

## A worldwide list of hermit crabs and their relatives (Anomura: Paguroidea) reported as hosts of Isopoda Bopyridae

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### Abstract

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Hermit crabs and their relatives in the anomuran superfamily Paguroidea are among the most frequently reported hosts of bopyrid isopods, all species of which are parasites of decapod crustaceans in general. This report serves, for the first time, to collect the widely scattered records of paguroid infestation into a single list with both host and parasite names updated to conform with the currently accepted nomenclature; each entry includes the geographical locality for the occurrence of each species of parasite on each species of host and the citation of the publication in which it was reported. The known host paguroids are in the Diogenidae (48 species plus 3 others not identified to species), Lithodidae (6), Paguridae (52 + 7), and Parapaguridae (3 + 1). Their parasites belong to three bopyrid subfamilies, the Pseudioninae (32 species occurring in the branchial chambers of hosts), the Athelginae (41 species clinging to the abdomens of their hosts), and the Bopyrophryxinae (one species attached simultaneously to branchiae and abdomen of their hosts).

### Keywords

Crustacea, Anomura, Paguroidea, Isopoda, Bopyridae, species list

### Introduction

The epicaridean isopod family Bopyridae contains just over 500 described species worldwide in ten subfamilies, all of which parasitise decapod crustaceans as adults. With one exception, all known species are external parasites. Seventy-four are known to infest hosts in the anomuran superfamily Paguroidea.

So far, there are reports of 48 species of Diogenidae plus three others identified only to genus serving as bopyrid hosts, six species of Lithodidae, 52 species of Paguridae plus seven identified only to genus or family, and three species of Parapaguridae plus one identified only to genus. Their parasites belong to three bopyrid subfamilies: Pseudioninae, the largest and probably most primitive subfamily, whose species are branchial parasites mainly of Anomura in general; the rather small and evidently fairly advanced subfamily Athelginae, all of whose species are dorsoabdominal parasites of paguroids alone; and the monotypic subfamily Bopyrophryxinae, whose single species is simultaneously a branchial and abdominal parasite of a parapagurid. Published records of the occurrences of paguroid-infesting bopyrid isopods have been very widely scattered; it is hoped that this compilation, by bringing them all together for the first time, will be useful to readers seeking information about both the hosts and their parasites.

The following is a list of all known Paguroidea hosts, their

recorded Bopyridae parasites, their known localities and references reporting them. The families of the superfamily Paguroidea are in accordance with the most recently published classification of Martin and Davis (2001). The names of the hosts and parasites have been corrected, as needed, to conform with the most current taxonomic opinion, so they are not necessarily those previously used in the original publications.

### Superfamily Paguroidea

#### Coenobitidae

No records known.

#### Diogenidae

*Allodardanus bredinii* Haig and Provenzano, 1965; *Parathelges tumidipes* Markham, 1972, Athelginae; Bermuda (Markham, 1978).

*Calcinus elegans* (H. Milne Edwards, 1848); *Parapagurion calcinicolae* Shiino, 1933, Pseudioninae; Seto, Japan (Shiino, 1933).

*C. morgani* Rahayu and Forest, 1998; *Propseudione rhombicosoma* Shiino, 1933, Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Pseudostegias macdermotti* Williams and Boyko, 1999, Athelginae; Bali, Indonesia (Williams and Boyko, 1999).

*C. laevimanus* (Randall, 1839): *Propseudione rhombicosoma* Shiino, 1933, Pseudioninae; Seto, Japan (Shiino, 1933). *Parathelges weberi* Nierstrasz and Brender à Brandis, 1923, Athelginae; Maiwara, Papua New Guinea (Danforth, 1971), Irian Jaya, Indonesia (Haig and Ball, 1988).

*C. latens* (Randall, 1839): *Pseudione calcinii* (Shiino, 1958), Pseudioninae; Japan (Shiino, 1958).

