. norvegica* may have been accidentally preyed upon while feeding on the houses. Steinberg (1995) examined the guts of *Scopalatum vorax* (Esterly, 1911), another scolecitrichid associated with giant larvacean houses, and found good evidence that it consumes some of the other copepods resident on houses, including *Microsetella* spp.

Ohtsuka *et al.* (1993) observed that *M. norvegica* was a common associate of both discarded and occupied oikopleurid houses (possibly *Oikopleura* (*Coecaria*) *gracilis* Lohmann, 1896, *O.* (*C.*) *longicauda* (Vogt, 1854) and/or *O.* (*Vexillaria*) *dioica* Fol, 1872), throughout the year at an offshore station near the Nansei Islands, whereas neither discarded nor occupied houses carried copepods at an inshore station in the central Seto Inland Sea at any time. Uye *et al.* (2002) investigated the seasonal population dynamics and production of *M. norvegica* in the Seto Inland Sea and noted that associations with marine snow aggregates did not occur, despite being one of the four numerically dominant species in this food-rich environment. This observation led the authors to suggest that attachment to larvacean houses or association with marine snow are facultative strategies in relatively oligotrophic offshore waters where suspended food is scarce. However, it has been advocated that the generally low egg production measured for *M. norvegica* in the field (≤ 1 eggs.ind^{-1}.d^{-1}; Nielsen & Andersen 2002) could be connected to the low feeding rates in the absence of aggregates and indicate food limitation outside areas and seasons of high aggregate abundance (Koski *et al.* 2005).

Maar *et al.* (2004) found that recycling of houses of *O. dioica* in the water column correlated non-linearly with the abundance of *M. norvegica*, but not with other copepod species in the Skagerrak. The species can potentially degrade up to 100% of the small < 0.5 cm aggregates in the North Sea (Koski *et al.* 2005), whereas in the Skagerrak the degradation rate of appendicularian houses by *M. norvegica* has been estimated to 34%.day^{-1} at intermediate turbulence levels (Maar *et al.* 2006). In a different study Koski *et al.* (2007) concluded that at the typical concentrations of *M. norvegica* in the North Sea (≤ 10^4 ind. m^{-2}), its role in marine snow degradation is likely to be small while potential house degradation rates by other zooplankton groups, such as invertebrate larvae, can be substantial.

Both *Microsetella* species are routinely separated by body size, relative length of caudal seta IV, ratio between body length and length of seta V, and the endopodal armature of the female leg 5 (Boxshall 1979; Wells 2007). Caution should be exercised when applying these criteria since it is known that several as yet undescribed species occur in the world's oceans. For example, Japanese "populations" traditionally identified as *M. norvegica* turned out to be a complex of different *Microsetella* species (R. Hirota, pers. commn).

Harpacticoids were also found to associate with other types of marine aggregates but were not identified to species level (Bochdansky & Herndl 1992; Shanks & Edmondson 1990).

(ii) Ascidiacea

Sea squirts are common hosts to copepods to the extent that they have been referred to as ascidian "hotels" (Gotto 1959). Their comparative immunity from predation, maintenance of a feeding current and usual capaciousness of many of their internal cavities afford protection, accessible food and a certain freedom of movement. Despite the considerable advantages offered by ascidians as hosts very few harpacticoids have been recorded as genuine commensals. Only three species, representing two genera and two families, have been confirmed to have exploited this particular niche but it is known that certain as yet undescribed members of the Ectinosomatidae are also associated with solitary ascidians (R. Huys, unpubl. data).

Family Miraciidae

Paramphiascella Lang, 1944

The genus currently accommodates 24 species (Wells 2007; Chullasorn 2010; Chullasorn *et al.* 2011) of which two are known as associates of ascidiacean hosts. Surprisingly, one species occupies compound ascidians while its congener is associated with a solitary ascidian. Both can be identified with the tabular keys provided by Wells (2007).

Paramphiascella commensalis (Seiwell, 1928)

Seiwell (1928) based the original description of *Amphiascus commensalis* on 11 females and three males found inside the branchial chamber of an unidentified species of *Aplidium* Savigny in Lamarck, 1816b (as *Amaroucium* H. Milne Edwards, 1841) (family Polyclinidae) collected near Woods Hole. The host, referred to as the "common sea pork" by Seiwell, is probably *Aplidium stellatum* (Verrill, 1871). The authenticity of the commensal relationship was confirmed by Wilson (1932) who collected additional material from *A. stellatum* in the Woods Hole area. Lang (1948) transferred the species without any comment to the genus *Paramphiascella* Lang, 1944. Sleeter & Coull (1973) found this species—as *Paramphiascoides* [*sic*] *commensalis*—in the burrows of the gribble *Limnoria tripunctata* in Duxbury Bay, Massachusetts (see also Coull 1977). According to Seiwell (1928) *Tisbe gracilis* (T. Scott, 1895) (as *T. wilsoni* Seiwell, 1928) cohabits with *P. commensalis* but this record is almost certainly accidental.

OD: Seiwell (1928—as *Amphiascus commensalis*): 2, 5; Plate 1 (Figs 1–14).
AD: Wilson (1932): 227–228; Fig. 153.
TL: U.S.A., Massachussetts, vicinity of Woods Hole; in branchial chamber of *Aplidium stellatum* (Verrill, 1871) (Polyclinidae).
BL: 740 µm (♀) [Seiwell 1928]; 740 µm (♀), 650 µm (♂) [Wilson 1932].

Paramphiascella pacifica Vervoort, 1962

This species was described on the basis of 22 adult females, 20 males and 25 copepodids obtained from the bottom of jars containing ascidiaceans collected from Nouméa in New Caledonia. In addition to this material, a single male was observed in the branchial cavity of *Ascidia sydneiensis* var. *samea* (Oka, 1935) where it was found together with some notodelphyid copepods. Being the predominant copepod in the collecting bottles and probably inspired by the great morphological similarity with *P. commensalis*, Vervoort (1962) was of the opinion that some form of association between *P. pacifica* and ascidiacean hosts seemed reasonable. He suggested that the species lives on the external mantle surface of large solitary tunicates, hovering around the oral and atrial siphons and occasionally being introduced in the host when water is pumped through the inhalant siphon by cilia lining the stigmatal openings of the branchial basket. Ovigerous females carry two egg sacs each containing five large eggs.

OD: Vervoort (1962): 430, 436–304; Figs 14c, 17–21, 22a, 23.
TL: France, Melanesia region, New Caledonia, Nouméa; from the bottom of collecting bottles with ascidiaceans.
BL: 555–630 µm (♀), 490–585 µm (♂), 390–435 µm (CoV).

Family Pseudotachidiidae

Xouthous Thomson, 1883

See p. 575 for a key to species.

Xouthous purpurocinctus (Norman & Scott, 1905)

This species was originally described (but not illustrated) by Norman & Scott (1905) as *Dactylopusia purpurocincta* based on a single female dredged off Salcombe, Devon (England). Norman & Scott (1906) provided an extended illustrated description of the same specimen and placed it in a new genus *Megarthrum* as *M. purpurocinctum* (Norman & Scott, 1905). Lang (1936a) relegated *Megarthrum* Norman & Scott, 1906 to a junior subjective synonym of *Idomene* Philippi, 1843 and cited the species as *Idomene purpurocincta* (Norman & Scott, 1905). Huys (2009b) showed that the type species of *Idomene*, *I. forficata* Philippi, 1943, does not belong to the Harpacticoida and, consequently, transferred the remaining species to its oldest available synonym, *Xouthous* Thomson, 1883. Sewell (1940) recorded a second female from Nancowry (Nankauri) Island in the central part of the Nicobar archipelago in the north-eastern Indian Ocean. Vervoort's (1964) record from Ifalik (Ifaluk) Atoll in the Caroline Islands (Federated States of Micronesia) further extended the range eastwards. Both Indo-Pacific records came from weed washings. Recently, Sarmento & Santos (2012) reported it from the phytal environment of the Porto de Galinhas reef off Pernambuco in north-eastern Brazil. Hall & Bell (1993) found it in association with the seagrass *Thalassia testudinum* Banks *ex* König, 1805 at Egmont Key, Florida and Suárez-Morales *et al.* (2006) reported it from an undisclosed locality from the Caribbean coast of Mexico. Kask *et al.* (1983) added a record from the Nanaimo estuary in Canada. Various authors (Haas *et al.* 2002; Cordell *et al.* 2009; Armbrust *et al.* 2010) have recorded *X. purpurocinctus* from Puget Sound, in western Washington State where it may have been introduced with ballast water. Lang (1965) provided a redescription of the female and the first description of the male, based on specimens collected from an intertidal pool in Monterey Bay, California. The second and only other record from Europe is that by Soyer (1971, 1975) from Banyuls-sur-Mer, France. The alleged cosmopolitan distribution of *X. purpurocinctus* is probably more apparent than real and it is conceivable that many identifications were based on its single unique characteristic, the conspicuous colour pattern of the prosome (*cf.* name). It is most probable that *X. purpurocinctus*, as currently constituted, will prove to be a complex of sibling and pseudosibling species (see key on p. 575 for differentiating characters between the Indo-Pacific records of this species).

Recently, Saito (2009) discovered *X. purpurocinctus* in very large numbers in the common cloacal cavity of the compound ascidian *Aplidium yamazii* (Tokioka, 1949) (family Polyclinidae) collected in Nomi-wan (33°21'28"N, 133°18'36"E), a cove of Tosa bay (Kochi Prefecture), Shikoku Island, Japan. The host is commonly found on boulders in the intertidal zone and typically occurs from December to August. Saito (2009) analyzed the seasonal abundance of *X. purpurocinctus* over a 2-year period (2005–2006) and found it to be present in all months with mean numbers per host ranging from 625 ± 847 in the 2005 season to 397 ± 357 in the 2006 season. In terms of dry weight copepod density was usually $> 10^3$ per gram of host tissue with a mean of 5.10×10^3 indiv.g^{-1} and maximum value 1.76×10^4 indiv.g^{-1}, corresponding to 3.4×10^2 and 1.2×10^3 indiv.cm^{-3} of host volume, respectively. Assuming that the volume of the common cloacal cavity occupies at most 27% of the host, Saito calculated that cloacal densities must be at least 1.3×10^3.cm^{-3}.

Xouthous purpurocinctus appeared to be present right from the initial appearance of the host and copepodids already co-occurred with adults in the cloacal cavity, suggesting that adult copepods entered the hosts immediately after the host colonies had been formed. Live observations showed that eggs carried by adult females hatched inside the host, and copepodids never left the cloacal cavity unless the host was treated with menthol (Saito 2009). Although these observations indicate that postembryonic development is completed inside the host it is unknown where adults reside when the ascidian colonies degenerate and disappear in July/August, and how initial colony formation and early infection are synchronized. An exponential negative correlation was seen between copepod density and host size, and the density varied less as host size increased. While proportional representation by adults varied greatly in small hosts, it tended to converge to about 25% with increasing host size. Saito (2009) claimed that these host size dependent correlations may be explained by naupliar recruitment inside the host and dispersal by adults. Laboratory observations showed that adult copepods often crawled on the surface of the common tunic and occasionally swam away from it, suggesting they are capable of migrating between colonies and are probably the infective stage in the life cycle.

OD: Norman & Scott (1905—as *Dactylopusia purpurocincta*): 295–296 (♀ and text only).

AD: Norman & Scott (1906—as *Megarthrum purpurocinctum* (Norman & Scott, 1905)): 175–176; Plates X (fig. 17), XII (fig. 10), XIII (fig. 10), XIV (fig. 9), XVIII (fig. 6), XIX (fig. 1), XX (figs 4–5). Sewell (1940—as *Xouthous purpurocinctum* (Norman & Scott, 1905)): 197–198; Text-fig. 29. Vervoort (1964—as *Idomene purpurocincta* (Norman & Scott, 1905)): 170–175; Figs 62–63. Lang (1965—as *I. purpurocincta*): 223–226; Figs 125–126; Plate III (Figs f–g). Note that the specimens of Sewell (1940), Vervoort (1964) and Lang (1965) may represent different species.

TL: England, Devon, Salcombe; dredging.

BL: 500 µm (♀) [Norman & Scott, 1905, 1906]; 380 µm (♀) [Sewell 1940]; 270–300 µm (♀) [Vervoort 1964].

Fish hosts

Parasitic copepods occur on fishes from all marine depth zones, from the intertidal zone to over 5,400 m depth (Boxshall 1998) and are common on all kinds of fish hosts, including hagfishes, elasmobranchs, holocephalans, as well as actinopterygians. The family Tisbidae contains the only known species of parasitic harpacticoid from a fish host. Leigh-Sharpe's (1936) record of *Parategastes haphe* on the gills of the brown comber, *Serranus hepatus* (Linnaeus, 1758), is to be considered accidental (see below).

Family Tisbidae

Neoscutellidium Zwerner, 1967

Zwerner (1967) placed the monotypic genus *Neoscutellidium* in the subfamily Tisbinae while Bodin (1997) considered it a member of the subfamily Idyanthinae (now Idyanthidae). Neither author provided a sound justification for the proposed subfamilial assignment. Avdeev (1983) recognized a close relationship between *Neoscutellidium* and the cholidyinid genus *Yunona*. Seifried (2003), without referring to Avdeev's work, formally placed *Neoscutellidium* in the tisbid subfamily Cholidyinae based on the shared (apomorphic) reductions observed in the antenna, maxillule, maxilla and maxilliped. The type and only species, *N. yeatmani* Zwerner, 1967, can be identified using the key on p. 502.

Neoscutellidium yeatmani Zwerner, 1967

Zwerner (1967) obtained seven female specimens from 92 sets of gills of the bathydemersal Antarctic eelpout *Lycodichthys dearborni* (DeWitt, 1962) (as *Rhigophila dearborni* DeWitt, 1962) (family Zoarcidae). The host is known only from the Ross Sea where it occurs between 550–588 m depth (Eastman & Hubold 1999), and is one of the most common fish species at McMurdo Sound (Matallanas & Olaso 2007). *Neoscutellidium yeatmani* has not been recorded again since its original description and the male is as yet unknown. Prehensile attachment to the host's gill filaments is achieved by using the large hook-like maxillae and maxillipeds. Both appendages are much larger than in other cholidyinids, being at least as long as the cephalic shield. The eggs (averaging four in number) are large (113 µm in diameter) and spherical, carried ventrally in a loose egg sac.

The Cholidyinae are currently considered a monophyletic clade within a paraphyletic Tisbinae (Seifried 2003), implying the former parasitic subfamily evolved from a free-living tisbinid ancestor. *Neoscutellidium yeatmani* is the only member of the Cholidyinae that utilizes a teleost as host. All other species are known to be associated with octopodan cephalopods (see above). Although comparative morphological analysis may shed some light on the basal relationships within the group, at this stage it remains conjectural whether teleosts or cephalopods were the ancestral hosts or any host switching occurred in the early evolution of the subfamily. *Yunona marginata*, *Octopinella tenax* and *N. yeatmani* are the most primitive members in the Cholidyinae, being the only ones that have all body somites expressed. Some characters such as the 9-segmented antennule in the female suggest that *N. yeatmani* is the most basal taxon in the subfamily, while others such as the armature on P1 exp-3, P3–P4 enp-2 and P3 enp-3 indicate that *Y. marginata* and especially *O. tenax* are more ancestral.

OD: Zwerner (1967): 153–156; Figs 1–11; Table I (♀ only).
TL: Antarctica, Ross Sea, McMurdo Sound (77°55'S, 166°39'E); on gills of *Lycodichthys dearborni* (DeWitt, 1962) (Zoarcidae).
BL: 697–913 µm (♀).

Marine tetrapods

Only six copepod species infect or otherwise associate with mammals (Benz *et al.* 2011) and half of them are members of the Harpacticoida. *Harpacticus pulex* Humes, 1964 was described from the sloughed skin tissue of a porpoise and a manatee, both captive-held at the Miami Seaquarium in Florida, however, the copepod is likely to be an opportunitistic scavenger rather than a genuine associate (Humes 1964; Morales-Vela *et al.* 2008). The two valid species of the family Balaenophilidae are known to be associated with marine mammals and reptiles (Suárez-Morales 2007) and appear to show low host specificity (Table 31). *Balaenophilus unisetus* Aurivillius, 1879a inhabits the baleen of several rorqual species (Mysticeti, Balaenopteridae) in the Northern and Southern Hemispheres while *B. manatorum* (Ortíz, Lalana & Torres Fundora, 1992) utilizes both sirenian and sea turtle hosts in the Caribbean, Mediterranean, and eastern and western Pacific. Schärer (2003) noted that the caudal third of the plastron in hawksbill sea turtles, *Eretmochelys imbricata* (Linnaeus, 1766), was overgrown by epibiota, mostly filamentous algae and harpacticoid copepods. The putative chelonian hosts were collected from the Mona and Monito Islands, Puerto Rico but no further information was given on the identity of the harpacticoids.

Family Balaenophilidae

The presence of nauplii, copepodid stages and ovigerous females on the baleen of rorquals and the skin of sea turtles indicates that balaenophilids live attached to the host throughout their life cycle (Aurivillius, 1879a, 1879b; Collett 1886; Lillie 1910; Vervoort & Tranter 1961; Gambell 1964; Bannister & Grindley 1966; Raga & Sanpera 1986; Dalla Rosa & Secchi 1997; Ogawa *et al.* 1997). Naupliar stages are highly modified, displaying a broad, dorsoventrally flattened body, and are equipped with strong claws on the antennae and mandibles. Only two stages have been described so far but it is likely that the naupliar phase goes through a 6-stage cycle as in other harpacticoids. The consistent absence of later naupliar stages on the hosts examined so far may indicate that they are involved in dispersal. Adult females bear paired egg sacs as in members of the Miraciidae and it has been suggested that balaenophilids may be included in this family (Willen 2000).

Balaenophilus Aurivillius, 1879a

There is controversy whether species of *Balaenophilus* are commensal or ectoparasitic, thus whether they derive their nutrients from host tissue, its associated epibiota, or both. Based on the presence of partly digested algal cells and numerous isolated plastids in the gut contents of specimens associated with blue whales from Western Australia, Vervoort & Tranter (1961) suggested that *B. unisetus* is commensal and probably feeds on the small, unicellular algae that develop on the baleen plates. Ogawa *et al.* (1997) observed packed brownish material, but no unicellular algae or remains of diatoms, in the gut of *B. manatorum* collected from juvenile *Caretta caretta* (Linnaeus, 1758) and in the gut of *B. unisetus* from the baleen of fin whales. The similar appearance with material scraped from loggerhead turtle's neck skin was regarded as evidence in support of a parasitic association of *Balaenophilus* spp. with their hosts. Badillo (2007) and Badillo *et al.* (2007) provided data on the gut contents of both species using SEM and immunohistochemistry analysis. In *B. unisetus* the gut was packed with pellets that were mostly made up of baleen tissue and high concentrations of coccoid bacteria. Positive staining for keratin was observed in the gut contents of all specimens, ranging from mild to strong immunolabelling, thus indicating ingestion of baleen tissue. In *B. manatorum* no pellets or food remains could be identified in the gut contents but some specimens were found manipulating fragments of flat tissue that roughly resembled the pericloacal epidermis of the sea turtle host. Histopathological analysis revealed a mild host reaction to the erosion of the epidermis, such as increased presence of fibroblasts and moderate infiltration of granulocytes and lymphocytes. Although this reaction appeared to increase with the density of the copepods it was only observed in very few host individuals. In one host showing lesions associated with *B. manatorum*, Badillo *et al.* (2007) showed that the copepods resided under the keratin layer of the decolorized maculae. This observation would indicate that the copepods feed on the dermal and hypodermal tissues rather than the α-keratin in the cornified outer layer of the epidermis as suggested by Badillo *et al.* (2007). Keratin is a structural protein that is resistant to digestion by the common proteolytic enzymes, and can only be degraded under very acidic or alkaline conditions at high temperatures well above 100°C during very long times. Such conditions do not exist in the digestion system of aquatic invertebrates. Badillo *et al.*'s (2007) hypothesis that the unique association of balaenophilids with marine tetrapods was driven by their ability to exploit epidermal keratin in permanently submerged microhabitats requires further testing since the current evidence appears to be inconclusive. At least on manatees there appears to be no evidence that *B. manatorum* causes skin damage or behaves as a scavenger feeding on sloughed skin since copepods typically settled on healthy skin areas (Suárez-Morales *et al.* 2010). The latter authors suggested that the copepods are merely commensal epibionts which use the manatee as a substratum to found a colony while having consistent access to suspended particles when the host feeds.

Balaenophilus species are often infested by epibiotic protists. Rice (1963, 1978; and in Mohr *et al.* 1963) first mentioned the occurrence of large numbers of an undescribed chonotrich on the legs of *B. unisetus*. The ciliate, which is normally found on cyamids, occurred on copepods collected from blue whales and fin whales. Bannister & Grindley (1966) stated that a very high percentage of adult *B. unisetus* on sei whales off Durban were heavily overgrown with long chains of bacteria (?), which gave them a hairy appearance, while *Ellobiopsis* sp. and a chonotrich ciliate were also common. Jankowski (1971) examined the epibionts on *B. unisetus* from the sei whale (*Balaenoptera borealis* Lesson, 1828) and the blue whale *(B. musculus* (Linnaeus, 1758)) collected off South Africa and described two new genera (*Talassochona* and *Inermichona*) and six new species of chonotrich ciliates. Each of these species appeared highly site specific, occupying narrow niches on the antennules, antennae, maxillipeds, swimming legs and urosome of the copepod host (see Fernandez-Leborans (2001) for details), however, experimentation has yet to confirm this conclusion. Ortíz *et al.* (1992) recorded peritrich ciliates on the swimming legs of the holotype of *B. manatorum*.

Ogawa *et al.*'s (1997) claim that the distal segment of both rami of leg 1 of *B. umigamecolus* bears three strong claws (one of which being very small), compared with only two in *B. unisetus*, is not readily observable in their illustrations (Wells 2007). The two species can be differentiated by the key below.

TABLE 31. Balaenophilidae associated with marine mammals and reptiles.

Copepod species	Host	Region	Locality	Reference
Balaenophilus unisetus	*Balaenoptera borealis* [1]	Antarctic	north of Graham Land	Bannister & Grindley (1966)
			south-east of Bouvet Island	Bannister & Grindley (1966)
		Norway	Finnmark, Sørvær whaling station	Collett (1886)
		South Africa	Durban whaling station	Matthews (1938), Mackintosh in Vervoort & Tranter (1961), Jankowski (1971)
			Durban and Saldanha whaling stations	Bannister & Grindley (1966)
		South Georgia		Matthews (1938), Mackintosh in Vervoort & Tranter (1961), Bannister & Grindley (1966)
		U.K.	Isle of Man, Langness	Chadwick (in Bruce *et al.* 1963)
		U.S.A.	off central California	Rice (1963)
	Balaenoptera edeni	Australia	undisclosed whaling stations	Ichihara (1966) [2]
		South Africa	Saldanha whaling station	Bannister & Grindley (1966)
	Balaenoptera physalus	Chile	Iquique	Bannister & Grindley (1966)
		South Africa	Durban and Saldanha whaling stations	Bannister & Grindley (1966)
		South Georgia		Bannister & Grindley (1966)
		Spain	Galicia, Caneliñas whaling station	Raga & Sanpera (1986), Badillo *et al.* (2007)
		U.S.A.	off central California	Rice (1963)
	Balaenoptera m. musculus	Australia	Western Australia, Carnarvon and Albany whaling stations	Vervoort & Tranter (1961)
			undisclosed whaling stations	Ichihara (1966) [2]
		Brazil	stranded near Chuí, Rio Grande do Sul	Dalla Rosa & Secchi (1997) [3]
		Ireland	County Mayo, South Inishkea whaling station	Lillie (1910) [4]

……*continued on the next page*

TABLE 31. (Continued)

Copepod species	Host	Region	Locality	Reference
		Norway	Finnmark, Vadsø whaling station	Aurivillius (1879a, b) [5]
			Finnmark, Sørvær whaling station	Cocks (1885)
		South Africa	Durban and Saldanha whaling stations	Bannister & Grindley (1966) [3]
			Durban whaling station	Jankowski (1971)
		South Georgia		Bannister & Grindley (1966)
		U.S.A.	off California and Baja California	Rice (1963, 1992)
	Balaenoptera m. brevicauda	Antarctic	Marion, Crozet and Kerguelen Islands	Ichihara (1966)
		Australia	undisclosed whaling stations	Ichihara (1966) [2]
		South Africa	off Durban	Gambell (1964)
Balaenophilus manatorum	*Trichechus manatus manatus*	Cuba	mouth of Sagua La Chica River	Ortíz *et al.* (1992) [6]
		Mexico	Quintana Roo, Ascención Bay	Suárez-Morales *et al.* (2010)
			Quintana Roo, Chetumal Bay	Suárez-Morales *et al.* (2010)
	Caretta caretta	Japan	Wakayama Prefecture	Ogawa *et al.* (1997) [7], Aznar *et al.* (2010)
		Spain	coast of Valencian Autonomous Community	Badillo *et al.* (2003 [8], 2007 [7]), Domènech *et al.* (2015)
	Chelonia mydas agassizii	Mexico	Jalisco State, Careyes (near Chamela)	Lazo-Wasem *et al.* (2007, 2011)
	Lepidochelys olivacea	Mexico	Jalisco State, Careyes (near Chamela)	Lazo-Wasem *et al.* (2007 [7], 2011)
			Jalisco State, south of Chamela	Suárez-Morales & Lazo-Wasem (2009), Suárez-Morales *et al.* (2010)

[1] Two subspecies have been identified – the Northern sei whale (*Balaenoptera borealis borealis* Lesson, 1828) and Southern sei whale (*B. borealis schlegelii* (Flower, 1865)). While their ranges do not overlap, morphological or genetic support for the southern-hemisphere subspecies at present is weak (Perrin *et al.* 2009); [2] records by Graham Chittleborough (*in litt.*); [3] these records probably refer to the pygmy blue whale, *Balaenoptera musculus brevicauda* Ichihara, 1966; [4] the host is also listed a second time under its junior synonym *Balaenoptera sibbaldii* (Gray, 1847); [5] the host is cited as *Balænoptera Sibbaldii* (Gray, 1847); [6] as *Harpactichechus manatorum* Ortíz, Lalana & Torres Fundora, 1992; [7] as *Balaenophilus umigamecolus* Ogawa, Matsuzaki & Misaki, 1997; [8] as *Balaenophilus* sp.

Key to species of *Balaenophilus* Aurivillius, 1879a

1. Body length (excluding caudal ramus setae) 2.05–2.50 mm in ♀, 1.95–2.35 mm in ♂; maximum length of caudal ramus about four times maximum width (in dorsal aspect); P4 exp-2 with inner seta . . . . *B. unisetus* Aurivillius, 1879a.
Body length (excluding caudal ramus setae) 0.90–1.40 mm in ♀, 1.00–1.25 mm in ♂; maximum length of caudal ramus about 1.5 times maximum width (in dorsal aspect); P4 exp-2 without inner seta . . . . *B. manatorum* (Ortíz, Lalana & Torres Fundora, 1992).

Balaenophilus unisetus Aurivillius, 1879a

The known baleen whale hosts utilized by *B. unisetus* are all members of the Balaenopteridae, with confirmed records from four of the 18 extant rorqual species (Table 31). Right whales (Balaenidae), pygmy right whales (Neobalaenidae) and gray whales (Eschrichtiidae) have not been reported as hosts yet but this may be due to sampling bias. Allen (1916) predicted that *B. unisetus* would be discovered on the baleen of the North Atlantic humpback whale *Megaptera novaeangliae novaeangliae* (Borowski, 1781) but there are no published reports substantiating such an association while other studies (Vervoort & Tranter 1961; Bannister & Grindley 1966) indicate that it is absent from the Southern humpback whale, *M. n. australis* (Lesson, 1828).

The species was first discovered by Aurivillius (1879a—Swedish translation in 1879b) who obtained innumerable specimens from the baleen plates of a Northern blue whale, *Balaenoptera musculus musculus* [as *Balænoptera Sibbaldii* (Gray, 1847)] landed in June 1878 at the Vadsø whaling station in the Varangerfjorden in northern Norway. All stages of development were found firmly adhering to the baleen where they formed large yellowish-white spots. Inspection of other blue whales landed at Vadsø initially did not reveal additional material (Aurivillius 1879a, 1879b) but Cocks (1885) rediscovered the species in large numbers on the same rorqual species at Sørvær whaling station on the western tip of the island of Sørøya, Finnmark in Norway. At the same whaling station Collett (1886) subsequently recorded countless numbers of *B. unisetus* on the baleen plates of the sei whale *Balaenoptera borealis*. Lillie (1910) examined the baleen of blue whales landed at the South Inishkea whaling station off the north-western coast of Ireland and commented that they were "…very frequently coated with the adult forms and nauplius larvae…" of *B. unisetus*. Note that in his paper *Balaenoptera musculus* and its junior synonym, *B. sibbaldii*, were still separated specifically and that—not surprisingly—*B. unisetus* was recorded on both. In his review of the baleen whales of New England waters, Allen (1916) did not add any new records but erroneously cited Lillie's (1910) under the parasites of the fin whale *Balaenoptera physalus* (Linnaeus, 1758), claiming that no external parasites had been discovered on *B. musculus*. Sars (1910) changed the specific epithet *unisetus* to *unisetis* but the latter is to be regarded as an incorrect subsequent spelling. His redesciption, based on Aurivillius' material, marked the end of the initial discovery phase of *B. unisetus* in the Northern Hemisphere with no further published records for over fifty years. Herbert C. Chadwick (in Bruce *et al.* 1963) found live specimens of *B. unisetus* on the baleen plates of *B. borealis* stranded at Langness on the south-eastern coast of the Isle of Man. Off the coast of California Rice (1963, 1992) recorded the species from *B. musculus* and sighted it for the first time on *B. physalus*. The occurrence on the latter host was recently confirmed by Raga & Sanpera (1986) and Badillo *et al.* (2007) who reported heavy infections of *B. unisetus* on the baleen plates of fin whales that were captured during commercial whaling operations in the period 1980–1984 off the coast of Galicia, north-western Spain, and landed at the currently disused Caneliñas whaling station. Badillo *et al.* (2007) recorded a 90% prevalence (*n* = 20).

The first records of *B. unisetus* from the Southern Hemisphere are those by Matthews (1938) who stated that it commonly infests the baleen of sei whales. It was searched for in 116 *B. borealis* at South Georgia and was found to be present in 100 host individuals, the infection varying from very slight to very heavy. *Balaenophilus* was looked for in only three whales at South Africa and was absent in one, but heavy infections of the naupliar stages were present in two sei whales at Durban. No variation in infection of *B. unisetus* could be correlated with season or with size, condition or sex of whale. Mackintosh (1942) examined whales at shore stations and in factory ships in the Southern Hemisphere and stated that "among the Discovery Committee's records [*B. unisetus*] is noted on blue and sei whales". No indication of the regularity of its occurrence was given but the author later stated (*in litt.*; *cf.* Vervoort & Tranter 1961: 83) that is was very common on the baleen plates of sei whales around South Georgia but had never been observed on other rorqual species in the region. Mackintosh also mentioned a single record from a sei whale in the Durban area. Vervoort & Tranter (1961) collected numerous individuals from the baleen plates of a blue whale landed at the whaling station at Carnarvon in Western Australia. According to additional commercial catch data *B. unisetus* 17appears to be a common epibiont of blue whales off the coast of Western Australia but is consistently absent on humpback whales which comprised the greater part of the catches at the whaling stations in this region (Vervoort & Tranter 1961). Ichihara (1961, 1963, 1966) pointed out the existence of two blue whale morphotypes in the Southern Hemisphere and established the subspecies *B. musculus brevicauda* Ichihara, 1966 for the pygmy form which he found to be regularly infested by *B. unisetus*. Antarctic blue whales remain largely south of 55°S, whereas pygmy blue whales are generally found north of 55°S (Ichihara 1966; Kato *et al.* 1995). Presumably all Southern Hemisphere blue whales on which *Balaenophilus* was found (Gambell 1964; Bannister & Grindley 1966; Ichihara 1966; Dalla Rosa & Secchi 1997), including Vervoort & Tranter's (1961) stunted variety of *B. musculus* from Western Australia, belong to the pygmy subspecies. Vervoort & Tranter (1961) reported that examination of some 1,500 Antarctic blue and fin whales during the 1946–1948 whaling seasons produced no specimens of *B. unisetus*. Ichihara (1966) suggested that *B. unisetus* does not occur on the baleen plates of ordinary blue whales in the Antarctic. He further claimed that its occurrence in the Southern Hemisphere may relate to the southern limit of the feeding migration of pygmy blue whales, and particularly to water temperature.

According to Bannister & Grindley (1966) *B. unisetus* is only occasionally found on fin whales and Bryde's whales (*Balaenoptera edeni* Anderson, 1878) in South Africa and South Georgia, its prevalence being less than two percent. Their data indicate that the sei whale forms the most important host in the Southern Hemisphere occurring as far south as Graham Land (58–65°S), *B. unisetus* having been observed in almost 80% of the individuals examined. Historically, two subspecies of *B. borealis* have been identified (Tomilin 1946; Rice 1998)—the Northern sei whale (*B. borealis borealis* Lesson, 1828) and the Southern sei whale (*B. b. schlegelii* (Flower, 1865)). While their ranges do not overlap, there are no strong lines of morphological or genetic evidence for recognition of the southern-hemisphere subspecies at present (Perrin *et al.* 2009), implying that *B. borealis* acts as host for *B. unisetus* across an immense latitudinal range, extending from the Arctic (Collett 1886) to the Antarctic (Bannister & Grindley 1966). In the Southern Hemisphere, heavy infestations of *B. unisetus* survive best on baleen whales which are more warm-water or subantarctic in distribution, explaining why some seem less prone to infection than others.

Balaenophilus unisetus can occur in extraordinary large numbers. According to Rice (1978) "Such uncountable millions … live on the baleen plates [of *B. musculus*] that these ectoparasites form a whitish scum". Where infestations are particularly heavy, individuals can be found spreading out over the gum at the outer margin of the baleen or at the corners of the mouth (Bannister & Grindley 1961; Badillo *et al.* 2007). Based on the presence of nauplii Bannister & Grindley (1961) inferred that breeding takes place during at least eight months of the year, and on at least four species of whales. Ovigerous females carry paired egg sacs, each containing about 20 slightly oval eggs (100 × 130 μm).

While *B. unisetus* assumes a virtually cosmopolitan distribution, its populations are remarkably uniform morphologically, irrespective of latitude or whale host species. Ogawa *et al.* (1997) pointed out that the socle supporting the antennule may have been misinterpreted as a supernumerary segment in some descriptions (Sars 1910; Lang 1948). They also remarked that the labrum and paragnaths were transposed in Vervoort & Tranter's (1961) redescription.

OD: Aurivillius (1879a): 5–16; plates I–IV [Translated in Swedish in Aurivillius (1879b): 8–26; Plates I–IV].

AD: Collett (1886): 256–257; Figs A–D. Sars (1910—as *Balænophilus unisetis*): 347–349; Plates CCXXIX–CCXXX. Vervoort & Tranter (1961): 70–82; Figs 1–6. Bannister & Grindley (1966): 297, 299; Fig. 1. Raga & Sanpera (1986): 493.

TL: on the baleen plates of a recently killed blue whale, *Balaenoptera musculus* (Linnaeus, 1758) (Balaenopteridae) landed at the Vadsø whaling station, Varangerfjorden, Øst-Finnmark, Norway.

BL: 2,250–2,500 μm (3,600–3,750 μm including caudal setae) (♀), 2,200 μm (3,750 μm including caudal setae) (♂), 150 × 270 μm (NI), 200–250 × 300–350 μm (NII), 660 μm (850 μm including caudal setae) (CoI), 830–850 μm (1,300 μm including caudal setae) (CoII), 1,150–1,250 μm (1,900–1,950 μm including caudal setae), 1,500 μm (2,400 μm including caudal setae) (CoIV), 1,850–2,150 μm (2,850–3,100 μm including caudal setae) (CoV) [Aurivillius 1879a, b]; 2,400 μm (♀) [Sars 1910]; 2,050–2,450 μm (♀), 2,050–2,130 μm (♂) [Vervoort & Tranter 1961]; 2,250 μm (♀), 2,100 μm (♂), 150 × 240 μm (NI), 250 × 320 μm (NII), > 650 μm (CoI)

[Bannister & Grindley 1966]; 2,210–2,390 µm (caudal setae 920–1,380 µm) (♀), 2,080–2,390 µm (caudal setae 1,000–1,250 µm) (ovigerous ♀), 1,950–2,330 µm (caudal setae 1,100–1,610 µm) (♂) [Raga & Sanpera 1986].

***Balaenophilus manatorum* (Ortíz, Lalana & Torres Fundora, 1992)**

Ortíz *et al.* (1992) obtained over one hundred copepods from the skin of a female Caribbean manatee, *Trichechus manatus manatus* Linnaeus, 1758, which had stranded in the estuary of the Sagua La Chica River, Cuba. The authors assigned the material to a new genus and species, *Harpactichechus manatorum*, which they placed in the Harpacticidae. Unfortunately, the description by Ortíz *et al.* (1992) was inadequate and Boxshall & Halsey (2004) believed that without further information *Harpactichechus* Ortíz, Lalana & Torres Fundora, 1992 must be ranked *genus incertae sedis* in the Harpacticidae. Wells (2007) recognized similarities with *B. unisetus* and relegated *Harpactichechus* to a junior synonym of *Balaenophilus*, effectively removing it to the Balaenophilidae. Simultaneously, Badillo *et al.* (2007) re-examined the type material of *H. manatorum* and likewise concluded that it belonged to *Balaenophilus*.

Ogawa *et al.* (1997) obtained more than 440 individuals of a new species, *Balaenophilus umigamecolus*, from washings of the neck skin of a juvenile loggerhead sea turtle in the Kushimoto Marine Park Center, Wakayama Prefecture, Japan. Descriptions were given of both adults, the first nauplius stage and copepodid stages III–V. Females outnumbered males by a ratio of 3.6:1 while the average number of eggs per sac was 30 (29–35). The species was subsequently discovered on wild populations of two chelonian hosts in the eastern Pacific, the olive ridley turtle, *Lepidochelys olivacea* (Eschscholtz, 1829) and the black (Pacific green) turtle, *Chelonia mydas agassizii* (Bocourt, 1868) (Lazo-Wasem *et al.* 2007, Suárez-Morales & Lazo-Wasem 2009). Both hosts were collected while nesting on the beaches of the Jalisco coast of western Mexico. Suárez-Morales (2007) compared the descriptions of *H. manatorum* by Ortíz *et al.* (1992) and of *B. umigamecolus* by Ogawa *et al.* (1997) and concluded that both species are conspecific, the valid combination therefore becoming *Balaenophilus manatorum* (Ortíz, Lalana & Torres Fundora, 1992). Badillo *et al.* (2003) recorded several hundreds of specimens of an unidentified species of *Balaenophilus* from stranded juvenile loggerhead turtles along the coasts of the Valencian Autonomous Community, Spain (40°31'N, 0°31'E to 37°51'N, 0°46'W). This material was variously considered a putative new species based on morphometric differences (Badillo 2007), conspecific with *B. umigamecolus* (Badillo *et al.* 2007) and finally identical to *B. manatorum* (Aznar *et al.* 2010; Domènech *et al.* 2015). Suárez-Morales *et al.* (2010) confirmed the common association of *B. manatorum* with manatees in Chetumal Bay, Quintana Roo, Mexico. Infestation was found in over 25% of the 54 manatees examined with incidence being highest in young adult females and males. Copepods were absent on juveniles.

Ogawa *et al.* (1997) noted variability in the Japanese material in the armature of the second and third antennulary segments in both sexes, the number of outer spinules ("smallest claws") on the third exopodal segment of leg 1 in both sexes, and the number of small setae on the caudal rami. Suárez-Morales & Lazo-Wasem's (2009) comparison of *B. manatorum* from sea turtles of the Mexican Pacific with the descriptions based on Cuban (Ortíz *et al.* 1992) and Japanese specimens (Ogawa *et al.* 1997) showed subtle differences in the antennule, antennary exopod and legs 1–5 but these were considered to be within the range of intraspecific variability expected in copepods associated with hosts that exhibit wide-ranging migration behaviour. Using both light and scanning electron microscopy Aznar *et al.* (2010) found that specimens of *B. manatorum* from Japan and the western Mediterranean are virtually identical, differing only in the spinular patterns on the pedigerous somites, but that both populations were distinguishable from the Mexican Pacific individuals by differences in maxillipedal morphology. They suggested that *B. manatorum* might represent a complex of sibling or pseudosibling species rather than a single cosmopolitan species, an issue that will probably remain unanswered until the arrival of molecular sequence data.

Lazo-Wasem *et al.* (2007) found a distinct correlation between the presence of *B. manatorum* and the coronuloidean barnacle *Stomatolepas elegans* (Costa, 1838) (as *S. praegustator* Pilsbry, 1916) that grows embedded in the turtle skin. They suggested that *B. manatorum* may either feed on the irritated skin around the embedded barnacles or, alternatively, were associated with the barnacles themselves. The possible negative effects of *Balaenophilus* on marine turtle health remain as yet unknown. Greenblatt *et al.*'s (2004) findings implicated the leech *Ozobranchus branchiatus* (Menzies, 1791), a common marine turtle ectoparasite, as a potential vector in transmitting the turtle herpes virus which causes fibropapillomatosis in green turtles in Hawaii. Fibropapillomatosis is a benign tumour disease of marine turtles, predominantly in *Chelonia mydas agassizii*, but has also been reported in *Caretta caretta* and *Lepidochelys olivacea*, all of which serve as hosts for *B. manatorum*. Lazo-Wasem *et al.* (2007, 2011) suggested a potentially similar vector role for *Balaenophilus*. Clusters of *B. manatorum* observed along skin folds on manatees in Mexico were not related to groups of barnacles or algal patches (Suárez-Morales *et al.* 2010).

Badillo *et al.* (2007) observed an 82.7% prevalence ($n = 52$) and a mean intensity of 863 (386–2,108) ind.host^{-1} in stranded immature *Caretta caretta* in the western Mediterranean. Copepods appeared mostly in the hinge region between the largest scales on the limbs and on the skin of the cloacal region. In one host, *B. manatorum* was associated with white lesions on the skin of the neck and the hindlimbs. The carapace and plastron were never infected. A recent study by Suárez-Morales *et al.* (2010) revealed that *B. manatorum* commonly forms conspicuous yellowish clusters of different size and density on Caribbean manatees in Chetumal Bay. The soft copepod masses are loosely adhered to the host and typically associated with long deep skin folds, including the area around the muzzle and nipples, and the bases of the caudal and pectoral fins, but not in the exposed body depressions such as the anus and genitalia. In contrast to the records from sea turtle hosts, those from Caribbean manatees are so far exclusively from brackish estuarine localities (Ortíz *et al.* 1992; Suárez-Morales *et al.* 2010), indicating that *B. manatorum* can survive osmotic stress when its hosts move from oceanic to low salinity coastal environments.