*C. lineapropodus* Morgan and Forest, 1991: *Parapagurion calcincola* Shiino, 1933, Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Anathelges muelleri* Nierstrasz and Brender à Brandis 1931, Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Athelges* sp., Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

*Ciliopagurus strigatus* (Herbst, 1804): *Athelges* sp., Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

*Clibanarius albidiitus* Nobili, 1901: *Bopyrissa magellonica* Nierstrasz and Brender à Brandis, 1931, Pseudioninae; Pacific coast, Costa Rica (Nierstrasz and Brender à Brandis, 1931).

*C. antillensis* Stimpson, 1862: *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Caribbean coast, Colombia (Markham, 1988).

*C. bimaculatus* (De Haan, 1849): *Asymmetrione asymmetrica* (Shiino, 1933), Pseudioninae; Tanabe Bay, Japan (Shiino, 1933). *Bopyrissa pyriforma* (Shiino, 1958), Pseudioninae; Hong Kong (Markham, 1982). *Pseudione clibanaricola* Shiino, 1933, Pseudioninae; Tanabe Bay, Japan (Shiino, 1933). *Pseudostegias setoensis* Shiino, 1933, Athelginae; Seto, Japan (Shiino, 1933); Hong Kong (Markham, 1982).

*C. digueti* Bouvier, 1898: *Pseudione* sp., Pseudioninae; Gulf of California, Mexico (Brusca, 1980).

*C. englaucus* Ball and Haig, 1972: *Asymmetrione asymmetrica* (Shiino, 1933), Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988).

*C. erythropus* (Latreille, 1818): *Bopyrissa fraiseii* (Carayon, 1943), Pseudioninae; Arcachon, France (Bourdon, 1968). *Parathelges cardonae* R. and M. Codreanu, 1968, Athelginae; Corsica (Codreanu, 1968); Baleares Islands (Bonnier, 1900); Mediterranean coast of Africa (Codreanu, 1961). *Parathelges racovitzai* Codreanu, 1940, Athelginae; Corsica (Altès, 1962).

*C. merguiensis* de Man, 1888: *Bopyrissa liberorum* Markham, 1985, Pseudioninae; Phuket, Thailand (Markham, 1985b). *Pseudostegias dulcilacuum* Markham, 1982, Athelginae; Phuket, Thailand (Markham, 1985b).

*C. padaverensis* de Man, 1888: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Phuket, Thailand (Markham, 1985b).

*C. signatus* Heller, 1861: *Asymmetrione shiinoi* Codreanu et al., 1965, Pseudioninae; Red Sea (Codreanu et al., 1965).

*C. striolatus* Dana, 1852: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Taiwan (Shiino, 1958).

*C. taeniatus* (H. Milne Edwards, 1848): *Pseudostegias setoensis* Shiino, 1933, Athelginae; Queensland, Australia (Dunbar and Coates, 2000).

*C. tricolor* (Gibbes, 1840): *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Florida, USA; Bahamas; Caribbean coast, Colombia (Markham, 1988). *Bopyrissa wolffi* Markham, 1978, Pseudioninae; Bermuda; Florida, USA; Bahamas; Quintana Roo, Mexico; Puerto Rico (Markham,

1978; Markham et al., 1990). *Parathelges occidentalis* Markham, 1972, Athelginae; Florida, USA; Bahamas; Quintana Roo, Mexico (Markham, 1972). *Stegias clibanarii* Richardson, 1904, Athelginae; Bermuda; Caribbean (Markham, 1979).

*C. virescens* (Krauss, 1843): *Pseudostegias setoensis* Shiino, 1933, Athelginae; Queensland, Australia (Dunbar and Coates, 2000). Unidentified, Indian Ocean coast, South Africa (Barnard, 1950).

*C. vittatus* (Bosc, 1802): *Bopyrissa wolffi* Markham, 1978, Pseudioninae; North Carolina and Texas, USA (Markham, 1978).