OD: Ortíz *et al.* (1992—as *Harpactichechus manatorum* Ortíz, Lalana & Torres Fundora, 1992): 118–126; Figs 1–7; Tabla 1. Ogawa *et al.* (1997—as *Balaenophilus umigamecolus* Ogawa, Matsuzaki & Misaki, 1997): 691–699; Figs 1–10. Lazo-Wasem *et al.* (2007—as *B. umigamecolus*): Fig. 1. Suárez-Morales & Lazo-Wasem (2009): 85–91; Figs 1–27. Aznar *et al.* (2010): 300–307; Figs 1–27; Table I.

TL: Cuba, Villa Clara province, estuary of Sagua La Chica River; on the skin of a stranded female Caribbean manatee, *Trichechus manatus manatus* Linnaeus, 1758 (Trichechidae).

BL: 1,100 µm (♀), 1,200 µm (♂) [Ortíz *et al.* 1992]; 1,140–1,320 µm (caudal setae 710–880 µm) (♀), 1,100–1,200 µm (caudal setae 710–900 µm) (♂), 89 × 127 µm (NI), 500 µm (CoIII), 650 µm (CoIV), 970 µm (CoV) [Ogawa *et al.* 1997]; 1,030–1,140 µm (♀), 1,180 µm (♂) [Suárez-Morales & Lazo-Wasem 2009—Mexican material]; 1,020–1,360 µm (caudal setae 752–920 µm) (♀), 1,050–1,250 µm (caudal setae 725–905 µm) (♂) [Aznar *et al.* 2010—Mediterranean material]; 1,200–1,380 µm (caudal setae 690–905 µm) (♀), 1,070–1,210 µm (caudal setae 782–908 µm) (♂) [Aznar *et al.* 2010—Japanese material]; 920–1,050 µm (♀), 1,010 µm (♂) [Suárez-Morales *et al.* 2010].

Unresolved cases

Some harpacticoids exhibit a morphology that is radically divergent from that of their congeners (*Paralaophonte harpagone*) or other members of the family they have been assigned to (*Caligopsyllus primus*, *Raptolaophonte ardua*). Their morphological adaptations are suggestive of an ecto-associated mode of life but in the absence of information on the presumed host their status as symbionts has to remain unconfirmed.

Caligopsyllus primus Kunz, 1975 (Paramesochridae)

Although the type specimens (one female and one male) were found in tidal pool sediment samples, Kunz (1981) was the first to postulate an ectoparasitic mode of life for *Caligopsyllus primus*. The species differs radically from other members of the Paramesochridae which are primarily mesopsammic. Various aspects of its morphology can be interpreted as adaptations to a parasitic life on invertebrate hosts, or at least to a life in intimate association with other organisms.

Unlike other paramesochrids, *C. primus* has a low-profile body shape which could help the copepod maintaining its position on the host, especially when water currents sweep over the host's surface. The laterally expanded cephalothorax is provided with a marginal membrane which might assist in sealing off the concavity beneath the cephalic shield and facilitate its adhesive function.

Morphologically, the adoption of an ecto-associated mode of life is usually linked to the evolution of attachment organs, *i.e.* the adaptation of existing appendages to a new role. In *Caligopsyllus* the primary attachment devices are the endopods of the first leg pair and the maxillipeds. The modified endopod of leg 1 appears to have lost its prehensility as found in other members of the family; instead it displays two strong, curved claws which could serve as anchors ensuring attachment to a presumed host. The robust maxillipeds have strong endopodal claws and probably serve as auxilliary limbs in holding onto the host.

It is conceivable that *C. primus* is an ecto-associate clinging to the host's surface with the aid of its prehensile appendages but remains capable of free movement over this surface. However, until the discovery of the presumptive host, one cannot preclude the possibility that the morphological adaptations of *Caligopsyllus* might serve as well for clinging to flat sediment grains or algae and the species is essentially free-living (Huys 1988b).

OD: Kunz (1975): 202–203; Plate 19 (Abb. 195–200), Plate 20 (Abb. 201–209).
AD: Huys (1988b): 5–13; Figs 1–6.
TL: South Africa, Eastern Cape Province; 21 km north-east of East London; shell gravel from tidal pools of a reef situated in the mouth of the Gonubie River.
BL: 360 µm (♀), 320 µm (♂) [Kunz 1975]; 385 µm (♀), 338 µm (♂) [Huys 1988b].

Raptolaophonte ardua **Cottarelli & Forniz, 1989 (Laophontidae)**

This genus *Raptolaophonte* has remained monotypic since its proposal for an unusual laophontid from a littoral sediment sample taken on Îsle Boddam, Salomon Atoll, Chagos Islands. *Raptolaophonte ardua* exhibits an extraordinary sexual dimorphism in leg 4 and an extreme reduction in the male leg 5. Cottarelli & Forniz (1989) pointed out the similarity in general body morphology between members of *Mexicolaophonte* Cottarelli, 1977 and *R. ardua*, however, the superficial resemblance in the stout and cylindrical body, and the strongly developed leg 1 and maxilliped, was postulated as the collective product of convergent evolution in the interstitial habitat. Cottarelli & Forniz (1989) attributed significant weight to the absence of sexual dimorphism on the endopod of leg 3, a character they thought could be indicative of phylogenetic affinity with the genera *Indolaophonte* Cottarelli, Saporito & Puccetti, 1986 and *Laophontina* Norman & Scott, 1905. This potential synapomorphy is not particularly robust and may be more apparent than real. In *Raptolaophonte* the entire endopod is absent while in the other two genera it is usually reduced (except in *I. ramai* Cottarelli, Saporito & Puccetti, 1986 where it is lost). It is virtually impossible to determine whether the loss of sexual dimorphism preceded the loss of the leg 3 endopod or whether the various reductions observed are the result of a single evolutionary event. Fiers (1998) offered a dissenting opinion by speculating that *R. ardua* is not genuinely mesopsammic but, under normal circumstances, lives in close association with an invertebrate host (probably a decapod crustacean). This assumption was based on the secondarily elongated P1 protopod and the extreme development of the maxilliped, both of which are characteristic for the primarily decapod associated genera *Coullia*, *Robustunguis* and *Xanthilaophonte*. Following the discovery of *Carcinocaris serrichelata*, Cottarelli *et al.* (2006) appear to have now accepted Fiers' (1998) arguments.

Fiers (1998) indicated that the lamelliform 1-segmented leg 4 in female *Raptolaophonte* is analogous to that found in late copepodids of laophontid genera that typically display a sexually dimorphic development in this leg. Although this can be regarded as evidence for a paedomorphic origin, it is in practice impossible to determine whether neoteny, progenesis or postdisplacement is the underlying heterochronic process. Pending live observations in association with the presumptive host and the discovery of copepodids, it is equally difficult to claim whether the female leg 4 morphology is an adaptation to postcopulatory mate guarding or, less likely, a further specialization to prevent the females (and their offspring) from becoming detached from their host.

It is not clear whether the marginal spiniform structures on the female leg 4 (Cottarelli & Forniz 1989: Fig. 20) represent ornamentation elements or reduced setae. The number (7) appears to be constant on either side but their position is not symmetrical between the left and right members. Other features in the original description that require confirmation include the slight sexual dimorphism of the maxillipedal claw, the morphology of the female genital field and the precise configuration of the male sixth legs. The free segment on the male leg 4 is interpreted here as the vestigial exopod (based on the serial homology with P2–P3).

OD: Cottarelli & Forniz (1989): 97–101; Figs 1–21.
TL: Indian Ocean, Chagos Islands, Salomon Atoll, Îsle Boddam; intertidal zone, depth <1 m; coarse coral sand.
BL: 330–400 µm (♀), 300–400 µm (♂).

Paralaophonte harpagone **Gheerardyn, Fiers, Vincx & De Troch, 2006 (Laophontidae)**

Gheerardyn *et al.* (2006) found this species in washings of dead coral rubble in two localities along the Kenyan coast. Both adults and and virtually all copepodid stages (CoII–V; CoI not found) display large, robust maxillipeds which protrude laterally from the cephalothorax and are backwardly directed, making them discernible in dorsal aspect. Powerful maxillipeds of similar dimension and orientation have previously been recorded in members of the genus *Microchelonia* (= *Namakosiramia*) which are known to utilize holothurian hosts. However, Gheerardyn *et al.* (2006) pointed out the many differences with *P. harpagone*, rendering a close relationship with *Microchelonia* spp. unlikely. The species was placed in the genus *Paralaophonte* on account of the sexual dimorphism on the P2 endopod, involving the modification of the distal inner seta on enp-2. This character is diagnostic for the *Paralaophonte-Loureirophonte* complex (Huys & Lee 2009). *Paralaophonte harpagone* occupies an isolated and phylogenetically advanced position in the genus as indicated by the absence of distinct sexually dimorphic features on leg 3 and the segmental reductions in the antennule and P1 exopod, and the reduced armature of legs 2–4.

Gheerardyn *et al.* (2006) suggested that *P. harpagone* may live as an associate of another invertebrate. Their inspection of the 1 mm fraction of the coral rubble washings revealed mostly peracarid crustaceans and small polychaetes but no copepods were found attached to them. Although the radically divergent morphology of the maxillipeds may suggest such a mode of life throughout the copepodid phase, the symbiotic association of *P. harpagone* remains speculative at present. The species is not related to the clade of *Paralaophonte* species (*majae/ormieresi/royi*) that are associated with majid crabs and have unmodified maxillipeds.

Variability was recorded in the exopodal armature of the male leg 2 with most males exhibiting left-right asymmetry on the distal segment (either two or three outer spines) (Gheerardyn *et al.* 2006). Aberrations were also noted in the male P3 endopod and P5 exopod.
OD: Gheerardyn *et al.* (2006): 2–4; Figs 1–4.
TL: Kenya, Kurwitu village (03°47'S, 39°49'E); dead coral rubble at less than 1 m depth.
BL: 356–415 µm (♀), 349–379 µm (♂).

Pholeteros

Lake (1977) and Lake & Coleman (1977) coined the collective term pholeteros (derived from the Greek *pholeteros*,—"one who lurks in a hole") to define the faunal assemblage found in the water of crayfish burrows. They claimed that crustaceans are the dominant group found in the pholeteros possibly because they have not evolved an effective method of drought resistance. Instead they adopted a strategy of drought evasion in spite of the stresses imposed on them by the burrow water environment, including its acidity, high organic content and very low oxygen concentrations. Members of the pholeteros must therefore be physiologically adapted to the conditions of this microhabitat. In many cases the burrow fauna appears to be some subset of the local aquatic community. Reid *et al.* (2006) redefined pholeteros as the fauna consisting of species that occur more often in the burrows than in surface water and are consistently present in the burrows (in the case of their study, during three or more months).

Crayfish tunnels may serve as refuges for many species of benthic copepods, including rather eurytopic, widely distributed ones, especially in dynamic, seasonally cyclic riverine floodplains. Reid (2001) reviewed the species of copepods reported from crayfish burrows in Europe, North America, Australia, and Tasmania, and from the burrows of land crabs on several islands in the Pacific Ocean. Several species have been recorded in washings of crayfish but are probably only accidentals and not even part of the pholeteros (*e.g.* Chappuis 1926; Jakubisiak 1939; Bassamakov 1973, 1975). As a rule, canthocamptid harpacticoids tend to predominate over other copepods found in crayfish burrows; however the species encountered are normally benthic or epibenthic in epigean waters, rather than true stygobionts (Reid *et al.* 2006).

Williams *et al.* (1974) found large populations of *Attheyella nordenskioldii* (Lilljeborg, 1902) in the burrows of the crayfish, *Fallicambarus fodiens* (Cottle, 1863) (as *Cambarus fodiens*), along the Moser Stream, a temporary stream in southern Ontario, Canada. The copepod oversummers as a near adult stage by secreting a circular drought resistant cyst around itself (Williams & Hynes 1976).

Horwitz *et al.* (1985) reported an undescribed species of *Antarctobiotus* Chappuis, 1930, which appeared to be common in the burrow water of two sympatric crayfish, *Engaeus tuberculatus* Clark, 1936 and *E. urostrictus* Riek, 1969, occurring in Sherbrooke Creek in the Dandenong Ranges, Victoria, Australia. Horwitz & Knott (1991) recorded an unidentified *Canthocamptus* species from crayfish tunnels at two sites in Lightning Plains, Western Tasmania. *Parastacoides tasmanicus inermis* Clark, 1939 was the dominant crayfish at both sites with two other species, *Astacopsis franklinii* (Gray, 1845) and *Engaeus cisternarius* Suter, 1977, co-occurring at the mixed forest site. *Canthocamptus* sp. was considered a genuine component of the pholeteros.

Reid *et al.* (2006) reported several copepods associated with the burrows of the South American *Parastacus defossus* (Parastacidae) near Lami, Porto Alegre, Rio Grande do Sul, Brazil. A total of 12 species of copepods (of which six were harpacticoids) were found either consistently or occasionally in the crayfish tunnels. *Attheyella* (*Chappuisiella*) *fuhrmanni* (Thiébaud, 1912) and *A.* (*C.*) cf. *godeti* (Delachaux, 1918) occurred more often in the burrows than in the surface water, and were present in the burrows during three or more sampling months. *Elaphoidella bidens* (Schmeil, 1893) appeared equally often in burrows and surface waters while *Attheyella* (*Chappuisiella*) *subdola* (Brian, 1927), *Attheyella* (*Chappuisiella*) sp. and *Epactophanes* sp. were only occasionally encountered; since these species showed no predilection for the burrows they were not considered part of a pholeteros. Reid *et al.* (2006) considered the large number of nauplii and copepodids in the burrows as evidence that some copepod species may be able to reproduce successfully within this cryptic microhabitat.

Yeatman (1983) collected several harpacticoids from crab holes in Fiji, Tonga and Western Samoa, including *Darcythompsonia inopinata* Smirnov, 1934, *Nitocra lacustris pacifica* Yeatman, 1983, *N. pseudospinipes* Yeatman, 1983, *Schizopera tobae* Chappuis, 1931, and *Tisbella pulchella* (Wilson, 1932). *Nannopus palustris* Brady, 1880 has been recorded from intertidal crab holes occupied by the ocypodid *Uca* (*Austruca*) *lactea* (De Haan, 1835) in Beolgyo, Goheung, Korea (Kim 2013).

It has been suggested that the possible use of crayfish tunnels as refuges may have led to the development of various degrees of commensalism between certain harpacticoid species and their crayfish hosts (Reid 2001; Huys *et al.* 2009). The colonization of these burrows conceivably facilitated habitual partnership with their original occupants. Huys *et al.* (2009) postulated that the "cancrincolids" and members of the *N. divaricata* lineage originated from a common ancestral stock, which lived in oligohaline cryptic habitats and displayed a propensity to enter into association with decapod crustaceans. Initially, species would have been primarily free-living and only occasionally loosely associated with the crustacean host (as still shown in present-day *N. hibernica*; *cf.* Chappuis 1926). Such symbiotic relationship may offer a safe haven for reproduction and against predators, a potential food source and a vehicle for dispersal into more favourable habitats (Defaye 1996).

Biogenic substrata

Sunken or submerged wood, bored and eroded by the biological activities of isopod crustaceans (Limnoriidae) and shipworms (Teredinidae), offers a firm yet ephemeral biogenic substratum for invertebrates in offshore waters. Although harpacticoid copepods have been reported from decaying wood on numerous occasions, only in a few cases (*Harrietella simulans*, donsiellinids) a direct symbiotic relationship with the wood-boring hosts could reasonably be confirmed (see above). For most species the microtopographically complex habitat appears to be the primary determining factor for habitation rather than dependence on the wood-borers themselves. Harpacticoids exploiting this habitat are likely to feed on wood particles, dead entombed gribbles or faecal pellets produced by the wood-borers.

Barnard & Reish (1957) were first to report the observation of marine copepods ingesting woody material. The harpacticoids were observed in culture dishes in which populations of the wood-boring gammarid amphipod *Chelura terebrans* Philippi, 1839 had been maintained but had died. The copepods (which somewhat misleadingly were called "wood-boring") had woody matter in their digestive tracts and were found browsing on the surface of the wood in a manner similar to that of *C. terebrans*; unlike active borers like teredinids or limnoriids, they made no discrete holes. Five species of wood-browsing copepods belonging to the genera *Tisbe*, *Sarsamphiascus*, and an unknown genus were isolated from timber test blocks suspended in Los Angeles and Long Beach harbours, California. The most frequently observed species was subsequently identified as *Tisbe gracilis* (Barnard & Reish 1960), coincidently one of the species Stephensen (1936) had reported previously from *Limnoria lignorum*. Although Volkmann (1979b) confirmed the occurrence of *T. gracilis* in southern California, she believed that the male described by Barnard & Reish (1960) is in reality *T. holothuriae*, while the female belongs to the *gracilis*-group. Like *Harrietella simulans* and *Donsiella limnoriae* it is possible that some *Tisbe* species have an indirect commensal relationship by feeding on the faecal pellets left behind in the burrows by their wood-boring peracarid hosts. This appears to be corroborated by Pinkster (1968) who described two new *Tisbe* species, *T. eurypleura* and *T. parviseta*, obtained from submerged wooden shipwrecks in the harbour of Marseille and wooden poles used for demarcating mussel beds in Wimereux, respectively. Pinkster's (1968) laboratory experiments showed that, although *T. eurypleura* showed a marked tendency towards clinging to *Limnoria tripunctata*, it can very well survive on wood in the absence of the isopod host. Volkmann-Rocco (1972b) suspected that both *T. eurypleura* and *T. parviseta* were identical with *T. holothuriae*. Specimens of *Tisbe* from Wimereux were found to be perfectly interfertile with *T. holothuriae*, reinforcing the supposition that Pinkster's species are not valid species (Volkmann 1974). In a later paper *T. eurypleura* was considered conspecific with *T. holothuriae* (Volkmann 1979b).

Crothers (1966) recorded *Harrietella simulans* (a true associate) and *Mesochra pygmaea* (Claus, 1863) (an accidental associate) on the gribble *Limnoria lignorum* in drift wood in West Dale Bay, Pembrokeshire, Wales. Sleeter & Coull (1973) and Rosenfield & Coull (1974) found *Paramphiascella fulvofasciata*, *P. commensalis* and *Paralaophonte congenera* in the burrows of *Limnoria tripunctata* in Duxbury Bay, Massachusetts. Although *P. fulvofasciata* was found to be feeding on dead, entombed *L. tripunctata*, its association cannot be considered a case of necrotrophic symbiosis (in which one of the symbionts dies and the other uses it as a souce of nutrients). Rearing experiments showed that it did not depend on the gribble (Rosenfield & Coull 1974; Dahms 1986) and was more than likely an accidental associate in Sleeter & Coull's (1973) study. The species has been recorded from both sides of the Atlantic and is a common inhabitant of *Laminaria* holdfasts (Dahms 1986, 1987). Ventham (2011) recorded considerable numbers on the red algae *Polysiphonia fucoides*, *Calliblepharis ciliata* and *Phyllophora crispa* (Hudson) P.S. Dixon, 1964 in the eastern English Channel (Sussex coast).

Raibaut (1962b, 1967) encountered *Nannomesochra arupinensis* (Brian, 1925) in submerged wood infested by *L. tripunctata* in the Bassin de Thau and Pinkster (1968) recorded *Amonardia normani* (Brady, 1872) in a similar habitat in the harbour of Marseille, France. Both species are usually found in phytal habitats (Lang 1948). Boer (1971: Table I) reported 18 species of harpacticoids in wood infested by *Limnoria lignorum* in northwestern France but only *Harrietella simulans* and *Donsiella limnoriae* were considered as genuine associates of the gribble. Kim (2013) recorded 30 species from a single fragment of decaying wood bored by shipworms and limnoriids collected in Korean waters, 20 of which were new to science (but not described). Named species included, among others, *Echinolaophonte mirabilis* (Gurney, 1927), *Laophonte denticornis* T. Scott, 1894b, *L. elongata barbata* Lang, 1934, *L. longistylata* Willey, 1935, *L. thoracica* Boeck, 1865, *Paralaophonte macera* (Sars, 1908b) and *Laophontodes bicornis* A. Scott, 1896.

Hicks (1988c) described three new species from a waterlogged teredinid bored log at 51 m depth off Kawhia, northwestern coast of New Zealand: *Paradactylopodia trioculata*, *Muohuysia xylophila* (Hicks, 1988c) [as *Stenhelia* (*Stenhelia*) *xylophila*] and *Laophonte lignosa*. The latter was placed in an incipient species group which included *L. confusa* Decho & Fleeger, 1986, *L. galapagoensis* Mielke, 1981 and *L. pseudooculata* Krishnaswamy, 1959, the latter of which incidentally was also found in floating logs infested by shipworms off the coast of Chennai, India (Krishnaswamy 1959).

Tegastes satyrus (Claus, 1860) was observed on the bacterial mats covering whale bones which had been recovered during a shallow-water whale-fall experiment (Willems *et al.* 2009). The bones originated from a Minke whale (*Balaenoptera acutorostrata* Lacépède, 1804) carcass sunk at continental shelf depth in the Kosterfjord, Sweden (see Dahlgren *et al.* 2006 for details) and were maintained at Tjärnö Marine Biological Laboratory in aquaria with chilled running seawater passing through sand-filters.

Recent studies have focused on deepwater harpacticoid communities associated with tubeworm and mussel aggregations around hydrocarbon seeps (Plum *et al.* 2015; Degen 2010; Degen *et al.* 2012) and hydrothermal vents (Gollner *et al.* 2006, 2007; Zekely *et al.* 2006; Degen 2010; Ivanenko *et al.* 2011, 2012; Degen *et al.* 2012), and with cold-water coral substrates (Gheerardyn *et al.* 2008b, 2009, 2010). Plum & Martínez Arbizu (2009) described a new tegastid species, *Smacigastes methanophilus*, associated with siboglinid tubeworm aggregations of *Escarpia* *laminata* Jones, 1985 and an undescribed species of the genus *Lamellibrachia* Webb, 1969 found at a natural oil seep in the Gulf of Mexico. Reviewing the rapidly increasing volume of literature on these biogenic substrata is beyond the scope of this paper and readers are encouraged to consult the publications listed above and the recent review by Buhl-Mortensen *et al.* (2010).

Accidental and doubtful records

Records from sponge hosts

Most harpacticoid copepods reported from sponges only display a rather loose form of association, the nature of which, in some cases, is still uncertain. Some of the species recorded below are potentially facultative associates but most are clearly accidental. The majority of bottom dwelling harpacticoid families have representatives that undergo active sustained vertical migration (Walters 1988), a behaviour that is linked to precopulatory mate guarding which takes place in the water column (Hicks 1988b). It is probable that their presence in sponge washings can often be attributed to contamination with sediment residues or overlying (hyperbenthic) water.

Thompson (1895) recorded *Diarthrodes pygmaeus* (Scott & Scott, 1895a) [as *Pseudowestwoodia pygmœa* Scott & Scott, 1895a], *Pseudodiosaccus propinquus* (Scott & Scott, 1893b) [as *Diosaccus propinquus* Scott & Scott, 1893b], *Ameira exigua* T. Scott, 1894b, *Sarsameira longiremis* (T. Scott, 1894b) [as *Ameira longiremis* T. Scott, 1894b], *Laophonte inopinata* T. Scott, 1892, and possibly a new *Laophonte* species in washings of sponges from Port Erin, Isle of Man. Additional sponge washings by Scott (1896b, 1896c) from the same area revealed *Eurycletodes* (*Oligocletodes*) *similis* (T. Scott, 1895) [as *Cletodes similis* T. Scott, 1895], *Laophonte serrata* [as *L. propinqua* Scott & Scott, 1895b] and *Asellopsis intermedia* (T. Scott, 1895) [as *Laophonte intermedia* T. Scott, 1895]. All these records were summarized by Moore (1937) and Bruce *et al.* (1963).

Thompson & Scott (1903) recovered *Longipedia coronata*, *Orthopsyllus linearis* (Claus, 1866) [as *Cletodes linearis* (Claus, 1866)], *Laophonte serrata* and *Applanola hirsuta* (Thompson & Scott, 1903) [as *Laophonte hirsuta* Thompson & Scott, 1903] from sponge washings in the Gulf of Mannar (Manaar), western Sri Lanka. Brian (1928a) reported *Robertgurneya similis* (A. Scott, 1896b) [as *Amphiascus tenax* var. *aegaea* Brian, 1928a] between sponge fragments collected off Rhodes. In another report, Brian (1928b) found *Paramphiascella vararensis* T. Scott, 1903b [as *Amphiascus affinis* Sars, 1906b] among pieces of sponge collected around the Dodecanese islands Rhodes, Astypalaia and Tilos; Lang (1948) doubted this identification and considered it a possible record of *Paramphiascella mediterranea* Lang, 1948.

Pearse (1934b) studied the associated fauna of five sponges at Dry Tortugas and found copepods in two of them. He recorded about 150 specimens of harpacticoids from a single loggerhead sponge *Spheciospongia vesparium* (Lamarck, 1815) (as *Speciospongia vespara* [*sic*]), including four or five species of the genus *Sarsamphiascus*, three species of the genus *Harpacticus*, two species of the genera *Ameira*, *Laophonte*, *Mesochra*, *Metis* Philippi, 1843 and *Thalestris* and one species of the genera *Dactylopusia* Norman, 1903, *Microthalestris* Sars, 1905b (= *Parastenhelia* Thompson & Scott, 1903), *Parathalestris*, *Parawestwoodia* Sharpe, 1910 (= *Diarthrodes*) and *Stenhelia* Boeck, 1865. He also recorded 15 *Metis ignea* Philippi, 1843 from the reef sponge *Spongia 'officinalis'* Linnaeus, 1759 (this is almost certainly *S.* (*Spongia*) *obliqua* Duchassaing & Michelotti, 1864 since *S. officinalis* does not occur in North America). All these copepods are typically found dwelling on seaweed and their association has to be considered accidental.

Krishnaswamy (1957) obtained a single female of *Ectinosoma melaniceps* and both adults and developmental stages of *Applanola hirsuta* from unidentified sponges collected in Sponge Bay in Krusadai Island, India.

Pesta (1959) listed various harpacticoids from biotic communities that included sponges belonging to the genera *Spongia* Linnaeus, 1759, *Halichondria* Fleming, 1828, *Ircinia* Nardo, 1833, *Aaptos* Gray, 1867 and *Penares* Gray, 1867, but this information is only indicative for the habitat where the copepods are suspected to be found and is no proof for a specific association.

Vervoort (1964) obtained four females of *Microlaophonte spongicola* Vervoort, 1964 (Laophontidae) from sponge washings on Ifaluk Atoll, Caroline Islands (Federated States of Micronesia) but this might be a chance association since the second species of this genus, *M. trisetosa* Boxshall, 1976, was described from laboratory cultures of the polychaete *Capitella* (as *Capitellides*) *giardi* (Mesnil, 1897) (Boxshall 1976). The species was subsequently recorded from mangrove debris on the Isle of Pines in Cuba (George in Boxshall (1976)) while Reid & Hribar (2006) discovered two females of *M. trisetosa* in a discarded car tire at Boot Key, Florida, possibly indicating that the species is common in the bottom sediments of mangrove forests in the Florida Keys. Vervoort's (1964) records of *Ameira longipes* Boeck, 1865, *Sarsamphiascus minutus* (Claus, 1863), *Laophonte dinocerata* Monard, 1926b, *Orthopsyllus dubius* Vervoort, 1964 and *Pseudocletopsyllus spiniger* Vervoort, 1964 from similar sponge washings on Ifaluk Atoll must also be treated as accidental.

TABLE 32. Harpacticoids recorded in washings of the demosponge *Semisuberites cribrosa* (Miklucho-Maclay, 1870) collected in Franz Josef Land (Chislenko 1977).

Family	Species
Ameiridae	*Ameira longipes* Boeck, 1865
	Ameira parascotti Chislenko, 1977
	Ameira parvula (Claus, 1866)
	Sarsameira major (Sars, 1907)
Ancorabolidae	*Laophontodes typicus* (T. Scott, 1894b)
Argestidae	*Eurycletodes* (*Oligocletodes*) *similis* (T. Scott, 1895)
Canthocamptidae	*Mesochra pygmaea* (Claus, 1863)
Dactylopusiidae	*Dactylopusia vulgaris* Sars, 1905b
Ectinosomatidae	*Ectinosoma melaniceps* Boeck, 1865
	Halectinosoma finmarchicum (T. Scott, 1903a)
Harpacticidae	*Harpacticus alevtinae* Chislenko, 1977
	Harpacticus uniremis Krøyer, 1842
	Zaus abbreviatus Sars, 1904b
Laophontidae	*Echinolaophonte horrida* (Norman, 1876)
	Laophonte aldonae Chislenko, 1977
	Laophonte inopinata T. Scott, 1892
	Paralaophonte hyperborea (Sars, 1909a)
	Paralaophonte innae Chislenko, 1977
	Paralaophonte macera (Sars, 1908b)
Miraciidae	*Amphiascoides golikovi* Chislenko, 1977
	Amphiascoides koltuni Chislenko, 1977
	Dactylopodamphiascopsis latifolius (Sars, 1909a)
	Paramphiascella hyperborea (T. Scott, 1903a)
	Robertsonia tenuis Brady, 1880
	Sarsamphiascus congener (Sars, 1909a)
	Stenhelia gibba Boeck, 1865
Parastenheliidae	*Parastenhelia spinosa* (Fischer, 1860)
Pseudotachidiidae	*Danielssenia typica* Boeck, 1873
Rhynchothalestridae	*Rhynchothalestris helgolandica* (Claus, 1863)
Thalestridae	*Amenophia peltata* Boeck, 1865

Yeatman (1970) obtained seven harpacticoid species from washings of the sponges *Halichondria* (*Halichondria*) *bowerbanki* Burton, 1930 and *Clathria* (*Clathria*) *prolifera* (Ellis & Solander, 1786), collected from rocks, pilings and bottom sand in Chesapeake Bay, Virginia: *Tisbe furcata*, *Harpacticus gracilis* Claus, 1863, *Dactylopusia tisboides* (Claus, 1863), *Amphiascopsis cinctus* (Claus, 1866), *Sarsamphiascus parvus* (Sars, 1906b), *Paralaophonte brevirostris* (Claus, 1863) and *P. congenera* (Sars, 1908b). Gut content analysis failed to identify any recognizable sponge cells, but indicated instead that all these copepods are either grazing on algae or scavenging and are not histophagic on their sponge hosts. Chislenko (1977) recorded thirty species of harpacticoid copepods from washings of the Arctic sponge *Semisuberites* [as *Phakellia*] *cribrosa* (Miklucho-Maclay, 1870) collected in Franz Josef Land, Arkhangelsk Oblast (Russia) (Table 32). It is clear, however, that a specific association of these species must remain in doubt.

Kim (2013) recorded *Laophonte dinocerata* in sponge washings from Jeju Island as well as *Paralaophonte obscura* Vervoort, 1962 in washings of various invertebrates including sponges, soft corals, sea pens, bryozoans and oysters.

The only freshwater record is that of Smirnov (1930) who found *Moraria mrazeki* T. Scott, 1903c in *Spongilla arctica* Annandale, 1915 in the Russian part of Lapland, but this species is normally free-living.

Records from cnidarian hosts

Although Sewell (1940) described *Eudactylopus fasciatus*, "from among weed growing on the stems of colonies of Stag's Horn Madrepore coral" in the Maldive Archipelago, it is unlikely that this species was actually associated with this coral (probably a species of *Acropora*) (Humes 1996). Noodt (1955) treated *E. fasciatus* as a subspecies of *E. robustus* (Claus, 1863). Bodin (1988, 1997) claimed that the males described by Sewell (1940) were not adult but this is incorrect since both adults and copepodid V stages were illustrated. Although most of Sewell's (1940) harpacticoids were recorded from weed washings, he also obtained three species from coral washings, *i.e. Amphiascopsis coralicola* (Sewell, 1940) (as *Amphiascus coralicola* Sewell, 1940) and *Metamphiascus hirsutus* (Thompson & Scott, 1903) from Henry Lawrence Island, Andaman Islands, and *Diosaccus hamiltoni* (Thompson & Scott, 1903) from Nancowry (Nankauri) Harbour, Nicobar Islands. None of these species is likely to be a genuine associate of corals.

Pesta's (1959) report on the harpacticoids from littoral caves in the Bay of Naples included several species (*Ectinosoma dentatum* Steuer, 1940, *E. melaniceps*, *Harpacticus gracilis*, *Tisbe furcata*, *T. gracilis*, *Tegastes* (?) *falcatus*, *Sarsamphiascus minutus*, *Metamphiascopsis hirsutus*, *Amphiascopsis cinctus*, *Paramphiascella vararensis*, *Ameira parvula* (Claus, 1866), *A. longipes* and *Paralaophonte brevirostris*) which had been obtained from biocoenoses characterized by the scleractinian coral genera *Astroides* Quoy & Gaimard, 1827 and *Leptopsammia* Milne Edwards & Haime, 1848b; however, there is no evidence for a close association between these species and their coral substrata.

Yeatman (1963) reported *Tisbe gracilis* on a dying moon jellyfish (*Aurelia aurita* (Linnaeus, 1758)) at Woods Hole, Massachusetts, but this species is generally regarded as a scavenger.

Hamond (1968) obtained *Marbefia carthyi* (Hamond, 1968) (as *Pseudonychocamptus carthyi* Hamond, 1968) in washings of intertidal colonies of the hydroid *Hartlaubella* (as *Laomedea*) *gelatinosa* (Pallas, 1766) (family Campanulariidae) attached to concrete lumps found under the Hunstanton pier, Norfolk (U.K.). The laophontid was subsequently found off St Mary's, Isles of Scilly in algal debris among bryozoans (*Cellaria* Ellis & Solander, 1786; *Lepralia* Johnston, 1838) and hydroids (*Sertularia* Linnaeus, 1758) and in fine sand with high silt content in Norfolk (Huys & Lee 2009). The only other record is that by Holmes & Minchin (1999) who collected a single female from a serpulid (*Serpula vermicularis* Linnaeus, 1767) reef in Killary Harbour, Co. Galway, Ireland. In a subsequent report on Norfolk harpacticoids, Hamond (1972) recorded several species in washings of another campanulariid hydroid, *Laomedea flexuosa* Alder, 1857, collected at Wells Rocks in Wells-next-the-Sea (Table 33). It is likely that the majority of these (mostly phytal) harpacticoids were associated with the bladder wrack *Fucus vesiculosus* to which the hydroids were attached than with the latter themselves.

Snelgrove & Lewis (1989) recorded a rich fauna of crustaceans, including many copepods, associated with the ramose hermatypic coral *Madracis myriaster* (Milne Edwards & Haime, 1850) [as *M. mirabilis* (Duchassaing & Michelotti, 1861)] along the west coast of Barbados where it forms dense beds on the outer edge of the fringing reefs. Among the 53 copepod species listed by the authors, harpacticoids were represented by members of the families Ectinosomatidae (*Pseudobradya* sp. and two unidentified species), Laophontidae (*Esola bulbifera*? (Norman, 1911), *Paralaophonte* sp.), Miraciidae (*Amphiascopsis* sp., *Sarsamphiascus paracaudaespinosus* (Roe, 1958), and one unidentified species), Peltidiidae (*Peltidium perturbatum* Geddes, 1968 and one unidentified species), Porcellidiidae (*Geddesia trisetosa* (Geddes, 1968)), Tetragonicipitidae (*Phyllopodopsyllus* sp.), Thalestridae (*Paramenophia platysoma* (Thompson & Scott, 1903), *Phyllothalestris mysis?* (Claus, 1863)) and Tisbidae (*Tisbe* sp.; ?*Tisbe* sp.). Some species were present in considerable numbers and *S. paracaudaespinosus* in particular occurred in high densities at every sampling site. This species was originally described from a littoral pool on Dalkey Island, Ireland (Roe 1958), casting some doubt on the accuracy of the identification of the Barbadian material. Both *P. perturbatum* and *G. trisetosa* were described from Ockelmann sledge samples collected near coral reef habitats in the Bahamas (Geddes 1968) but their association with scleractinian corals requires confirmation. Snelgrove & Lewis (1989) compared polluted with unpolluted coral beds and found that *Peltidium* sp., *G. trisetosa*, *Paralaophonte* sp. and *Amphiascopsis* sp. were most strongly influenced by eutrophication. Based on their pronounced density differences between sites they regarded them as possible indicator species of eutrophy.

TABLE 33. Harpacticoid species recorded in washings of invertebrates collected in Wells-next-the-Sea, Norfolk by Hamond (1972). *Bi* = *Bowerbankia imbricata* (Adams, 1798) (Bryozoa); *Ap* = *Anguinella palmata* van Beneden, 1845 (Bryozoa); *Lf* = *Laomedea flexuosa* Alder, 1857 (Hydrozoa).

Harpacticoid species	*Bi*	*Ap*	*Lf*
Longipedia weberi A. Scott, 1909	+		
Ectinosoma dentatum Steuer, 1940	+	+	
Ectinosoma melaniceps Boeck, 1865	+	+	
Ectinosoma normani Scott & Scott, 1896	+		
Halectinosoma gothiceps (Giesbrecht, 1881)	+		
Harpacticus littoralis Sars, 1910		+	+
Harpacticus uniremis Krøyer, 1842		+	
Zaus goodsiri Brady, 1880		+	
Tisbe furcata (Baird, 1837)	+		
Alteutha interrupta (Goodsir, 1845)	+	+	+
Parategastes sphaericus (Claus, 1863)		+	
Parathalestris clausii (Norman, 1869)			+
Phyllothalestris mysis (Claus, 1863)		+	
Ambunguipes rufocincta (Brady, 1880)		+	
Diarthrodes pygmaeus (Scott & Scott, 1895a)	+	+	+
Paradactylopodia brevicornis (Claus, 1866)		+	
Paradactylopodia latipes (Boeck, 1865)			+
Amonardia phyllopus (Sars, 1906a)		+	
Amphiascoides nanus (Sars, 1906c)	+	+	+
Diosaccus tenuicornis (Claus, 1863)		+	
Sarsamphiascus minutus (Claus, 1863)	+	+	+
Ameira scotti Sars, 1911	+	+	
Mesochra pygmaea (Claus, 1863)	+	+	+
Laophonte baltica Klie, 1929	+	+	+
Laophonte elongata Boeck, 1873	+	+	
Laophonte inopinata T. Scott, 1892	+		+
Heterolaophonte longisetigera (Klie, 1950)		+	+
Paralaophonte brevirostris (Claus, 1863)	+	+	+
Paronychocamptus curticaudatus (Boeck, 1865)	+		
Pseudonychocamptus koreni (Boeck, 1873)	+	+	+

Recently, Schizas *et al.* (2015) recorded a new species of *Longipedia* in washings of whole colonies of the scleractinian coral *Agaricia lamarcki* Milne Edwards & Haime, 1851 collected at 46–52 m depth near the shelf edge of south-western Puerto Rico. Since small sponges, algae and sediment were attached to the colonies, the level of association of *L. gonzalezi* Schizas, Dahms, Kangtia, Corgosinho & Galindo Estronza, 2015 with the coral could not be established. Nogueira *et al.* (2015) listed various harpacticoids associated with three species of *Mussismilia* Ortmann, 1890, exhibiting different growth morphologies, in two coral reefs of the Bahia State, Brazil. Except for their *Tegastes* sp. 1 it is unlikely that any of the other species (including three species of *Halectinosoma* Vervoort, 1962 and *Quinquelaophonte* Wells, Hicks & Coull, 1982, in addition to members of the Normanellidae, Euterpinidae, Pseudotachidiidae, Porcellidiidae and Canuelidae) are genuine associates of these Brazilian endemic scleractinian corals. An apparently diverse assemblage of unidentified harpacticoids was recorded in an earlier study of *Mussismilia hispida* (Verrill, 1901) off the coast of the State of São Paulo (Nogueira 2003).

Records from polychaete hosts

Brady (1880) reported *Tegastes falcatus* (as *Amymone sphærica*) amongst the filigree worm, *Filograna implexa* (family Serpulidae), dredged in 63 m off Robin Hood's Bay, Yorkshire. Similarly, Scott & Scott (1893b) collected *Amenophia peltata* Boeck, 1865 [as *Thalestris peltata* (Boeck, 1865)], *Mesocletodes monensis* Thompson, 1893 [as *Laophonte monensis* (Thompson, 1893)] and *Pseudocletodes vararensis* Scott & Scott, 1893b from washings of *F. implexa* brought up in a trawl net in the Moray Firth. An unusual association was reported by Dumitrescu & Marcus (1967) who observed a juvenile of the syllid *Salvatoria clavata* (Claparède, 1863) [as *Grubea clavata* (Claparède, 1863)] firmly attached to the dorsal surface of a male *Heterolaophonte stroemii paraminuta* Noodt, 1955. This isolated case is puzzling since neither of the two explanations (phoresis or ectoparasitism) offered by the authors appears credible.

Moore & O'Reilly (1993) found *Bulbamphiascus imus* (Brady, 1872) to be associated with the sedentary polychaete *Capitella capitata* (O. Fabricius, 1780) near the Garnock Valley sewer outfall in Irvine Bay, Scotland. In five cases *C. capitata* was found sharing its membranous tube with one to four copepods. Both copepodids and adults of *B. imus* were found between the worm and its tube at various points along the length of the host. Using a contingency table test Moore & O'Reilly (1993) inferred that *B. imus* makes active migrations along the *C. capitata* tubes. They also speculated that a commensal mode of life inside the polychaete tube may have preadapted *B. imus* to the low oxygen environment of organically enriched sediments. This is unlikely since *B. imus* is known to thrive in such habitats in the absence of an obligatory association with *C. capitata* tubes (*e.g.* Marcotte & Coull 1975; Moore & Pearson 1986).

Records from molluscan hosts

Thompson & Scott (1903) obtained a highly diverse copepod fauna from washings of pearl oysters (*Pinctada imbricata/fucata/radiata* species complex) in the Gulf of Mannar, between the south-eastern tip of India and the west coast of Sri Lanka. A total of 45 species (36 new), representing 14 families, were found in the oysters (Table 34). Similarly, Korringa (1951) recorded 27 species, representing 16 families, from oysters (*Ostrea edulis* Linnaeus, 1758) in the Oosterschelde estuary, The Netherlands, and particularly *Longipedia minor* Scott & Scott, 1893c appeared to be a regular inhabitant of the oyster shell habitat.