*Clibanarius* sp. aff. *longitarsus* (De Haan, 1849): *Pseudione novaeguineensis* Danforth, 1971, Pseudioninae; Maiwara, Papua New Guinea (Danforth, 1971).

*Clibanarius* sp. aff. *tricolor* (Gibbes, 1840): *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Ascension Island (Markham, 1978).

*Clibanarius* sp.: *Asymmetrione* sp., Pseudioninae; Puntarenas, Costa Rica (Markham, 1975). *Bopyrella magellonica* Nierstrasz and Brender à Brandis, 1931, Pseudioninae; Puntarenas, Costa Rica (Nierstrasz and Brender à Brandis, 1931).

*Clibanarius* sp.: *Pseudione brandaoi* Brian and Darteville, 1941, Pseudioninae; Congo (Brian and Darteville, 1941).

*Clibanarius* sp.: *Pseudostegias atlantica* Lemos de Castro, 1965, Athelginae; Ceará and Alagoas, Brazil (Lemos de Castro, 1965).

*Dardanus arrosor* (Herbst, 1796): *Asymmetrione dardani* Bourdon, 1968, Pseudioninae; Atlantic coast, Morocco (Bourdon, 1968). *Parathelges carolii* Codreanu, 1968, Athelginae; Naples, Italy (Codreanu, 1968).

*D. fucosus* Biffar and Provenzano, 1972: *Parathelges tumidipes* Markham, 1972, Athelginae; Jamaica (Markham, 1972).

*D. gardineri* Alcock, 1905: *Athelges aegyptius* Codreanu et al., 1965, Athelginae; Red Sea (Codreanu et al., 1965). *Athelges caudalis* Barnard, Athelginae; Inhambane, Mozambique (Barnard, 1955).

*D. megistos* (Herbst, 1804): Athelginae, unidentified; unspecified locality, Australia (Jones and Morgan, 1994).

*Dardanus* sp.: *Pagurion tuberculata* Shiino, 1933, Pseudioninae; Tanabe Bay, Japan (Shiino, 1933).

*Diogenes edwardsii* (De Haan, 1849): *Bopyrissa pyriforma* (Shiino, 1958), Pseudioninae; Mie Prefecture, Japan (Shiino, 1958); Hong Kong (Markham, 1982); southwest Korea (Kim and Kwon, 1988). *Athelges takanoshimensis* Ishii, 1914, Athelginae; Hong Kong (Markham, 1982). *Pseudostegias dulcilacuum* Markham, 1982, Athelginae; Hong Kong (Markham, 1982).

*D. merguiensis* de Man, 1888: *Bopyrissa dawydoffi* (Codreanu and Codreanu, 1963), Pseudioninae; Thanh Hoa, Vietnam (Codreanu and Codreanu, 1963).

*D. pugilator* (Roux, 1829): *Bopyrissa diogeni* (Popov, 1927), Pseudioninae; Black Sea; Channel Islands (Bourdon, 1968). *Athelges paguri* (Rathke, 1843), Athelginae; Roscoff, France (Bourdon, 1967). *Parathelges racovitzai* Codreanu, 1940, Athelginae; Black Sea, Romania (Codreanu, 1940).

*Isocheles pilosus* (Holmes, 1900): *Asymmetrione ambodis-torta* Markham, 1985, Pseudioninae; California, USA (Markham, 1985a).

*Paguristes anahuachis* Glassell, 1938: *Pseudione* sp., Pseudioninae; Gulf of California, Mexico (Brusca, 1980).

*P. emerita* (Linnaeus, 1767): *Athelges pelagosae* Babić, 1912, Athelginae; Adriatic Sea (Babić, 1912).

*P. hummi* Wass, 1955: unidentified. Florida, USA (Camp et al., 1977).

*P. markhami* Sandberg, 1996: Athelginae, unidentified; Turks and Caicos Islands (Markham, 1978).