In a paper dealing with new parasitic copepods from the Naples region, Leigh-Sharpe (1936) reported a new harpacticoid, *Ismardis spartacus*, from the gonad and mantle cavity of the rayed Mediterranean limpet, *Patella caerulea* Linnaeus, 1758. Being unable to assign the new species to any of the existing harpacticoid families recognized at the time, he also proposed a new family Ismardidae without any further discussion of its relationships. Lang (1948), who changed the spelling to Ismardiidae, suspected that *I. spartacus* belonged to the Thalestridae but failed to make a firm recommendation for this assignment. He remarked on several deficiencies in Leigh-Sharpe's (1936) original description and consequently considered the Ismardidae as unidentifiable, relegating the family as *incertae sedis* in the Harpacticoida. Huys & Song (2004) re-examined the type material and concluded that the species should be allocated to the genus *Harpacticus*, and the genus *Ismardis* Leigh-Sharpe, 1936 and the family Ismardidae be relegated to junior synonyms of *Harpacticus* and Harpacticidae, respectively. *Harpacticus spartacus* (Leigh-Sharpe, 1936) is conspecific with the "schwächeren" form of the Mediterranean *H. nicaeensis* Claus, 1866. The reliable records (Claus 1866; Leigh-Sharpe 1936; Steuer 1937) suggest that *H. spartacus* is distributed throughout the Mediterranean from the French coast in the west to Egypt in the east and that its discovery in a patellid was merely a chance association or contamination (Leigh-Sharpe did not extract the copepods himself).

Pesta (1959) recorded several species from a littoral cave substratum dominated by mussels of the genus *Lithophaga* Röding, 1798 (as *Lithodomus* Cuvier, 1816), *i.e. Ectinosoma dentatum*, *Tisbe gracilis*, *Tegastes* (?) *neapolitanus* (Claus, 1863), *Sarsamphiascus minutus*, *Metamphiascopsis hirsutus*, *Paramphiascella vararensis*, *Emertonia coelebs* (Monard, 1935b) and *Paralaophonte brevirostris*. Many of these species were also found on coral-based substrata (see above) and have been recorded from a wide range of other habitats.

Bresciani & Lützen (1962) found *Thalestris longimana* abundantly in washings of the common whelk, *Buccinum undatum*, collected in Kristineberg Harbour, Sweden. They also recorded one female of *Stenhelia gibba* Boeck, 1865 inside the branchial cavity of the mytilid *Musculus subpictus* (Cantraine, 1835) (as *Modiolaria marmorata* (Forbes, 1838)) obtained near Flatholmen, Bohuslän.

TABLE 34. Harpacticoids recorded in washings of pearl oysters collected in Sri Lanka (Thompson & Scott 1903).

Name used by Thompson & Scott (1903)	Currently valid name	Family
Ameira minor Thompson & Scott, 1903	*Ameira minor* Thompson & Scott, 1903 [1]	Ameiridae
Ameira tenuipes Thompson & Scott, 1903	*Ameira tenuipes* Thompson & Scott, 1903 [1]	Ameiridae
Ceylonia aculeata Thompson & Scott, 1903	*Lourinia armata* (Claus, 1866)	Louriniidae
Cletodes linearis (Claus, 1866)	*Orthopsyllus linearis* (Claus, 1866)	Orthopsyllidae
Dactylopusia æmula Thompson & Scott, 1903	*Xouthous aemula* (Thompson & Scott, 1903)	Pseudotachidiidae
Dactylopusia ceylonica Thompson & Scott, 1903	*Amphiascopsis cinctus* (Claus, 1866)	Miraciidae
Dactylopusia dentata Thompson & Scott, 1903	*Diosaccus dentatus* (Thompson & Scott, 1903)	Miraciidae
Dactylopusia hamiltoni Thompson & Scott, 1903	*Diosaccus hamiltoni* (Thompson & Scott, 1903)	Miraciidae
Dactylopusia havelocki Thompson & Scott, 1903	*Amphiascopsis cinctus* (Claus, 1866)	Miraciidae
Dactylopusia hirsuta Thompson & Scott, 1903	*Metamphiascopsis hirsutus* (Thompson & Scott, 1903)	Miraciidae
Dactylopusia laticaudata Thompson & Scott, 1903	*Xouthous laticaudatus* (Thompson & Scott, 1903)	Pseudotachidiidae
Dactylopusia platysoma Thompson & Scott, 1903	*Paramenophia platysoma* (Thompson & Scott, 1903)	Thalestridae
Dactylopusia robusta Thompson & Scott, 1903	*Diosaccus robustus* (Thompson & Scott, 1903)	Miraciidae
Ectinosoma normani Scott & Scott, 1896	*Ectinosoma normani* Scott & Scott, 1896	Ectinosomatidae
Ectinosoma propinquum Scott & Scott, 1896	*Halectinosoma propinquum* (Scott & Scott, 1896)	Ectinosomatidae
Laophonte hirsuta Thompson & Scott, 1903	*Applanola hirsuta* (Thompson & Scott, 1903)	Laophontidae
Laophonte inornata A. Scott, 1902	*Laophonte inornata* A. Scott, 1902	Laophontidae
Laophonte serrata (Claus, 1863)	*Laophonte serrata* (Claus, 1863)	Laophontidae
Parastenhelia hornelli Thompson & Scott, 1903	*Parastenhelia hornelli* Thompson & Scott, 1903	Parastenheliidae
Parastenhelia similis Thompson & Scott, 1903	*Parastenhelia hornelli* Thompson & Scott, 1903	Parastenheliidae
Peltidium angulatum Thompson & Scott, 1903	*Peltidium angulatum* Thompson & Scott, 1903	Peltidiidae
Peltidium ovale Thompson & Scott, 1903	*Peltidium ovale* Thompson & Scott, 1903	Peltidiidae
Peltidium perplexum Thompson & Scott, 1903	*Peltidium perplexum* Thompson & Scott, 1903	Peltidiidae
Peltidium serratum Thompson & Scott, 1903	*Peltidium serratum* Thompson & Scott, 1903 [2]	Peltidiidae

……*continued on the next page*

TABLE 34. (Continued)

Name used by Thompson & Scott (1903)	Currently valid name	Family
Peltidium speciosum Thompson & Scott, 1903	*Peltidium speciosum* Thompson & Scott, 1903	Peltidiidae
Porcellidium acuticaudatum Thompson & Scott, 1903	*Kensakia acuticaudata* (Thompson & Scott, 1903)	Porcellidiidae
Porcellidium brevicaudatum Thompson & Scott, 1903	*Kioloaria brevicaudata* (Thompson & Scott, 1903) **comb. nov.**	Porcellidiidae
Porcellidium fimbriatum Claus, 1863	*Porcellidium fimbriatum* Claus, 1863	Porcellidiidae
Porcellidium ravanæ Thompson & Scott, 1903	*Ravania ravanae* (Thompson & Scott, 1903)	Porcellidiidae
Pseudothalestris imbricata (Brady, 1883)	*Diarthrodes ponticus* (Kričagin, 1873)	Dactylopusiidae
Stenhelia brevicornis Thompson & Scott, 1903	*Typhlamphiascus brevicornis* (Thompson & Scott, 1903)	Miraciidae
Stenhelia dentipes Thompson & Scott, 1903	*Typhlamphiascus dentipes* (Thompson & Scott, 1903)	Miraciidae
Stenhelia gracilicaudata Thompson & Scott, 1903	*Typhlamphiascus gracilicaudatus* (Thompson & Scott, 1903)	Miraciidae
Stenhelia knoxi Thompson & Scott, 1903	*Robertsonia knoxi* (Thompson & Scott, 1903)	Miraciidae
Stenhelia longicornis Thompson & Scott, 1903	*Stenhelia longicornis* Thompson & Scott, 1903 [3]	Miraciidae
Stenhelia minuta Thompson & Scott, 1903	*Sarsamphiascus angustipes* (Gurney, 1927)	Miraciidae
Stenhelia perplexa Thompson & Scott, 1903	*Stenhelia perplexa* Thompson & Scott, 1903 [4]	Miraciidae
Tegastes chalmersi Thompson & Scott, 1903	*Parategastes chalmersi* (Thompson & Scott, 1903)	Tegastidae
Tegastes donnani Thompson & Scott, 1903	*Syngastes donnani* (Thompson & Scott, 1903)	Tegastidae
Tegastes imthurni Thompson & Scott, 1903	*Syngastes imthurni* (Thompson & Scott, 1903)	Tegastidae
Tegastes nigrans (Scott & Scott, 1894)	*Parategastes sphaericus* (Claus, 1863)	Tegastidae
Tegastes twynami Thompson & Scott, 1903	*Syngastes twynami* (Thompson & Scott, 1903)	Tegastidae
Tetragoniceps dubia Thompson & Scott, 1903	*Tetragoniceps dubius* Thompson & Scott, 1903	Tetragonicipitidae
Tetragoniceps minor Thompson & Scott, 1903	*Phyllopodopsyllus minor* (Thompson & Scott, 1903)	Tetragonicipitidae
Thalestris mysis Claus, 1863	*Phyllothalestris mysis* (Claus, 1863)	Thalestridae

[1] *species incertae sedis* in *Ameira* Boeck, 1865; [2] *species incertae sedis* in *Peltidium* Philippi, 1839; [3] Miraciidae *incertae sedis*; [4] *species incertae sedis* in *Sarsamphiascus* Huys, 2009b.

Yeatman (1963) observed *Tisbe gracilis* feeding on mucous material in mussels at Woods Hole, Massachusetts. This species is a facultative scavenger which can occur in large numbers in marine aquaria. Willey (1930) collected it in "almost unlimited numbers in submerged bottles baited with fragments of fish and bivalve molluscs". Given the difficulties in separating members of the *T. gracilis* sibling species complex it is not certain whether Willey and Yeatman were dealing with the same species or with *T. gracilis* at all. Volkmann (1979b) suspected that both authors were dealing with either *T. biminiensis* Volkmann-Rocco, 1973 or *T. acanthifera* Vervoort, 1962. During experimental rearing of the common cuttlefish *Sepia officinalis* Linnaeus, 1758, Richards (1976) observed high numbers of *T. gracilis* which were primarily associated with and feeding on degenerative, abortive eggs of the cephalopod. Although this report is largely anecdotal, the presence of *T. gracilis* appeared to enhance the survival of eggs that were undergoing normal development by removing the mucilaginous decomposing matter. However, it would seem attraction to dead and decaying animal matter might be mediated rather more through the decomposing activities of microorganisms associated with this material than the material itself.

Branch (1975b) recorded an unidentified species of *Harpacticus* from three species of the limpet genus *Scutellastra* collected in Kommetjie and Kalk Bay, Cape Town (Western Cape Province, South Africa). *Harpacticus* sp. occurred in low numbers in *S. argenvillei*, *S. barbara* and *S. cochlear* (5, 9 and 7 individuals per 100 limpets per year, respectively). Branch (1975b) also mentioned a second copepod species, "*Pelteutha* sp.", in association with these hosts and a fourth limpet species, *S. longicosta* (9, 3, 9 and 1 individuals per 100 limpets.yr^{-1}, respectively). *Pelteutha* is probably a typographical error and in reality refers to "*Alteutha*" as there is no such genus in the Harpacticoida.

Francisco *et al.* (2010) observed *Bathylaophonte azorica* Lee & Huys, 1999 in the labial palp tissue of *Mytilus galloprovencialis* Lamarck, 1819 from the Aveiro Estuary in Portugal. The annual prevalence was low (0.3%) and the copepod apparently did not produce lesions. However, it is highly unlikely that their identification is correct since *B. azorica* was originally described from hydrothermal vents at 845–1715 m depth south-west of the Azores (Lee & Huys 1999). Their photograph (Fig. 4) showing short caudal rami (*vs* 3.8 times as long as wide in *B. azorica*) confirms that they were dealing with a different member of the Laophontidae.

Krapivin (2012) reported adults and nauplii of various copepods, mostly harpacticoids, from *Mytilus edulis* in the littoral and sublittoral zones of the Kandalaksha and Onega Gulfs of the White Sea. None of the benthic species was identified due to their low numbers but the pelagic *Microsetella norvegica* was observed inside the mussels at all of the 16 sampling sites. Up to 78.6 % of the sampled bivalves contained *M. norvegica* in their mantle cavity and around the labial palps but the intensity was generally low (1–12 ind.host^{-1}). *Microsetella norvegica* is a widely distributed holoplanktonic species that is known to feed on discarded and occupied larvacean houses (see above) or is otherwise associated with marine snow aggregates; its association with *M. edulis* is to be considered accidental.

Records from bryozoan hosts

Klie (1934) recorded numerous specimens of *Schizopera clandestina* Klie, 1923 (Miraciidae) in washings of encrusting colonies of the cheilostomatid bryozoan, *Einhornia crustulenta* (Pallas, 1766) [as *Membranipora crustulenta* Pallas, 1766] (family Electridae), collected from a pontoon in the old harbour of Bremerhaven. Schäfer (1936) considered *S. clandestina* a saprophyte which obtains nutrients from dead or decomposed organic matter. In Europe it typically inhabits brackish water habitats (*e.g.* Lang 1948; Hockin 1982; Little 1986) and its "association" with a bryozoan substratum is probably accidental (Soyer 1968). The species was also recorded from eastern Asia (Tai & Song 1979; Chang 2009a, 2009b, 2010) and Australia (Halse *et al.* 2002) but at least some of these records require confirmation (Karanovic & Cooper 2012).

Médioni & Soyer (1968: 334–341, Figs 10–13) described a new species *Idomene parasimulans* (Pseudotachidiidae) based on a single female obtained by scraping the surface of bryozoans and red algae in the vicinity of Banyuls-sur-Mer. The authors themselves admitted that the nature of its association with bryozoans was inconclusive. *Xouthous parasimulans* (Médioni & Soyer, 1968) (for new combination *cfr.* Huys 2009b) is closely related to the Antarctic *X. simulans* (Brady, 1910) from which it can be differentiated by the number of inner setae on P2 enp-2. The presence of only one inner seta on this segment is shared by *X. purpurocinctus* (provided Norman & Scott's (1906) observation is correct—see key to species on p. 575). *Xouthous parasimulans* has not been recorded again since its original description.

Hamond (1972) reported a large number of harpacticoids in washings of two ctenostomatid species, *Amathia* (as *Bowerbankia*) *imbricata* (Adams, 1798) (family Vesiculariidae) and *Anguinella palmata* van Beneden, 1845 (family Nolellidae), from Wells Rock in Wells-next-the-Sea, Norfolk, U.K (Table 33). *Longipedia minor* and *Pseudonychocamptus proximus* (Sars, 1908) had previously been recorded among *Amathia imbricata* in the Tamar River, southwest England (Marine Biological Association, 1931, 1957). Given their documented occurrence as free-living species in other habitats, it is unlikely that any of them are obligate associates of the bryozoans.

Records from crustacean hosts

Hendrickx & Fiers (2010) remarked that great care should be exercised in sampling crustacean hosts to avoid contamination by free-living copepods originating from the surrounding sediment. Lack of attention to this is the root cause why the literature is rife with antecdotal records of harpacticoids associated with decapods in particular.

(i) Gill chamber inhabitants

Krøyer (1864: 408–410; Plate XVII (fig. 9a–b)) encountered females of a new species, "*Canthocamptus? Hippolytes*", on the gills of a caridean shrimp which he cited as *Hippolyte aculeata* (O. Fabricius, 1780), a junior subjective synonym of the currently valid name, *Lebbeus groenlandicus* (J.C. Fabricius, 1775) (family Hippolytidae). Since Krøyer based his description on only a few individuals collected from an unspecified locality in western Greenland, he consequently left the generic assignment and symbiotic association unconfirmed. Hansen (1923) re-examined the type material and concluded that Krøyer's specimens belonged to the tisbid genus *Machairopus* Brady, 1883, currently a junior synonym of *Scutellidium*, and was probably close to the species previously described by Sars (1905a) as *Machairopus minutus*. Lang (1948) considered both species conspecific and introduced the valid combination, *Scutellidium hippolytes* (Krøyer, 1864). Both Hansen (1923) and Lang (1948) considered the association with the caridean host accidental since *S. hippolytes*, as well as its congeners (except for *S. patellarum*—see above), are predominant members of epiphytic faunal communities (*e.g.* Itô 1976b; Hicks 1977a; Gunnill 1982). Krøyer (1864) also described a second copepod, *Psilomallus hippolytes*, from the same hippolytid shrimp host but its affinities have remained obscure until now. Boxshall & Halsey (2004) considered *Psilomallus* a *genus inquirendum* without any further comment. The tagmosis indicates that *P. hippolytes* does not belong to the Copepoda, a supposition made earlier by Wilson (1920).

Chappuis (1926) recorded six species in washings of the gill chamber and carapace of the noble crayfish, *Astacus astacus* (as *A. fluviatilis*) from four localities in northern Germany (Dieksee, Schöhsee and the River Schwentine near Fegetasche in Schleswig-Holstein, and Pudagla on the island of Usedom in Mecklenburg-Vorpommern) but only *Nitocra hibernica* can be considered a facultative symbiont of the crayfish host. The other five species all belong to the Canthocamptidae and are commonly found free-living in a variety of freshwater habitats: *Attheyella (Attheyella) crassa* (Sars, 1863) (as *Canthocamptus crassus* Sars, 1863), *Attheyella (Mrazekiella) dentata* (Poggenpoll, 1874) [as *Canthocamptus northumbricus* Brady, 1880)], *A. (M.) trispinosa* (Brady, 1880) (as *Canthocamptus trispinosus* Brady, 1880), *Bryocamptus (Bryocamptus) minutus* (Claus, 1863) (as *Canthocamptus minutus* Claus, 1863) and *Canthocamptus staphylinus* (Jurine, 1820). Similar accidental records from crayfish hosts are those by Jakubisiak (1939) who recorded *A. (M.) trispinosa* [as *A. (Brehmiella) trispinosa* (Brady, 1880)] from *A. astacus* (as *A. fluviatilis*) in ponds around Wągrowiec, and *Halectinosoma abrau* (Krićagin, 1877) [as *Ectinosoma abrau* (Krićagin, 1877)] from the same host near Poznań, in western Poland.

Pearse (1934a) found *Amphiacus* [*sic*] *intermedius* (T. Scott, 1897) between the gill lamellae of *Microphrys bicornutus* (family Majidae) in Dry Tortugas, Florida, but stated that it was probably an accidental guest. Wilson (1935) referred to specimens collected by A.S. Pearse from the same locality and host and identified them as *Cancrincola jamaicensis*, however upon re-examination of this material Humes (1958) concluded that it did not belong to this genus. Williams (1965) cited Pearse's (1934a) report and misquoted the species as "*Anthiacus intermedius*". The currently valid name of this copepod is *Paramphiascella intermedia* (T. Scott, 1897) (family Miraciidae). It was originally described from Kilbrannan Sound, between the Kintyre Peninsula and the island of Arran, Scotland (T. Scott 1897) and typically lives in muddy substrata (Lang 1948). Pearse (1934a) observed three additional accidental guests in the gill chambers of decapods at Dry Tortugas: *Mesochra lilljeborgi* Boeck, 1865 on *Plagusia depressa* (J.C. Fabricius, 1775) (family Plagusidae), *Tegastes* (as *Tergastes* [*sic*]) *calcaratus* Sars, 1910 on *Ocypode quadrata* (J.C. Fabricius, 1787) [as *Ocypode albicans* Bosc, 1802] (family Ocypodidae), and an unidentified copepod on *Moreiradromia antillensis* (Stimpson, 1858) [as *Dromidia antillensis* Stimpson, 1858] (family Dromiidae).

Yeatman (1963) recorded *Tisbe gracilis* from the gill chamber of spiny lobsters at Woods Hole, Massachusetts.

Dvoretsky (2012) reported *Halectinosoma* (as *Ectinosoma*) *neglectum* (Sars, 1904a), *Harpacticus uniremis* Krøyer, 1842, *Tisbe furcata* and *Zaus abbreviatus* Sars, 1904b from the great spider crab *Hyas araneus* (Linnaeus, 1758) (Brachyura: Oregoniidae) collected in Dalnezelenetskaya Bay, a semi-enclosed gulf in eastern Murman. Although *H. uniremis* showed the highest prevalence (39.6%; $n = 48$), both *T. furcata* (79.3 ± 18.3 ind.host^{-1}) and *H. neglectum* (44.5 ± 25.5 ind.host^{-1}) were found to have a higher mean intensity. Over 98% of all specimens were recorded on the gills with occasional copepods present on the carapace, limbs and abdomen. There is little doubt that these associations are accidental.

In their study of copepods associated with the red king crab *Paralithodes camtschaticus* (Anomura: Lithodidae) in Dalnezelenetskaya Bay (Barents Sea), Dvoretsky & Dvoretsky (2013) recorded several harpacticoid species that displayed low prevalence and intensity levels, including *Microsetella norvegica*, *Ectinosoma normani*, *Zaus abbreviatus* and *Dactylopusia vulgaris*. The first three species were invariably found attached to the gills while *D. vulgaris* occurred primarily on the limbs, carapace and mouthparts. All four species were considered accidental associates. Conversely, *Harpacticus uniremis* was classified as a commensal due to its higher prevalence (24.1–24.7%) and mean intensity (6 (range 1–21) to 12.3 (1–21) ind.host^{-1} over a 2-year period). Prevalence and mean intensity both increased with crab size. There were no significant differences between the intensities of *H. uniremis* on crabs with new and old shells. Over 97% of all specimens recorded were found on the gills; occasional individuals also occurred on the mouthparts and the limbs. The species is considered fairly eurytopic, being found among algae or in sandy and muddy sediments along the coasts of north-west Europe and throughout the sub-Arctic and to the boreal Pacific (Huys *et al.* 1996). Its association with *P. camtschaticus* should be regarded as accidental.