*P. monoporus* Morgan, 1987: *Bopyrissa* (?) sp., Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Parapagurion calcincola* Shiino, 1933, Pseudioninae; Phuket, Thailand (Markham, 1985b). *Parathelges whiteleggei* Nierstrasz and Brender à Brandis, 1931, Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

*P. oculatus* (Fabricius, 1775): *Asymmetrione foresti* (Bourdon, 1968), Pseudioninae; Western Mediterranean (Bourdon, 1968).

*P. oxyophthalmus* Holthuis, 1959: *Parathelges piriformis* Markham, 1972, Athelginae; Caribbean coast, Colombia (Markham, 1978).

*P. perspicax* (Nobili, 1906): *Allathelges pakistanensis* Kazmi and Markham, 1999, Athelginae; Karachi, Pakistan (Kazmi and Markham, 1999).

*P. robustus* Forest and de Saint Laurent, 1967: *Pseudione biacuta* Bourdon, 1979, Pseudioninae; Uruguay (Bourdon, 1979).

*P. subpilosus* Henderson, 1888: *Pseudostegias otagoensis* Page, 1985, Athelginae; Otago, New Zealand (Page, 1985).

*P. tortugae* Schmitt, 1933: *Asymmetrione desultor* Markham, 1975 (?), Pseudioninae; Abrolhos Bank, Brazil (Bourdon, 1979). *Parapagurion imbricata* Markham, 1978, Pseudioninae; Cuba (Markham, 1978).

*Strigopagurus boreonotus* Forest, 1995: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Chesterfield Islands (Markham, 1994).

## Lithodidae

*Dermaturus mandtii* Brandt, 1850: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska (Markham, 1975). Unidentified branchial parasite, Pseudioninae?; Hokkaido, Japan (Minemizu, 2000).

*Hapalogaster dentata* (De Haan, 1844): *Pseudostegias hapalogasteri* Shiino, 1950, Athelginae; Mie, Japan (Shiino, 1950).

*Lithodes murrayi* Henderson, 1888: Unidentified, Pseudioninae?; Crozet Islands (Vinuesa, 1989).

*L. santolla* (Molina, 1872): unidentified, Pseudioninae?; Beagle Channel, Argentina (Vinuesa, 1989).

*Neolithodes diomediae* (Benedict, 1894): *Pseudione tuberculata* Richardson, 1904, Pseudioninae; Pampas, Argentina (Richardson, 1904); South Georgia (Vinuesa, 1989).

*Paralomis granulosa* (Jacquinot, 1847): *Pseudione tuberculata* Richardson, 1904, Pseudioninae; Beagle Channel, Argentina (Roccatagliata and Lovrich, 1999).

## Paguridae

*Anapagurus breviaculeatus* Fenizia, 1937: *Athelges tenuicaudis* Sars, 1898, Athelginae; Mediterranean coast, Spain (García-Gómez, 1994).

*A. chiroacanthus* (Lilljeborg, 1856): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; Denmark; English Channel (Bourdon, 1968). *Athelges tenuicaudis* Sars, 1898, Athelginae; Scandinavia; British Isles; France (Sars, 1898).

*A. hyndmanni* (Bell, 1846): *Athelges tenuicaudis* Sars, 1898, Athelginae; Atlantic coast, France (Bourdon, 1964).

*A. japonicus* Ortmann, 1892: unidentified branchial, Pseudioninae?; Sagami Bay, Japan (Miyake, 1978).

*A. laevis* (Bell, 1845): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; English Channel; Spain (Bourdon, 1968). *Athelges paguri* (Rathke, 1843), Athelginae. Britain (Naylor, 1963).

*Aniculus aniculus* (Herbst, 1791): *Parathelges aniculi* (Whitelegge, 1897), Athelginae; Funafuti Atoll (Whitelegge, 1897).

*Catapagurodes fragilis* (Melin, 1939): unidentified abdominal, Athelginae?; Sagami Bay, Japan (Miyake, 1978).