(ii) External epibionts

Epibiosis is a common facultative association in marine environments where wave turbulence has caused many lightweight organisms to evolve some adaptations for attachment to solid, relatively stable surfaces provided by other living organisms. The calcified body surface or bristly carapace of certain crabs and lobsters appears to be a particularly suitable habitat for such epibionts.

Scott (1902) reported *Heterolaophonte stroemii* (Baird, 1837) (as *Laophonte curticauda* Boeck, 1865) from the pleopods of the common shore crab *Carcinus maenas* (Linnaeus, 1758) obtained in Scottish waters and noted that it was found on almost every crab examined. Even though the nature of the association remains to be proven, the potential of *C. maenas*—being listed among the 100 "world's worst alien invasive species" (Global Invasive Species Database 2014)—to introduce its associated fauna into other regions of the world should not be underestimated. The shore crab is native to the north-east Atlantic Ocean and Baltic Sea, but has colonised similar habitats in Australia, South Africa, South America and both Atlantic and Pacific coasts of North America. Interestingly, *H. stroemii* assumes a boreo-mediterranean distribution in Europe (*e.g.* Lang 1948; Alper *et al.* 2010) but has been recorded from three sites near Seattle (Chappuis 1958), the Gulf of Saint Lawrence in Canada (Brunel *et al.* 1998), various localities in the Woods Hole region (Wilson 1932) and Tampa Bay in Florida (Bell *et al.* 1988). Recently, the species was also found in the setal mats on the claws of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards, 1853a) in the River Thames (R. Huys, unpubl. data). Normant *et al.* (2007) reported that 86.8% of the crustacean epibionts found in the mittens of *E. sinensis* from the Gulf of Gdańsk (Poland) belonged to the Harpacticoida; however, no species identifications were provided. Finally, in a brief report on marine harpacticoids of Iceland, Apostolov (2014) recently stated that *H. stroemii* "…attended the crab *Carcinus maenas*"; it is unclear whether this statement refers to his own material (only two females were examined) or Scott's (1902) observation.

Scott (1902) recorded *Laophonte setosa* Boeck, 1865 (as *Laophonte similis* Claus, 1866) from the pleopods of the great spider crab *Hyas araneus* in the Bay of Nigg, Aberdeen (Scotland). Lang (1948) considered this record accidental.

Jakubisiak (1932) obtained 28 species, representing 19 genera and 12 families, from washings of spider crabs (*Maja brachydactyla*) which had mostly been collected from Roscoff, Brittany. Except for the laophontids, *Hemilaophonte janinae* and *Paralaophonte royi*, the remaining species are merely accidental records: *Longipedia minor*, *Canuella perplexa*, *Ectinosoma melaniceps*, *E. normani*, *Harpacticus gracilis*, *H. littoralis* Sars, 1910, *Tisbe furcata*, *T. longicornis* (Scott & Scott, 1895b), *T. elegantula* (Sars, 1905a), *Ambunguipes rufocincta* (Norman in Brady, 1880), *Dactylopusia tisboides*, *D. vulgaris*, *Diarthrodes minutus*, *D. pygmaeus*, *Diosaccus tenuicornis* (Claus, 1863), *Amonardia phyllopus* (Sars, 1906b), *Amphiascoides debilis* (Giesbrecht, 1881), *Paramphiascella hispida* (Brady, 1880), *Sarsamphiascus parvus*, *Ameira parvula*, *Mesochra lilljeborgi*, *Heterolaophonte stroemii*, *Laophonte cornuta* Philippi, 1840, *L. setosa*, *Paralaophonte brevirostris*, and *Laophontodes typicus* (T. Scott, 1894b). Ingle (1983, 1996) also listed *Diarthrodes nobilis* and erroneously attributed this record to Jakubisiak (1932) instead of the author's (1936) publication. Monard (1935b) examined spider crabs (*M. brachydactyla*) kept in the aquarium of the biological station in Roscoff and found *Amonardia phyllopus*, *Parathalestris clausii*, *Laophonte setosa* and *Laophontodes typicus*. From similar washings of the mediterranean spider crab, *Maja squinado*, Fiers (1992a) obtained several new species of the genera *Coullia* and *Laophonte*, amongst other members of the Laophontidae which are not considered as typical associates (*Laophonte cornuta*, *L. elongata*, *Pseudonychocamptus proximus*). Feltkamp (1960) observed *Pseudobradya parvula* Sars, 1920a and *Paralaophonte brevirostris* on the gills of *M. squinado* and the xanthid *Xantho pilipes* in Banyuls-sur-Mer.

Stephensen (1936) found a few specimens of *Dactylopusia neglecta* Sars, 1905b (Dactylopusiidae) and three different species of *Tisbe* (*T. furcata*, *T. gracilis* and *T.* sp.) on the gribble, *Limnoria lignorum*, near Trondheim; at least some of these records are undoubtedly accidental.

Bassamakov (1973) recorded three accidental canthocamptid guests on the carapace of *A. astacus* from the Kolarov (*C. staphylinus*, *Bryocamptus (Rheocamptus) tatrensis* (Minkiewicz, 1916)) and Dospat Rivers (*Attheyella (Attheyella) wierzejskii* (Mrázek, 1893)) in Bulgaria. A similar study of the epibiont copepod fauna of *A. leptodactylus* carapace washings revealed *C. staphylinus*, *A. (A.) crassa* and *Onychocamptus mohammed* (Blanchard & Richard, 1891) on crayfishes from Lake Shabla in north-eastern Bulgaria (Bassamakov 1975).

Chislenko (1977) recorded single female specimens of *Paralaophonte hyperborea* (Sars, 1909a) in two Arctic trawl samples from Frans Josef Land which contained *Lebbeus polaris* (Sabine, 1824) (family Hippolytidae) and *Sabinea septemcarinata* (Sabine, 1824) (family Crangonidae). It is not clear whether the laophontid was recovered from the washings of the decapods or the sediment associated with them.

Fiers (1991) recorded undescribed *Coullia* species from washings of unidentified decapods collected in the Eastern Pacific. Apostolov (1996) recorded seven harpacticoid species from carapace washings of the grapsid *Pachygrapsus marmoratus* (J.C. Fabricius, 1787) and the eriphiid *Eriphia verrucosa* (as *Eryphia spinifrons* (Herbst, 1785) [*sic*] = *Eriphia spinifrons* Rathke, 1837) collected from the Bulgarian Black Sea coast: *Ameira parvula*, *Dactylopusia tisboides*, *Harpacticus littoralis*, *Heterolaophonte stroemii*, *Laophonte setosa*, *Parathalestris harpactoides* (Claus, 1863) and *Delavalia elisabethae* Por, 1960. All these species are typically free-living and their presence on the decapods must be considered accidental.

Kim (2013) obtained two members of the genus *Laophonte*, *L. inopinata* and *L. inornata* A. Scott, 1902 from barnacle washings off Jeju Island, Korea.

(iii) Hermit crab washings

Samuelsen (1970) observed *Thalestris gibba* in the upper whorls of the gastropod shells inhabited by the hermit crab *Pagurus cuanensis* at both Hillersholmen and Liholmane in Raunefjorden, Norway. It is questionable whether this identification is correct since *T. gibba* is a free-living species, often associated with algae, and *P. cuanensis* is a confirmed host for *Sunaristes paguri*.

Hicks (1989) examined a female specimen labelled *Dactylopodella flava* from the late R. Hamond's offshore station W.34 in Norfolk, England, stating that it was collected at 36 m depth in washings of *Buccinum* shells. It is unknown whether the gastropod shells were inhabited by *Pagurus bernhardus* and thus *D. flava* is another associate of the hermit crab host.

According to Kim (2013) *Sarsamphiascus polaris* (Sars, 1909a) and *Amphiascopsis southgeorgiensis* (Lang, 1936a) are occasionally found in washings of hermit crabs in Korea.

Records from echinoderm hosts

Barel & Kramers (1977) listed six harpacticoid species (*Euterpina acutifrons* (Dana, 1847) was erroneously classified as a calanoid) in their survey of echinoderm associates of the north-eastern Atlantic but all of them are based on previously published accidental records.

(i) Records from sea urchins. Willey (1930) recorded a number of harpacticoids among the spines and the maskweeds or litter covering the test of *Arbacia* sp. in Bermuda, including *Tisbe bermudensis* Willey, 1930, *Scutellidium ligusticum* (Brian, 1920) [as *Tisbe ligustica* Brian, 1920], *Robertgurneya similis* [as *Amphiascus erythræus* (A. Scott, 1902)], *Paramphiascella robinsonii* (A. Scott, 1902) [as *Amphiascus robinsoni* (A. Scott, 1902)], *Lourinia armata* (Claus, 1866) [as *Ceyloniella armata* (Claus, 1866)], *Laophonte cornuta* and *Paralaophontodes echinatus* (Willey, 1930) [as *Laophonte echinata* Willey, 1930]. It is likely that the host urchin was misidentified since *Arbacia punctulata* (Lamarck, 1816b) does not occur in Bermuda; Willey (1930) was probably dealing with a species of *Lytechinus* Agassiz, 1863 instead (Volkmann 1979a).

Noodt (1954a) recorded 57 individuals of *Tisbe gracilis* and three specimens of a new species, *Amonardia pentasetosa* Noodt, 1954a, between the spines of the sea urchin *Loxechinus albus* from the Chilean coast. Both species are to be considered accidental records.

Volkmann-Rocco (1972a) noted that *Tisbe* species became particularly abundant in the running sea water system of the Duke University Marine Laboratory when sea urchins (*Arbacia* spp.) or blue crabs (*Callinectes sapidus* Rathbun, 1896) were introduced into the aquaria, suggesting a potentially loose or temporary association between these hosts and the copepods. *Tisbe biminiensis* was recovered from the test of a spatangoid sea urchin (*Meoma* Gray, 1851) by Volkmann (1979b). Holmes (1996) obtained *Tisbe angusta* (Sars, 1905a) in washings of the European edible sea urchin, *Echinus esculentus* Linnaeus, 1758, from Lough Hyne, Co. Cork, Ireland, but believed that the copepods were more closely associated with the green algae (*Ulva* sp.) with which the echinoids had covered themselves rather than the urchins themselves.

Bell & McClintock (1982) recorded high densities of harpacticoids on the tests of two echinoids, *Arbacia punctulata* and *Lytechinus variegatus* (Lamarck, 1816b), in Tampa Bay, Florida. The copepods on the two sea urchins overlapped broadly in species composition but relative abundance differed. Ten species representing seven families were encountered but it is doubtful if the “association” goes beyond mere external utilization of the echinoid body surface. *Harpacticus* sp. A. was the dominant copepod on *L. variegatus*, being represented by ovigerous females, copulating males and stage V copepodids, while an undescribed miraciid ranked first on *A. punctulata*. At least some of the dominant species were also found in other habitats in Tampa Bay, including the imbricate, shell-sediment matrix of the epibenthic tube-caps produced by the onuphid polychaete *Diopatra cuprea* (Bosc, 1802).

(ii) Records from sea cucumbers. Edwards (1891) described three new species, *Dactylopus bahamensis*, *Esola longicauda* and *Abacola holothuriae*, which he found embedded in mucus inside the body cavity of *Actinopyga agassizii* (Selenka, 1867) (as *Mülleria Agassizii*) (family Holothuriidae) from Great Abaco Island in the northern Bahamas. The first two species were considered free-living while the third was ranked as a semi-parasite and placed in its own family Abacolidae. Richard (1892) also suggested a semi-parasitic life style but recognized *Abacola* Edwards, 1891 as a junior subjective synonym of *Ilyopsyllus* Brady & Robertson, 1873. Scott (1909) proposed a new family Ilyopsyllidae to accommodate *Ilyopsyllus* but Sars (1910) remarked that both taxon names were preoccupied by the family-group name Metinae and its type genus *Metis*, respectively, both of which having previously been proposed by Boeck (1873). The current records of *Metis holothuriae* suggest a cosmopolitan distribution (*e.g.* Lang 1948) but the large amount of variation that has been reported for this species appears to reinforce the existence of a species complex (Mielke 1989; Wells 2007). None of these records was associated with a holothurian, supporting the notion that Edwards’ (1891) observation must have been accidental (Humes 1957b). Lang (1948: 1586) did not include this species in his list of symbiotic harpacticoids. Violante-Huerta & Suárez-Morales (2016) reported it as an opportunistic epibiont on captive Caribbean manatees (*Trichechus manatus manatus*) in Mexico (see below). It should also be noted that Edwards’ description of

Dactylopus bahamensis remained unnoticed by 20th-century workers, including Lang (1948, 1965), and the species does not feature in the Caribbean copepod checklists of Reid (1990) and Suárez-Morales *et al.* (2006) or the tabular keys of Wells (2007). Edwards' (1891) illustrations are somewhat difficult to interpret; however, his figure of leg 1 indicates that *D. bahamensis* cannot be included in the genus *Dactylopusia*. It is here tentatively considered as *species incertae sedis* in the Dactylopusiidae.

Monticelli (1892) reported *Tisbe furcata* from the body cavity of *Ocnus planci* (Brandt, 1835) [as *Cucumaria planci* (Brandt, 1835)] (family Cucumariidae) in the Gulf of Naples, however, in the absence of any illustrations it is impossible to corroborate this record. Since the species has yet to recorded from the Mediterranean (Volkmann-Rocco 1971) the possibility remains that Monticelli's material may actually have been *Tisbe cucumariae* Humes, 1957b (Humes 1980).

Humes (1957b) described two new species of *Tisbe* from washings of holothurian hosts in the western Mediterranean. Both species are now known to be widely distributed and are frequently collected in benthic samples independent of any associated host.

Tisbe cucumariae **Humes, 1957b**

Humes (1957b) recovered 12 females and 17 males from the washings of an unspecified number of individuals of *Ocnus planci* (as *Cucumaria planci*) in the vicinity of Banyuls-sur-Mer. According to Volkmann (1979a, 1979b) the species is only a "facultative parasite" or a scavenger which is often associated with tunicates and molluscs (Fava & Volkmann 1975) but also found free-living among algae. Pesta (1959) recorded it from several substrata covered with sponges, scleractinian corals and barnacles. The confirmed records suggest a wide distribution in the warm-temperate regions of the Northern Hemisphere, including the Mediterranean, both seaboards of the U.S.A., Bermuda and the Korean peninsula (Volkmann-Rocco 1972a, Volkmann 1979a, 1979b). The species has often been confused with other members of the *T. gracilis* species group, in particular *T. gracilis* itself (*e.g.* Battaglia 1957, 1958; Battaglia & Malesani 1959, 1962; Coull 1970; Coull & Herman 1970, Marcotte & Coull 1975; Pesta 1959). Volkmann (1974) examined the modified spine of the male leg 2 endopod using scanning electron microscopy.

OD: Humes (1957b): 16–20; Plates IV–V (Figs 32–53).

AD: Pesta (1959—as *T. gracilis*): 106–108; Figs 24–28. Vilela (1968): 42–44; Plate XVI. Volkmann-Rocco (1973): 77, 84, 90; Figs 2B, 8B. Volkmann (1974): 322, 324; Fig. 4f–h. Volkmann (1979b): 170–172, 248–251, 262–263, 268–271; Figs 19B, 20B, 26B, 29B, 30B.

TL: France, Languedoc-Roussillon region, Pyrénées-Orientales, Banyuls-sur-Mer; washings of *Ocnus planci* (Brandt, 1835) (Cucumariidae).

BL: 828–876 µm (♀), 828–876 µm (♂) [Humes 1957b]; 690 µm (♀) [Vilela 1968]; 850–1,020 µm (♀), 820–88 µm (♂) [Volkmann 1979b]; 840 µm (♀), 840 µm (♂) [Humes 1980].

Tisbe holothuriae **Humes, 1957b**

Humes (1957b) obtained over 1,000 individuals from washings of the common holothurian, *Holothuria* (*Holothuria*) *stellati* Delle Chiaje, 1824 (family Holothuriidae) in the vicinity of Banyuls-sur-Mer. The species was originally reported from the anterior part of the digestive tube, but this was later corrected to the surface of the integument by Changeux (1961: 18). Similar numbers were recorded in washings of about 20 individuals of *H. stellati* and the co-existing *H.* (*H.*) *tubulosa*. All developmental stages, including ovigerous females and nauplii, were found swarming over the body surface and among the podia and the dorsal papillae, indicating that *T. holothuriae* is capable of completing its life cycle on these hosts. The association is not obligatory for development, however, since *T. holothuriae* may complete its development free among algae or in culture in the laboratory (Volkmann-Rocco 1971).

Ovigerous females from Banyuls-sur-Mer have a dorsoventrally flattened egg sac which extends to the caudal rami and contains about 90 eggs (Humes 1957b); Uhlig & Noodt (1966) found fewer eggs (45–65; up to 80 under optimal rearing conditions) in populations from Helgoland. Changeux (1961) observed fragments of diatom tests and calcified host ossicles in the faecal pellets, suggesting that *T. holothuriae* feeds on the host integument itself as well as bacteria and diatoms inhabiting its surface. The species was never found on *Holothuria* (*Panningothuria*) *forskali* Delle Chiaje, 1824. Changeux (1961) speculated that either *H. forskali* produced a chemical substance that dissuades copepods from approaching or settling, or that the absence of suitable food sources such as diatoms on its body surface makes it a less attractive host.

Tisbe holothuriae belongs to a complex of sibling species which can only be distinguished through careful comparison of the males (Volkmann 1975; Volkmann-Rocco 1971, 1972b). Not surprisingly, it has been misidentified on numerous occasions and, in some cases, has been described under different names. *Tisbe helgolandica* Uhlig & Noodt, 1966 from Helgoland (Germany) and *T. lancii* Marcotte, 1974 from the Bay of Piran, northern Adriatic are junior synonyms of *T. holothuriae* (Volkmann-Rocco 1971). In addition, both *T. eurypleura* Pinkster, 1968 from Marseille and *T. parviseta* Pinkster, 1968 from Wiméreux are potential (Volkmann-Rocco 1972b; Volkmann 1974) or actual (Volkmann 1979b) synonyms. Populations from the U.K. (Plymouth), France (Banyuls-sur-Mer, Sigean), Italy (Venice Lagoon, Gargano) and Bermuda, previously identified as *T. furcata* by Corkett (1968), Coull (1970), Coull & Herman (1970), and Battaglia and co-workers (*e.g.* Battaglia 1962; Battaglia & D'Avella 1964; Battaglia & Parise 1968; Parise & Lazzaretto 1967), in reality refer to *T. holothuriae* (Volkmann 1979a; Volkmann-Rocco 1971). The species often occurs sympatrically with *T. battagliai* Volkmann-Rocco, 1972b in phytal habitats in the Mediterranean. Volkmann-Rocco (1972b) summarized confirmed distribution records and subsequently considered it cosmopolitan (Volkmann 1979a).

The species is characterized by an almost total absence of barriers to gene flow. Transatlantic crosses between populations from North Carolina (Beaufort) and Helgoland showed complete interfecundity. Certain Atlantic and mediterranean populations are not only interfertile, but even produce F_1 hybrids which are heterotic (Battaglia & Volkmann-Rocco 1973). Hybrid offspring of *T. holothuriae* populations from Plymouth and Lake Varano (southern Italy) are perfectly viable and significantly more tolerant of osmotic shock than are the parental populations (Battaglia & D'Avella 1964—originally identified as *T. furcata* but see Volkmann-Rocco (1971)).

OD: Humes (1957b): 10–15; Plates I–III (Figs 1–31).

AD: Petkovski (1964b): 8, 10–11; Abb. 22–25. Uhlig & Noodt (1966—as *T. helgolandica*): 134–137; Plates 1–2 (Figs 1–8). Marcotte (1974—as *T. lancii*): 66–72; Figs 2–4. Volkmann (1974): 320–322; Figs 1–2.

TL: France, Languedoc-Roussillon region, Pyrénées-Orientales, Banyuls-sur-Mer; washings of *Holothuria* (*Holothuria*) *stellati* Delle Chiaje, 1824 (Holothuriidae). Changeux (1961: 18) pointed out in a footnote that the copepods were found on the integument of the host and not in the anterior part of the oesophagus as Humes (1957b) had stated.

BL: 852–1,020 µm (♀), 612–672 µm (♂) [Humes 1957b]; 830 µm (♀), 560 µm (♂) [Uhlig & Noodt 1966]; 740 µm (♀), 540 µm (♂) [Marcotte 1974]; 930 µm (♀), 640 µm (♂) [Humes 1980].

(iii) Records from brittle stars. Bresciani & Lützen (1962) recorded three females and one male of *Thalestris longimana* from two ophiuroidean hosts, *Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789) and *Ophiopholis aculeata* (Linnaeus, 1767), collected in Humlesäcken on the west coast of Sweden. Gorzula (1978) observed *Tisbe furcata*, *T. gracilis*, *T. tenera* (Sars, 1905a), *Teissierella* (?) sp. (or *Monardius*?) and an unidentified tegastid on the black brittle star, *Ophiocomina nigra* (Abildgaard in Müller, 1789), in the Firth of Clyde, Scotland. All species occurred in very low numbers (totaling 19 out of 3,555 copepod specimens examined) and are to be treated as accidental records.