*Iridopagurus caribensis* (A. Milne Edwards, 1893): *Stegophrynxus hyptius* Thompson, 1902, Athelginae; Western Florida, USA (García-Gómez, 1983).

*I. iris* (A. Milne Edwards, 1880): *Pseudionella* sp., Pseudioninae; Venezuela (Markham, 1978).

*I. margaritensis* García-Gómez, 1983: *Parathelges occiden-talis* Markham, 1972, Athelginae; Venezuela (Markham, 1972). *Stegophrynxus hyptius* Thompson, 1902, Athelginae; Curaçao (García-Gómez, 1983).

*I. occidentalis* (Faxon, 1893): unidentified; Cocos Island, Costa Rica (García-Gómez, 1983).

*Iridopagurus* sp.: *Asymmetrione desultor* Markham, 1975, Pseudioninae; Belize (Markham, 1988).

*Lophopagurus (Lophopagurus) lacertosus* (Henderson, 1888): unidentified branchial, Pseudioninae?; New Zealand (Forest et al., 2000). Unidentified abdominal, Athelginae?; New Zealand (Forest et al., 2000).

*L. (L.) lacertosus* (Henderson, 1888)?: *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; New Zealand (Page, 1985). *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Page, 1985).

*L. (L.) thompsoni* (Filhol, 1885)?: *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Pike, 1961).

*L. (Australeremus) cooki* (Filhol, 1883): *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Page, 1985).

*L. (A.) triserratus* (Ortmann, 1892): *Pseudione intermedia* Nierstrasz and Brender à Brandis, 1932, Pseudioninae; Sagami and Misaki, Japan (McLaughlin and Gunn, 1992).

*Manucomplanus ungulatus* (Studer, 1863): *Parathelges occidentalis* Markham, 1972, Athelginae; North Carolina, USA (Markham, 1972).

*Pagurus aleuticus* (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska and Washington, USA (Markham, 1975).

*P. annulipes* (Stimpson, 1860): *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; North Carolina and

Georgia, USA (Adkison and Heard, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; North Carolina, USA; Gulf of Mexico (Markham, 1974).

*P. arenisaxatilis* Harvey and McLaughlin, 1991: *Stegophryxus* sp., Athelginae; Gulf of California, Mexico; Pacific coast, Costa Rica (Harvey and McLaughlin, 1991).

*P. armatus* (Dana, 1851): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Nyblade, 1974).

*P. beringanus* (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Markham, 1975). *Athelges paguri* (Rathke, 1843), Athelginae; Norway to Belgium; Britain (Sars, 1898; Pérez, 1934).

*P. brevidactylus* (Stimpson, 1859): *Asymmetrione desultor* Markham, 1975, Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Parathelges foliatus* Markham, 1972, Athelginae; Barbados; Curaçao (Markham, 1978). *Parathelges piriformis* Markham, 1972, Athelginae; Bermuda (Markham, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1978).

*P. capillatus* (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Nyblade, 1974).

*P. criniticornis* (Dana, 1852): *Pseudionella deflexa* Bourdon, 1979, Pseudioninae; Southern Brazil (Bourdon, 1979).

*P. cuanensis* (Bell, 1845): *Athelges bilobus* Sars, 1898, Athelginae; Denmark; English Channel (Bourdon, 1967). *Athelges cladophorus* Gerstaecker, 1862, Athelginae; British Isles (Bonnier, 1900). *Athelges paguri* (Rathke, 1843), Athelginae; France (Hesse, 1876).

*P. dubius* (Ortmann, 1892): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Korea (Kim and Kwon, 1988). *Parathelges enoshimensis* Shiino, 1950, Athelginae; Korea (Kim and Kwon, 1988).

*P. hirsutiusculus* Dana, 1851: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska and Washington, USA (Markham, 1975).

*P. japonicus* (Stimpson, 1859): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Seto, Japan (Shiino, 1958).

*P. kulkanii* Sankoli, 1962: *Parathelges neotenuicaudis* (Shyamasundari et al., 1993), Athelginae; Eastern India (Shyamasundari et al., 1993); Karachi, Pakistan (Markham and Kazmi, 1998).

*P. lanuginosus* De Haan, 1849 (s. l.): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Tokyo Bay, Japan (Shiino, 1958).

*P. longicarpus* Say, 1817: *Asymmetrione desultor* Markham, 1975, Pseudioninae; North Carolina, USA (Markham, 1975). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Massachusetts to Georgia, USA (Markham, 1974).

*P. maclaughlinae* García-Gómez, 1982: *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1988).

*P. maculosus* Komai and Imafuku, 1996: *Athelges takanoshimensis* Ishii, 1914, Athelginae; Honshu, Japan (Nagasawa et al., 1996).

*P. megalops* (Stimpson, 1858): unidentified; Sagami Bay, Japan (Miyake, 1978).

*P. middendorffi* Brandt, 1851: *Pseudione hyndmanni* (Bate and Westwood, 1868)?, Pseudioninae; Hokkaido, Japan (Shiino, 1958). *Athelges takanoshimensis* Ishii, 1914, Athelginae; Eastern Russia; Japan; Korea (Kim and Kwon, 1988).

*P. ochotensis* Brandt, 1851: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska, USA (Markham, 1975).

*P. pectinatus* (Stimpson, 1858): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Japan; Korea (Kim and Kwon, 1988).

*P. prideauxii* Leach, 1815: *Pseudione hyndmanni* (Bate and Westwood, 1868)?, Pseudioninae; Scotland (Henderson, 1886). *Athelges prideauxii* Giard and Bonnier, 1890, Athelginae; Scotland; France; Italy (Pike, 1953). *Athelges* sp., Athelginae; Norway (Samuelson, 1970).

*P. provenzanoi* Forest and de Saint Laurent, 1967: *Asymmetrione desultor* Markham, 1975, Pseudioninae; Antigua; Bonaire; Curaçao (Markham, 1978). *Parathelges piriformis* Markham, 1972, Athelginae; Bahamas (Markham, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Curaçao (Markham, 1978).

*P. pubescens* (Krøyer, 1838): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; Norway; Iceland; Faeroe Islands; Britain (Bourdon, 1968).

*P. stimpsoni* (A. Milne Edwards and Bouvier, 1893): *Asymmetrione desultor* Markham, 1975, Pseudioninae; Florida, USA (Markham, 1975). *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1974).

*P. brachiomastus* (Thallwitz, 1892): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Korea (Kim and Kwon, 1988).

*P. venturensis* Coffin, 1957: *Pseudione* sp., Pseudioninae; California, USA (Miller, 1975).

*P. vetaultae* Harvey and McLaughlin, 1991: *Stegophryxus* sp., Athelginae; Pacific coast, Costa Rica (Harvey and McLaughlin, 1991).

*Pagurus* sp.: *Pseudione intermedia* Nierstrasz and Brender à Brandis, 1932, Pseudioninae; Misaki, Japan (Shiino, 1972).

*Pagurus* sp.: *Pseudionella attenuata* Shiino, 1949, Pseudioninae; Seto, Japan (Shiino, 1949).

*Pagurus* sp.: *Anathelges resupinatus* (Müller, 1871), Athelginae; Florianópolis, Brazil (Müller, 1871).

*Pagurus* sp.: *Parathelges enoshimensis* Shiino, 1950, Athelginae; Enoshima, Japan (Shiino, 1950).

*Pagurus* sp.: *Stegophryxus thompsoni* Nierstrasz and Brender à Brandis, 1931, Athelginae; Valparaíso, Chile (Nierstrasz and Brender à Brandis, 1931).

*Pagurus* sp.: *Parathelges whiteleggei* Nierstrasz and Brender à Brandis, 1931, Athelginae; Java Sea (Nierstrasz and Brender à Brandis, 1931).