(iv) Records from starfishes. Bresciani & Lützen (1962) reported one female and one male of *Parathalestris harpactoides* and one female of *Stenhelia gibba* from $MgCl_2$ washings of *Crossaster papposus* (Linnaeus, 1767) (as *Solaster papposus* Müller & Troschel, 1842) collected from Stenskärsrännan in the Gullmarsfjorden area, Sweden. They also recorded 12 individuals of the planktonic harpacticoid *Euterpina acutifrons* from the slimy covering of a single *Astropecten irregularis* (Pennant, 1777) near the island of Bonden. All these records are unquestionably accidental.

Records from ascidian hosts

Aurivillius (1882) frequently encountered *Tisbe furcata* inside *Ascidiella aspersa* (O.F. Müller, 1776) [as *Phallusia patula* (O.F. Müller, 1776)] (family Ascidiidae) off the Bohuslän coast of Sweden. In later reports (Aurivillius 1885a, 1885b) he also reported it inside the branchial cavity of *Molgula manhattensis* (De Kay, 1843) (as *M. ampulloides* van Beneden, 1846) (family Molgulidae) in the Kara and Laptev Seas (Arctic Ocean).

Seiwell (1928) described a new species, *Tisbe wilsoni*, from the branchial chamber of *Aplidium stellatum* collected in the Woods Hole area. His description lacks sufficient detail to confirm the distinctiveness of the species and his illustration of the female leg 2 in reality refers to leg 1 of the cohabiting *Paramphiascella commensalis* (*cf.* Lang 1948: 366). Bowman (1962) re-examined the male holotype and noted that the sexual dimorphism on leg 2 had been overlooked, being very similar to that in *T. gracilis*. Volkmann (1979b) examined the female allotype and confirmed it as belonging to *T. gracilis*, stating that Seiwell's drawings seem to represent a copepodid V female rather than an adult. *Tisbe wilsoni* is no longer recognized as a distinct species and considered a junior synonym of *T. gracilis* (Coull 1977; Wells 2007). The latter species exhibits a tendency towards a rather loose form of association with other invertebrates (*e.g.* Stephensen 1936; Noodt 1954a; Yeatman 1936; Richards 1976) but there is no evidence that these "symbiotic" records are genuine. Pending direct observation its association with *A. stellatum* should also be categorized as accidental.

Stephensen (1932) recorded a single ovigerous female of "*Amphiascus* (*nanus* G.O. Sars?)" in a jar containing *Dendrodoa pulchella* (Rathke, 1806). Although Stephensen's identification of the species, currently known as *Amphiascoides nanus* (Sars, 1906c), needs confirmation, the association with the styelid is undoubtedly accidental.

Monard (1935b) observed *Paramphiascopsis longirostris* (Claus, 1863), *Ameiropsis brevicornis* Sars, 1907, *Laophonte elongata* Boeck, 1873 and *L. dominicalis* Monard, 1935b on the tunic of *Ascidia mentula* O.F. Müller, 1776 (family Ascidiidae) in the aquarium tanks of the marine biological station of Roscoff. Given the many records from a variety of sediment substrata of the first three species, their occurrence on the tunicate is almost certainly accidental (Lang 1948). *Laophonte dominicalis* has not been reported again since its original description; it was found externally on the test and not inside the ascidian as claimed by Lang (1948).

Krishnaswamy (1957) recorded ten harpacticoid species from the compound ascidian, *Polyclinum indicum* Sebastian, 1952, collected in Chennai Port, India, including *Echinolaophonte armiger* (Gurney, 1927), *Ectinosoma melaniceps*, *Melima indica* (Krishnaswamy, 1957) (as *Stenhelia* (*Delavalia*) *indica*), *Sarsamphiascus parvus* (as *Mesamphiascus parvus*), *Tisbe furcata* and *T. gracilis*.

Vervoort (1962) reported on three calanoid and 13 harpacticoid species obtained together with ascidiaceans at Nouméa, New Caledonia. However, he clarified that the copepods were mainly obtained from the bottom of collecting bottles with tunicates and that there was no definite information concerning the conditions under which the copepods actually lived. Except for *Paramphiascella pacifica* (see above) there is no reason to suggest that the remaining species are actually associated with ascidiaceans. Volkmann (1979b) stated that *Tisbe acanthifera* is "… associated with ascidians, but also on algae (*e.g. Cymopolia*) and muddy bottom".

Holmes (1980) found *Peltidium purpureum* Philippi, 1839 in the solitary tunicate *Ascidiella aspersa* (O.F. Müller, 1776) in Lough Ine (Hyne), a sea lough in West Cork, Ireland. Although *A. aspersa* is known to serve as host to no less than 14 cyclopoid species (Gotto 2004), the association with *P. purpureum*, a species that typically lives on intertidal and shallow subtidal algae (Huys *et al.* 1996), is clearly accidental.

Marchenkov (1997, 1999) recorded two undescribed species of unknown affinity ("Harpacticoida fam. gen. sp. 1 and 2") from two ascidians in the White Sea. Both harpacticoid species were found in the branchial sac of the solitary ascidiacean *Molgula retortiformis* Verrill, 1871 in the Kandalaksha Gulf and the Onega Gulf. The first species was also obtained from the tunic of the colonial species *Synoicum pulmonaria* (Ellis & Solander, 1786) (Polyclinidae). It is likely that these are accidental records since at least one of these species (sp. 1) was also recorded from the mantle cavity of two bivalves in the same sampling areas (see above).

Records from hemichordate hosts

Holland *et al.* (2005) observed two intact, possibly commensal, harpacticoid copepods in the post-hepatic intestine of a deepwater enteropneust. The host, an adult female of *Torquarator bullocki* Holland, Clague, Gordon, Gebruk, Pawson & Vecchione, 2005, was collected at a depth of 1,901 m in the northeastern Pacific (42.58°N, 126.78°W). Unfortunately no morphological evidence was provided which could have substantiated the validity of this record. Copepods rarely utilize enteropneusts as hosts and the only three species that are known to parasitize acorn worms all belong to the cyclopoid family Ividae (Tung *et al.* 2014).

Records from vertebrate hosts

Zaus goodsiri Brady, 1880

Pearse (1951) found two specimens, one female and one male, in a dish in which a squirrelfish, *Holocentrus adscensionis* (Osbeck, 1765) (Beryciformes), collected in Bimini, had been kept for examination. The author claimed that they probably came from the fish but this is highly unlikely. *Zaus goodsiri* is a north-west European species that is frequently found amongst algae and communities of other sessile organisms on rocky shores from the lower intertidal down to a depth of 30 m (Huys *et al.* 1996).

Metis holothuriae (Edwards, 1891)

Violante-Huerta & Suárez-Morales (2016) recently reported the presence of this species as an epibiont on six captive manatees at two locations in the state of Quintana Roo, Mexican Caribbean. Eleven adult and two copepodid V females were recovered from the dorsal skin surface of the Caribbean manatee, *Trichechus manatus manatus*. Violante-Huerta & Suárez-Morales (2016) suggested that *M. holothuriae* is probably an opportunistic symbiont which consumes the detritus associated with the algal biofilm on the manatee skin rather than the skin itself. The species was not reported from free-ranging Caribbean manatees.

Harpacticus pulex Humes, 1964

Humes (1964) collected several hundreds of individuals (including ovigerous females) of a new species, *Harpacticus pulex*, from the sloughed skin of a common bottlenose dolphin *Tursiops truncatus* (Montagu, 1821) (Delphinidae) kept in the Miami Seaquarium. The same copepod was found in smaller numbers on a Florida manatee, *Trichechus manatus latirostris* (Harlan, 1824) which was also kept in the same oceanarium. After the captive manatee had developed a skin infection copepods established themselves in the ulcerated areas of the skin. Zeiller (1981) noted two cases of captive manatees at the Miami Seaquarium where unidentified copepods were associated with skin lesions. It was not determined whether they were responsible for the lesions or secondarily invaded them. The situation was remedied by changing the tank water to freshwater and adding copper sulfate (Zeiller 1981). Graham (2005; her Figs 3-88, 3-89) observed unidentified copepods inhabiting the stratum corneum of two manatees caught off the west coast of Florida. The copepods appeared to pose no health threat since there was no associated injury to the skin or inflammation. Bledsoe *et al.* (2006) observed biofouling harpacticoid copepods on 63% of the free-ranging Florida manatees in Tampa, as compared to 30% of captive manatees in the Homosassa Springs Wildlife State Park, however, it is unclear whether *H. pulex* was among them.

Harpacticus pulex does not differ significantly from its 36 valid congeners and lacks any morphological adaptations that could underpin the association with its putative hosts. It is conceivable that *H. pulex* was attracted by the ulcerative skin lesions of the mammals and does not normally occur as a dermal parasite on these hosts in their natural environment. Like some other copepods (*e.g. Tisbe*) it likely causes opportunistic infestations related to captive conditions rather than being a primary pathogen in free-ranging animals. Evidence is support of this is offered by the fact that only adults and no copepodids were found, and that the species was found on two different hosts in the same conditions of captivity and only in relation to damaged, sloughed skin (Morales-Vela *et al.* 2008). An alternative explanation offered by Humes (1964) surmises that the copepods live in small numbers on these mammals under natural conditions and that their abundance increases under the artificial conditions in captivity. Some Florida manatees can support extensive growths of a blue-green alga *Lyngbya martensiana* Meneghini ex Gomont, 1892 (Cyanobacteria), on their backs, indicating that they have spent most of their time in rivers and estuaries, while others have the red alga, *Compsopogon caeruleus* (Balbis ex C. Agardh) Montagne, 1846b, growing from the tips of hairs and vibrissae (Hartman 1979). *Lyngbya* is known to harbour a rich associated fauna, including amphipods, isopods, dipteran larvae, nematodes, ostracods, copepods and protozoans (Husar 1978). Members of the family Harpacticidae in general, and the genus *Harpacticus* in particular, are known as true algae-dwelling forms in so far that their dominant occurrence supports the concept of geographic parallelism in phytal assemblages (Hicks 1980). A pre-existing phoretic population of *H. pulex* inhabiting the algal growths on the manatee could therefore have become secondarily associated with the skin lesions of the sirenian host.

Frost (1967) found individuals of *H. pulex*, including ovigerous females and males clasping copepodids, with *Harpacticus littoralis* in washings of algae from the intertidal zone near the Scripps Institution of Oceanography in San Diego, California. Without giving any justification he declared *H. pulex* to be similar to *H. boehleri* Pesta, 1916, an incompletely described species from the Togolese coast. The authenticity of Frost's (1967) identification and the recent record of *H. pulex* from the south-western coast of Turkey (U.N.Ö. Köroğlu, unpubl. data) are, however, questionable. *Harpacticus pulex* belongs to a large group of 21 species displaying (a) a 9-segmented antennule in the female, (b) only one inner seta on P2 enp-2 in the female, and (c) 7,8,8 setae/spines on the distal exopodal segment of P2–P4. Existing identification keys for this complex are characterized by the extensive use of meristic characters, whose veracity depends on the accuracy of the descriptions and illustrations; both may be doubtful for some older literature (Wells 2007). Caudal ramus shape (max. length/max. width ratio about 1.5 in dorsal view) and maxillipedal basis length (max. length/max. width < 2) single out *H. pulex*, however, any identification made must be checked against the original description.

OD: Humes (1964): 517–526; Figs 1–32.
TL: U.S.A., Florida, Miami Seaquarium on the island of Virginia Key in Biscayne Bay; sloughed surface of the skin of *Tursiops truncatus* (Montagu, 1821) (Delphinidae).
BL: 840–940 µm (♀), 810–1,020 µm (♂).

Parategastes haphe Leigh-Sharpe, 1936

Leigh-Sharpe (1936) based his description on a single female found on the gills of the brown comber *Serranus hepatus* (Linnaeus, 1758) (family Serranidae) collected in the vicinity of Naples. Genus level taxonomy in the Tegastidae has tradionally been based on swimming leg segmentation (Wells 2007). It is therefore not surprising that Lang (1948) considered *P. haphe* a *species incertae sedis* because Leigh-Sharpe explicitly stated that the "other pereiopods [legs 1–4 are] present but cannot be distinguished". The grounds on which Leigh-Sharpe decided to assign the species to *Parategastes* remain a mystery since there is nothing in his very concise description that supports such a placement. His claim that the first pedigerous somite is free is undoubtedly based on an observational error and probably resulted from a misinterpretation of the transverse chitinous band commonly found in the posterior part of the cephalic shield. Leigh-Sharpe (1936) also stated that the rami of the fifth legs "… are modified in relation to the parasitic habit, acting like blunt scissor-blades, a portion of the gill of the host being clipped between their concave edges" but this observation is incorrect since their morphology is grossly similar to that in other tegastids (Lang 1948). There is no doubt that the presence of *P. haphe* on the gills of *S. hepatus* was accidental.

OD: Leigh-Sharpe (1936): 67–68; Fig. 7.
TL: Italy, Campania, vicinity of Naples; on gills of *Serranus hepatus* (Linnaeus, 1758) (Serranidae).
BL: 440 µm (♀) [based on original habitus illustration; measured in lateral aspect along dorsal curvature].

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APPENDIX 1. Symbiotic harpacticoids arranged by family with their host organisms.

Family	Harpacticoid species	Host organism
Ameiridae		
	Abscondicola humesi Fiers, 1990	*Discoplax hirtipes* (Dana, 1851a)
		Discoplax rotunda (Quoy & Gaimard, 1824)
	Antillesia cardisomae Humes, 1958	*Cardisoma guanhumi* Latreille, 1828
	Cancrincola jamaicensis Wilson, 1913	*Cardisoma armatum* Herklots, 1851
		Cardisoma guanhumi Latreille, 1828
		Sesarma huzardi (Desmarest, 1825)
	Cancrincola plumipes Humes, 1941	*Armases cinereum* (Bosc, 1802)
		Sesarma reticulatum (Say, 1817)
		Sesarma sp. (nr. *reticulatum*)
	Cancrincola abbreviata Humes, 1957a	*Metagrapsus curvatus* (H. Milne Edwards, 1837)
		Sesarma angolense Brito Capello, 1864
		Sesarma huzardi (Desmarest, 1825)
	Cancrincola longiseta Humes, 1957a	*Goniopsis cruentata* (Latreille, 1803)
		Goniopsis pelii (Herklots, 1851)
		Metagrapsus curvatus (H. Milne Edwards, 1837)
		Sesarma huzardi (Desmarest, 1825)
	Neocancrincola platensis Mañé-Garzón & Sobota, 1974	*Cyrtograpsus angulatus* Dana, 1851a
		Neohelice granulata (Dana, 1851a)
	Nitocra bdellurae (Liddell, 1912)	*Bdelloura candida* (Girard, 1850)
		Bdelloura propinqua Wheeler, 1894
	Nitocra divaricata divaricata Chappuis, 1923	*Astacus astacus* (Linnaeus, 1758)
		Astacus leptodactylus Eschscholtz, 1823
		Astacus sp.
		Austropotamobius torrentium (Schrank, 1803)

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Nitocra divaricata caspica Behning, 1936	*Astacus leptodactylus caspicus* Eichwald, 1838
	Nitocra hibernica (Brady, 1880)	*Astacus astacus* (Linnaeus, 1758)
		Astacus leptodactylus Eschscholtz, 1823
		Pacifastacus leniusculus (Dana, 1852a)
	Nitocra medusaea Humes, 1953	*Aurelia* sp.
	Nitocra sphaeromata Bowman, 1988	*Sphaeroma peruvianum* Richardson, 1910
	Ameiridae gen. et sp. nov. (this study)	*Blepharipoda liberata* Shen, 1949
Balaenophilidae		
	Balaenophilus unisetus Aurivillius, 1879a	*Balaenoptera borealis* Lesson, 1828
		Balaenoptera edeni Anderson, 1878
		Balaenoptera physalus (Linnaeus, 1758)
		Balaenoptera musculus musculus (Linnaeus, 1758)
		Balaenoptera musculus brevicauda Ichihara, 1966
	Balaenophilus manatorum (Ortíz, Lalana & Torres Fundora, 1992)	*Caretta caretta* (Linnaeus, 1758)
		Chelonia mydas agassizii (Bocourt, 1868)
		Lepidochelys olivacea (Eschscholtz, 1829)
		Stomatolepas elegans (Costa, 1838)
		Trichechus manatus manatus Linnaeus, 1758
Canthocamptidae		
	Attheyella carolinensis Chappuis, 1932	*Cambarus asperimanus* Faxon, 1914
		Cambarus distans Rhoades, 1944
		Cambarus sciotensis Rhoades, 1944
		Cambarus tenebrosus Hay, 1903
		Cambarus sp.
	Attheyella pilosa Chappuis, 1929	*Cambarus asperimanus* Faxon, 1914
		Cambarus tenebrosus Hay, 1903
		Cambarus sp.
		Orconectes rusticus rusticus (Girard, 1852)

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Pholetiscus orientalis Humes, 1947	*Episesarma mederi* (H. Milne Edwards, 1853b)
		Episesarma palawanense (Rathbun, 1914)
		Perisesarma eumolpe (De Man, 1895)
	Pholetiscus rectiseta Humes, 1956	*Neosarmatium africanum* Ragionieri, Fratini & Schubart, 2012
	Pholetiscus wilsoni (Pearse, 1930)	*Chiromantes haematocheir* (De Haan, 1833)
		Parasesarma pictum (De Haan, 1835)
Canuellidae		
	Brianola elegans Hamond, 1973b	*Diogenes senex* Heller, 1865
	Brianola stebleri (Monard, 1926a)	*Pagurus bernhardus* (Linnaeus, 1758)
	Brianola sydneyensis Hamond, 1973b	*Diogenes senex* Heller, 1865
	Canuella perplexa Scott & Scott, 1893c	*Pagurus bernhardus* (Linnaeus, 1758)
	Coullana pori (Hamond, 1973b)	*Diogenes senex* Heller, 1865
	Echinosunaristes bathyalis Huys, 1995	*Paleopneustes* sp.
	Intersunaristes dardani (Humes & Ho, 1969a)	*Calcinus latens* (Randall, 1840)
		Clibanarius virescens (Krauss, 1843)
		Dardanus deformis (H. Milne Edwards, 1836)
		Dardanus guttatus (Olivier, 1812)
		Dardanus lagopodes (Forskål, 1775)
		Dardanus megistos (Herbst, 1804)
		Dardanus scutellatus (H. Milne Edwards, 1848)
	Parasunaristes chelicerata (Por & Marcus, 1973)	*Siphonoecetes* sp.
	Scottolana scotti (Sewell, 1940)	*Upogebia darwinii* (Miers, 1884)
	Sunaristes inaequalis Humes & Ho, 1969a	*Calcinus latens* (Randall, 1840)
		Clibanarius carnifex Heller, 1861
		Clibanarius virescens (Krauss, 1843)
		Dardanus megistos (Herbst, 1804)
		Dardanus scutellatus (H. Milne Edwards, 1848)

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Sunaristes japonica Ho, 1986a	*Clibanarius bimaculatus* (De Haan, 1849)
		Pagurus filholi (De Man, 1887)
		Pagurus japonicus (Stimpson, 1858)
		Pagurus lanuginosus De Haan, 1849
		Pagurus middendorffii Brandt, 1851
		Pagurus rubrior Komai, 2003
		Pagurus similis (Ortmann, 1892)
	Sunaristes paguri Hesse, 1867	*Clibanarius erythropus* (Latreille, 1818)
		Diogenes pugilator (Roux, 1828)
		Paguristes eremita (Linnaeus, 1767)
		Pagurus bernhardus (Linnaeus, 1758)
		Pagurus cuanensis Bell, 1845
	Sunaristes tranteri Hamond, 1973b	*Calcinus gaimardii* (H. Milne Edwards, 1848)
		Calcinus latens (Randall, 1840)
		Calcinus minutus Buitendijk, 1937
		Calcinus sp.
		Ciliopagurus strigatus (Herbst, 1804)
		Dardanus guttatus (Olivier, 1812)
		Dardanus lagopodes (Forskål, 1775)
	Sunaristes sp. *sensu* Hamond (1973b)	*Pagurus novizealandiae* (Dana, 1851b)
	Sunaristes-like copepod *sensu* Shields (2011), Shields *et al.* (2006)	*Panulirus* spp.
	Canuellidae gen. et sp. nov. 1 (this study)	*Amphiura* sp.
	Canuellidae gen. et sp. nov. 2 (this study)	*Aspidosiphon muelleri muelleri* Diesing, 1851
Dactylopusiidae		
	Dactylopusia vulgaris Sars, 1905b	*Lanice conchilega* (Pallas, 1766)
	Dactylopusioides fodiens Shimono, Iwasaki & Kawai, 2004a	*Dictyota coriacea* (Holmes) I.K. Wang, H.-S. Kim & W.J. Lee, 2004
		Dictyota dichotoma (Hudson) J.V. Lamouroux, 1809