*Parapagurodes constans* (Stimpson, 1858): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Tokyo Bay, Japan (Shiino, 1958).

*P. laurentae* McLaughlin and Haig, 1973: *Stegophryxus hyphalus* Markham, 1974, Athelginae; California, USA; Baja California, Mexico (Markham, 1974).

*P. makarovi* McLaughlin and Haig, 1973: *Stegophryxus hyphalus* Markham, 1974, Athelginae; California, USA; Baja California, Mexico (Markham, 1974).

*Propagurus haigae* (McLaughlin, 1997): Unidentified branchial, Pseudioninae?; New Caledonia (McLaughlin and de Saint Laurent, 1998).

*Pylopagurus unguilatus* (Studer, 1883): *Parathelges occidentalis* Markham, 1972, Athelginae; North Carolina, USA (Markham, 1972).

*Tomopagurus cokeri* (Hay, 1917): Athelginae, unidentified; Quintana Roo, Mexico (Markham, 1978).

Pagurid, unidentified: *Anathelges mossambica* Barnard, 1956, Athelginae; Mozambique (Barnard, 1956).

Pagurid, unidentified: *Stegophryxus minutus* Markham, 1992, Athelginae; Hong Kong (Markham, 1992).

## Family Parapaguridae

*Oncopagurus bicristatus* (A. Milne Edwards, 1880); *Pleurocryptella paguri* Bourdon, 1979?, Pseudioninae; Azores (Bourdon, 1981).

*O. monstrosus* (Alcock, 1905): *Bopyrophryxus branchiabdominalis* Codreanu, 1965, Bopyrophryxinae; Kei Islands, Indonesia (Codreanu, 1965).

*Parapagurus pilosimanus* Smith, 1879: *Pleurocryptella paguri* Bourdon, 1979, Pseudioninae; Azores (Bourdon, 1979).

*Parapagurus* sp.: *Parapagurion imbricata* Markham, 1978, Pseudioninae; Caribbean coast, Colombia (Markham, 1978).

## Pylochelidae

No records known.

## Discussion

It is difficult to infer many generalisations about the occurrence of the parasites considered, because they do not fit into discernible patterns. Of the species of the Pseudioninae known to infest paguroids, most belong to genera not known from hosts outside of that superfamily. The exceptions are the nine species of *Pseudione*, among whose other species (totalling more than 50) are parasites of many other anomurans, numerous thalassinideans and some deep-water carideans; and *Pleurocryptella paguri* Bourdon, known from one or two species of *Parapagurus*, whose congeneric species are all parasites of galatheids. Despite their markedly different appearance from other paguroids, the lithodids bear parasites closely related to those of hosts in other pagroid families; all of their branchial parasites are assignable to *Pseudione* (*P. giardi* Calman being reported as a parasite of both a lithodid and several species of hermit crabs); and the single lithodid-infesting abdominal bopyrid, *Pseudostegias hapalogasteri* Shiino, is in a genus whose other species infest hermit crabs. Most genera of parasites containing more than single species infest both diogenids and pagurids, but all seven species of the pseudionine genus *Bopyrissa* infest only diogenids, while all four species of the athelgine genus *Stegophryxus* infest only pagurids. The most widespread species is *Pseudione hyndmanni* (Bate and Westwood), reported from six host species of pagurids in

western Europe (Bourdon, 1968), another in New Zealand (Page, 1985), and possibly one in Japan (Shiino, 1958). It seems to be an analogue of the closely similar *Pseudione giardi* Calman, which infests five species of *Pagurus* and the lithodid *Dermaturus mandtii* in northwestern North America (Markham, 1975; Nyblade, 1974). Among abdominal parasites, *Athelges* spp. infest many different pagurids in Europe (Sars, 1898; Bourdon, 1967), while *A. takanoishimensis* Ishii infests ten species of pagurids in the western Pacific (Kim and Kwon, 1988; Nagasawa et al., 1996; Shiino, 1958).

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