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Dactylopusioides macrolabris (Claus, 1863)	*Dictyota dichotoma* (Hudson) J.V. Lamouroux, 1809
		Sargassum fusiforme (Harvey) Setchell, 1931
	Dactylopusioides malleus Shimono, Iwasaki & Kawai, 2007	*Dictyopteris undulata* Holmes, 1896
		Dictyota ciliolata Sonder *ex* Kützing, 1859
		Dictyota dichotoma (Hudson) J.V. Lamouroux, 1809
	Dactylopusioides sp. *sensu* Takemori & Iwasaki (2009)	*Palmaria palmata* (Linnaeus) Weber & Mohr, 1805
	Diarthrodes cystoecus Fahrenbach, 1954	*Callophyllis crenulata* Setchell, 1923
		Callophyllis edentata Kylin, 1925
		Cryptopleura lobulifera (J. Agardh) Kylin, 1924
		Cryptopleura ruprechtiana (J. Agardh) Kylin, 1924
		Cryptopleura spatulata N.L. Gardner, 1927
		Cryptopleura stenoglossum (J. Agardh) Kylin, 1924
		Gloiocladia fryeana (Setchell) Sánchez & Rodríguez-Prieto, 2007
		Gloiocladia laciniata (J. Agardh) Sánchez & Rodríguez-Prieto, 2007
		Halosaccion glandiforme (S.G. Gmelin) Ruprecht, 1850
		Halymenia (?) sp.
	Diarthrodes feldmanni Bocquet, 1953	*Cryptopleura ramosa* (Hudson) L. Newton, 1931
		Erythroglossum laciniatum (Lightfoot) Maggs & Hommersand, 1993
		Haraldiophyllum bonnemaisonii (Kylin) A.D. Zinova, 1981
		Rhodophyllis divaricata (Stackhouse) Papenfuss, 1950
		Rhodymenia pseudopalmata (J.V. Lamouroux) P.C. Silva, 1952
		Stenogramma interruptum (C. Agardh) Montagne, 1846a
	Diarthrodes nobilis (Baird, 1846)	*Ceramium virgatum* Roth, 1797
		Heterosiphonia plumosa (J. Ellis) Batters, 1902
Darcythompsoniidae		
	Leptocaris brevicornis (Douwe, 1905)	*Spartina alterniflora* Loiseleur-Deslongchamps, 1807
Ectinosomatidae		
	Microsetella norvegica (Boeck, 1865)	*Flaccisagitta enflata* (Grassi, 1881)

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
		Megalocercus abyssorum Chun, 1887
		Oikopleura (*Coecaria*) *fusiformis* Fol, 1872
		Oikopleura (*Coecaria*) *gracilis* Lohmann, 1896
		Oikopleura (*Coecaria*) *longicauda* (Vogt, 1854)
		Oikopleura (*Vexillaria*) *dioica* Fol, 1872
	Microsetella rosea (Dana, 1847)	*Bathochordaeus* spp.
	Peltobradya bryozoophila Médioni & Soyer, 1968	*Cellepora pumicosa* (Pallas, 1766)
		Patinella radiata (Audouin, 1826)
		Flustra foliacea (Linnaeus, 1758)
		Schizomavella linearis (Hassall, 1841)
	Ectinosomatidae gen. et sp. nov. *sensu* O'Reilly (1995)	*Hydroides norvegica* Gunnerus, 1768
Hamondiidae		
	Hamondia superba Huys, 1990a	unidentified sponges
Harpacticidae		
	Discoharpacticus mirabilis Noodt, 1954a	*Loxechinus albus* (Molina, 1782)
	Harpacticus sp. *sensu* Glynn (1968)	*Acanthopleura granulata* (Gmelin, 1791)
		Chiton tuberculatus Linnaeus, 1758
	Paratigriopus hoshidei Itô, 1969	*Chthamalus challengeri* Hoek, 1883
	Zaus sp. *sensu* Takemori & Iwasaki (2009)	*Palmaria palmata* (Linnaeus) Weber & Mohr, 1805
Laophontidae		
	Carcinocaris dussarti Cottarelli & Bruno, 2011	*Leptodius affinis* (De Haan, 1835)
	Carcinocaris minipedia Björnberg & Santos, 2009	*Eurypanopeus depressus* (Smith, 1869)
		Panopeus americanus Saussure, 1858
		Panopeus herbstii H. Milne Edwards, 1834
	Carcinocaris serrichelata Cottarelli, Bruno & Berera, 2006	unidentified xanthids
	Coullia sp. *sensu* Fiers (1991, 1992a)	*Maja squinado* (Herbst, 1788)
		unidentified decapods

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Harrietella simulans (T. Scott, 1894b)	*Limnoria borealis* Kussakin, 1963
		Limnoria carinata Menzies & Becker, 1957
		Limnoria lignorum (Rathke, 1799)
		Limnoria quadripunctata Holthuis, 1949a
		Limnoria sexcarinata Kühne, 1975
		Limnoria tripunctata Menzies, 1951
	Hemilaophonte janinae Jakubisiak, 1932	*Maja brachydactyla* Balss, 1922
	Heterolaophonte brevipes Roe, 1958	*Austrominius modestus* (Darwin, 1854)
		Semibalanus balanoides (Linnaeus, 1767)
	Heterolaophonte lalanai Varela & Ortíz, 2008	*Acanthopleura granulata* (Gmelin, 1791)
		? *Chiton tuberculatus* Linnaeus, 1758
	Inermiphonte drachi (Médioni & Soyer, 1966)	*Turbicellepora armata* (Hincks, 1860)
	Laophonte adamsiae Raibaut, 1966	*Adamsia palliata* (O.F. Müller, 1776)
	Loureirophonte majacola Fiers, 1993	*Maja brachydactyla* Balss, 1922
	Microchelonia californiensis (Ho & Perkins, 1977)	*Apostichopus parvimensis* (Clark, 1913)
	Microchelonia koreensis (Kim, 1991)	*Apostichopus japonicus* (Selenka, 1867)
		Holothuria (*Mertensiothuria*) *hilla* Lesson, 1830
	Mictyricola typica Nicholls, 1957	*Mictyris platycheles* H. Milne Edwards, 1852
	Mictyricola proxima Nicholls, 1957	*Mictyris longicarpus* Latreille, 1806
	Paralaophonte majae Petkovski, 1964a	*Maja squinado* (Herbst, 1788)
	Paralaophonte ormieresi Raibaut, 1969	*Maja squinado* (Herbst, 1788)
	Paralaophonte royi (Jakubisiak, 1932)	*Maja brachydactyla* Balss, 1922
	Raibautius commensalis (Raibaut, 1963) **comb. nov.**	*Eriphia verrucosa* (Forskål, 1775)
		Xantho hydrophilus (Herbst, 1790)
		Xantho pilipes A. Milne-Edwards, 1867
		Xantho poressa (Olivi, 1792)
	Robustunguis minor Fiers, 1992b	*Pilumnus minutus* De Haan, 1835
		(?) *Pilumnus* sp.

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Robustunguis ungulatus Fiers, 1992b	*Pilumnus sayi* Rathbun, 1897
		unidentified xanthids
	Robustunguis sp. 1 *sensu* Hendrickx & Fiers (2010)	*Pilumnus townsendi* Rathbun, 1923
	Robustunguis sp. 2 *sensu* Hendrickx & Fiers (2010)	*Daira americana* Stimpson, 1860
	Xanthilaophonte carcinicola Fiers, 1991	*Pilumnus vespertilio* (J.C. Fabricius, 1793)
	Xanthilaophonte trispinosa (Sewell, 1940)	*Daldorfia horrida* (Linnaeus, 1758)
		Mictyris longicarpus Latreille, 1806
		Mictyris sp.
		Pilumnopeus makianus (Rathbun, 1931)
		Pilumnus hirtellus (Linnaeus, 1761)
		Pilumnus tomentosus Latreille, 1825
		Pilumnus vespertilio (J.C. Fabricius, 1793)
		Phymodius monticulosus (Dana, 1852b)
		unidentified xanthid
	Laophontidae gen. et sp. nov. (this study)	*Blepharipoda liberata* Shen, 1949
Miraciidae		
	Amphiascus giesbrechti Sars, 1906b	unidentified polychaetes
	Amphiascus paromolae (Soyer, 1973)	*Paromola cuvieri* (Risso, 1816)
	Amphiascus soyeri (Lang, 1965)	*Eunicella stricta* (Bertoloni, 1810)
	Amphiascus waihonu (Hicks, 1986b)	*Choristella marshalli* McLean, 1992
	Amphiascus sp. *sensu* Shields (2011), Shields *et al.* (2006); Jeffs *et al.* (2013)	*Jasus edwardsii* (Hutton, 1875)
		Sagmariasus verreauxi (H. Milne Edwards, 1851)
	Distioculus minor (T. Scott, 1894a)	*Trichodesmium* spp.
	Macrosetella gracilis (Dana, 1847)	*Trichodesmium* spp.
	Miracia efferata Dana, 1849	*Trichodesmium* spp.
	Oculosetella gracilis (Dana, 1849)	*Trichodesmium* spp.
	Paramphiascella commensalis (Seiwell, 1928)	*Aplidium stellatum* (Verrill, 1871)
	Paramphiascella pacifica Vervoort, 1962	*Ascidia sydneiensis* var. *samea* (Oka, 1935)

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Sarsamphiascus ampullifer (Humes, 1953)	*Homarus americanus* H. Milne Edwards, 1837
	Sarsamphiascus elongatus (Itô, 1972)	*Telmessus cheiragonus* (Tilesius, 1815)
Peltidiidae		
	Alteuthellopsis corallina Humes, 1981b	*Acropora exigua* (Dana, 1846)
		Astreopora sp.
		Gardineroseris planulata (Dana, 1846)
		Goniastrea retiformis (Lamarck, 1816a)
		Merulina ampliata (Ellis & Solander, 1786)
		Montipora verrilli Vaughan, 1907
		Platygyra daedalea (Ellis & Solander, 1786)
		Platygyra sp.
		Pocillopora damicornis (Linnaeus, 1758)
		Stylophora pistillata Esper, 1797
	Alteuthoides affinis Kim & Kim, 1998	*Callyspongia elegans* (Thiele, 1899)
	Alteuthoides kootare Hicks, 1986a	*Symplectella rowi* Dendy, 1924
		Symplectella sp.
Porcellidiidae		
	Clavigofera echinophila (Humes & Gelerman, 1962)	*Echinometra mathaei* (Blainville, 1825)
	Kioloaria brevicaudata (Thompson & Scott, 1903) **comb. nov.**	*Calcinus gaimardii* (H. Milne Edwards, 1848)
		Calcinus latens (Randall, 1840)
		Calcinus minutus Buitendijk, 1937
		Ciliopagurus strigatus (Herbst, 1804)
		Clibanarius virescens (Krauss, 1843)
		Dardanus deformis (H. Milne Edwards, 1836)
		Dardanus guttatus (Olivier, 1812)
		Dardanus lagopodes (Forskål, 1775)
		Dardanus megistos (Herbst, 1804)
		Dardanus scutellatus (H. Milne Edwards, 1848)

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
		Pagurus sp.
	Kioloaria cumulus (Harris, 2014a) **comb. nov.**	*Pagurus sinuatus* (Stimpson, 1858)
	Kioloaria iwasakii (Harris, 2014a) **comb. nov.**	*Pagurus sinuatus* (Stimpson, 1858)
	Kioloaria jejuensis **sp. nov.**	*Dardanus impressus* (De Haan, 1849)
	Kioloaria paguri (Ho, 1986a) **comb. nov.**	*Clibanarius bimaculatus* (De Haan, 1849)
		Pagurus filholi (De Man, 1887)
		Pagurus japonicus (Stimpson, 1858)
	Kioloaria similis (Kim & Kim, 1996) **comb. nov.**	*Pagurus pectinatus* (Stimpson, 1858)
		Pagurus similis (Ortmann, 1892)
	Kioloaria tapui (Hicks & Webber, 1983) **comb. nov.**	*Areopaguristes pilosus* (H. Milne Edwards, 1836)
		“*Areopaguristes setosus*” (H. Milne Edwards, 1848)
		Diacanthurus rubricatus (Henderson, 1888)
		Diacanthurus spinulimanus (Miers, 1876)
		Lophopagurus cookii (Filhol, 1883)
		Lophopagurus stewarti (Filhol, 1883)
		Lophopagurus thompsoni (Filhol, 1885)
		Paguristes barbatus (Heller, 1862)
		Pagurus novizealandiae (Dana, 1851b)
		Pagurus traversi (Filhol, 1885)
		Pagurus sp. A
		Pylopagurus sp.
		unidentified Paguridae
	Porcellidium sp. *sensu* Villiers *et al.* (1998)	*Patella* (*Scutellastra* ?) sp.
	Porcellidium sp. *sensu* Williams & McDermott (2004)	*Calcinus gaimardii* (H. Milne Edwards, 1848)
	Porcellidiidae sp. *sensu* Ho (1986a)	*Aniculus miyakei* Forest, 1984
		Pagurus japonicus (Stimpson, 1858)

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
Pseudotachidiidae		
	Apodonsiella indica Hicks, 1988a	*Paralimnoria andrewsi* (Calman, 1910)
	Donsiella limnoriae Stephensen, 1936	*Limnoria borealis* Kussakin, 1963
		Limnoria lignorum (Rathke, 1799)
		Limnoria quadripunctata Holthuis, 1949a
		Limnoria tripunctata Menzies, 1951
	Donsiella anglica Hicks, 1988a	*Limnoria quadripunctata* Holthuis, 1949a
		Limnoria tripunctata Menzies, 1951
	Donsiella bisetosa Hicks, 1988a	*Limnoria sexcarinata* Kühne, 1975
	Donsiella victoriae Hicks, 1988a	*Limnoria quadripunctata* Holthuis, 1949a
		Limnoria tripunctata Menzies, 1951
		Limnoria sp.
	Donsiella phycolimnoriae Hicks, 1990	*Limnoria stephenseni* Menzies, 1957
	Donsiella sp. *sensu* Brunel (1963), Brunel *et al.* (1998)	*Limnoria borealis* Kussakin, 1963
	Idomenella rostrata (T. Scott, 1893)	*Pagurus bernhardus* (Linnaeus, 1758)
	Oligoxylora cooksoni Hicks, 1988a	*Limnoria quadripunctata* Holthuis, 1949a
	Pseudonsiella aotearoa Hicks, 1988a	*Limnoria carinata* Menzies & Becker, 1957
	Pseudonsiella longicaudata Kim & Kim (1997)	*Limnoria* sp. (probably *L. lignorum* (Rathke, 1799))
	Xouthous purpurocinctus (Norman & Scott, 1905)	*Aplidium yamazii* (Tokioka, 1949)
	Xylora bathyalis Hicks, 1988a	*Limnoria sexcarinata* Kühne, 1975
	Xylora neritica Hicks, 1988a	*Limnoria carinata* Menzies & Becker, 1957
		Limnoria sexcarinata Kühne, 1975
	Xylora longiantennulata Kim & Kim, 1997	*Limnoria* sp. (probably *L. lignorum* (Rathke, 1799))
Tachidiidae		
	Cithadius cyathurae Bowman, 1972	*Cyathura polita* (Stimpson, 1856)
Tegastidae		
	Aglaogastes cnidicus (Humes, 1981b) **comb. nov.**	*Aglaophenia cupressina* Lamouroux, 1816
	Parategastes conexus Humes, 1984	*Stereonephthya ulicoides* Thomas & Dean, 1931

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Tegastes acroporanus Humes, 1981a	*Acropora florida* (Dana, 1846)
	Tegastes falcatus (Norman, 1869)	*Flustra foliacea* (Linnaeus, 1758)
		unidentified suctorian
	Tegastes gemmeus Humes, 1984	*Cyphastrea ocellina* (Dana, 1846)
		Montipora verrucosa (Lamarck, 1816a)
	Tegastes georgei Marcus & Masry, 1971	*Stylophora* sp.
	Tegastes knoepffleri Médioni & Soyer, 1968	*Schizobrachiella sanguinea* (Norman, 1868)
	Tegastes paulipes Humes, 1984	*Pocillopora verrucosa* (Ellis & Solander, 1786)
	Tegastes pygmaeus Marcus, 1977	? *Acropora palmata* (Lamarck, 1816a)
	Tegastes singularisaetus Marcus, 1977	? *Acropora palmata* (Lamarck, 1816a)
	Tegastes sp. *sensu* Varela (2010)	*Plexaurella grisea* Kunze, 1916
Thalestridae		
	Amenophia orientalis Ho & Hong, 1988	*Undaria pinnatifida* (Harvey) Suringar, 1873
	Parathalestris croni (Krøyer, 1842)	macroalgal clumps
	Parathalestris infesta Ho & Hong, 1988	*Undaria pinnatifida* (Harvey) Suringar, 1873
	Parathalestris sp. *sensu* Takemori & Iwasaki (2009)	*Palmaria palmata* (Linnaeus) Weber & Mohr, 1805
	Thalestris hokkaidoensis Takemori & Iwasaki, 2009	*Palmaria palmata* (Linnaeus) Weber & Mohr, 1805
	Thalestris rhodymeniae (Brady, 1894)	*Halosaccion glandiforme* (S.G. Gmelin) Ruprecht, 1850
		Palmaria palmata (Linnaeus) Weber & Mohr, 1805
	Thalestris sp. *sensu* Torii & Yamamoto (1975), Kang (1981)	*Undaria pinnatifida* (Harvey) Suringar, 1873
	Thalestris sp. *sensu* Takemori & Iwasaki (2009)	*Palmaria palmata* (Linnaeus) Weber & Mohr, 1805
Tisbidae		
	Amplipedicola pectinata Avdeev, 2010	*Muusoctopus* cf. *profundorum* (Robson, 1932)
		Enteroctopus dofleini (Wülker, 1910)
	Avdeevia antarctica Bresciani & Lützen (1994)	*Megaleledone setebos* (Robson, 1932)
	Brescianiana rotundata Avdeev, 1982a	*Graneledone boreopacifica* Nesis, 1982
	Cholidya polypi Farran, 1914	*Bathypolypus ergasticus* (Fischer & Fischer, 1892)
		Graneledone boreopacifica Nesis, 1982

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
		Tetracheledone spinicirrhus Voss, 1955
		Bathypolypus arcticus (Prosch, 1849)
		Graneledone sp. A
		Graneledone sp. B
		unknown octopodid
	Cholidyella intermedia (Bresciani, 1970)	unidentified Cirroteuthidae
	Cholidyella nesisi Avdeev, 1986	*Muusoctopus profundorum* (Robson, 1932)
		Muusoctopus fuscus (Taki, 1964)
	Cholidyella incisa Avdeev, 1982a	*Graneledone boreopacifica* Nesis, 1982
	Cholidyella breviseta Avdeev, 1986	*Opisthoteuthis californiana* Berry, 1949
	Genesis vulcanoctopusi López-González, Bresciani & Huys, 2000	*Vulcanoctopus hydrothermalis* González & Guerra, 1988
	Neoscutellidium yeatmani Zwerner, 1967	*Lycodichthys dearborni* (DeWitt, 1962)
	Octopinella tenax Avdeev, 1986	*Muusoctopus hokkaidensis* (Berry, 1921)
		Muusoctopus profundorum (Robson, 1932)
		Octopus longispadiceus (Sasaki, 1917)
		Octopus sp.
		Sasakiopus salebrosus (Sasaki, 1920)
	Paraidya major (Sewell, 1940)	*Dardanus guttatus* (Olivier, 1812)
		Dardanus lagopodes (Forskål, 1775)
		Dardanus megistos (Herbst, 1804)
	Paraidya minor (Sewell, 1940)	*Dardanus guttatus* (Olivier, 1812)
		Dardanus lagopodes (Forskål, 1775)
		Dardanus megistos (Herbst, 1804)
	Paraidya occulta (Humes & Ho, 1969b)	*Dardanus guttatus* (Olivier, 1812)
		Dardanus lagopodes (Forskål, 1775)
		Dardanus megistos (Herbst, 1804)
	Paraidya sp. *sensu* Humes (1972)	unidentified hermit crabs
	Sacodiscus humesi Stock, 1960	*Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1791

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APPENDIX 1. (Continued)

Family	Harpacticoid species	Host organism
	Sacodiscus ovalis (Wilson, 1944)	*Homarus americanus* H. Milne Edwards, 1837
	Scutellidium patellarum Branch, 1974	*Cymbula granatina* (Linnaeus, 1758)
		Cymbula miniata (Born, 1778)
		Cymbula oculus (Born, 1778)
		Scutellastra argenvillei (Krauss, 1848)
		Scutellastra barbara (Linnaeus, 1758)
		Scutellastra cochlear (Born, 1778)
		Scutellastra longicosta (Lamarck, 1819)
		Scutellastra tabularis (Krauss, 1848)
	Scutellidium sp. *sensu* Park *et al.* (1990), Rho *et al.* (1993)	*Undaria pinnatifida* (Harvey) Suringar, 1873
	Tisbe celata Humes, 1954	*Mytilus edulis* Linnaeus, 1758
	Tisbe elongata (A. Scott, 1896b)	*Homarus gammarus* (Linnaeus, 1758)
	Tisbe japonica Ho, 1982	*Patiria pectinifera* (Müller & Troschel, 1842)
	Tisbe sp. *sensu* Huys in Huys & Song (2004)	*Mytilus edulis platensis* Orbigny, 1846
	Tisbe sp. *sensu* Jansen *et al.* (1998)	*Paralithodes camtschaticus* (Tilesius, 1815)
	Tripartisoma ovale Avdeev, 1983	*Pareledone charcoti* (Joubin, 1905)
		Pareledone harrissoni (Berry, 1917)
		Pareledone turqueti (Joubin, 1905)
	Tripartisoma trapezoidale Avdeev, 1983	*Pareledone harrissoni* (Berry, 1917)
Unidentified		
	unidentified harpacticoid [*cf.* Hobbs & Villalobos (1958)]	*Tehuana lamellifrons* (Rathbun, 1893)
	unidentified harpacticoid [*cf.* McDermott (2005, 2009)]	*Pinnixa chaetopterana* Stimpson, 1860

APPENDIX 2. References containing original descriptions of host and other non-copepodan taxa listed in the text and in Appendix 1.

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