First record of the hyperparasite *Liriopsis pygmaea* (Cryptoniscidae, Isopoda) from a rhizocephalan parasite of the false king crab *Paralomis granulosa* from the Beagle Channel (Argentina), with a redescription

LAURA PERESAN & DANIEL ROCCATAGLIATA

Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, C1428EHA, Buenos Aires, Argentina

(Accepted 19 January 2004)

Abstract

The Cryptoniscidae are epicaridean isopod parasites or hyperparasites of other crustaceans. *Liriopsis* Schultze in Müller, 1859, one of the genera included in this family, now contains two nominal species: *L. pygmaea* (Rathke, 1843) and *L. monopthalma* (Fraisse, 1878). Both of these species infest rhizocephalan cirripeds, which are in turn parasites of hermit crabs. Among the false king crabs, *Paralomis granulosa* (Jacquinot, 1847), captured commercially in the Beagle Channel in 1996–1998, we found 31 specimens of the rhizocephalan *Briarosaccus callosus* Boschma, 1930 infested by one or more specimens of *L. pygmaea*. Neither *L. pygmaea* nor *L. monopthalma* has been reported previously for the southern seas. Although unidentified isopod hyperparasites have been found on *B. callosus* infesting other lithodids from Crozet Islands, South Georgia Island and Canadian Atlantic waters, this is the first time that one of these hyperparasites has been identified as a member of the genus *Liriopsis*. Since the differences between *L. pygmaea* and *L. monopthalma* remain obscure, the epicaridium and cryptoniscus larvae and three females stages of *L. pygmaea* are herein described from the material collected in the Beagle Channel.

Keywords: *Liriopsis pygmaea*, Cryptoniscid isopod, Beagle Channel

Introduction

Cryptoniscid isopods belong to the suborder Epicaridea and are parasites or hyperparasites of a great variety of other crustaceans (Grygier and Bowman 1990). They are protandrous hermaphrodites, functional males when young and later changing into females. Egg-bearing females lose their isopod appearance and take a sac-like shape (Caullery 1908).

Grygier (1993) reviewed the nomenclature of the family Cryptoniscidae. The genus *Liriopsis* Schultze in Müller, 1859 includes two nominal species, *L. pygmaea* (Rathke, 1843) and *L. monopthalma* (Fraisse, 1878); however, the differences between these two species remain obscure.
Liriopsis pygmaea has been reported from Norway, Denmark, the British Isles (Clyde Sea and English Channel), France (Roscoff), and the Pacific coast of the USA (Friday Harbor area and southeastern Alaska), parasitizing mainly the rhizocephalan Pelogaster paguri Rathke, 1842, which in turn is parasitic on hermit crabs (Rathke 1843; Lilljeborg 1859; Sars 1899; Pérez 1929, 1931; Pike 1961; Bourdon 1963; George and Strömberg 1968; Nielsen and Strömberg 1973; Warrenchuk and Shirley 2000). Besides, Liriopsis pygmaea has been found on the rhizocephalans Septosaccus cuenoti Duboscq, 1912 and Peltogasterella gracilis (Boschma, 1927), also infesting hermit crabs (Pérez 1929, 1931; George and Strömberg 1968). In addition, unidentified Liriopsis species have been reported on rhizocephalans infesting a hermit crab from the Faroe Islands and galatheid anomurans from Norway (Brinkmann 1936; Brinkmann Jr, 1984; Høeg and Lützen 1985; Lange 1999).

While examining commercial captures of the false king crab, Paralomis granulosa (Jacquinot, 1847), taken in the Beagle Channel in 1996–1998, we found some rhizocephalans identified as Briarosaccus callosus Boschma, 1930 parasitized by one or more epicaridean isopods. This is the first time that an epicaridean parasite of B. callosus has been identified as a member of the genus Liriopsis.

Hyperparasites on B. callosus infesting other lithodids from Crozet Islands, South Georgia and the Canadian Atlantic have been variously called ‘a large Bopyrid (?)’, ‘cryptoniscid isopods’, ‘cryptonisciens’, ‘Liriopsinae’ or simply ‘isopods’ (see Boschma 1962; Arnaud and Do-Chi 1977; Pohle 1992a, 1992b; Otto and MacIntosh 1996; Watters 1998). However, the photograph provided by Pohle (1992a: Figure 4) most likely depicts a member of the genus Liriopsis.

Since previous descriptions of Liriopsis pygmaea are incomplete, both the epicaridium and cryptoniscus larvae, and three female stages, are herein described from specimens collected on the rhizocephalan B. callosus infesting the false king crab P. granulosa from the Beagle Channel.

Materials and methods

A total of 29 570 specimens of Paralomis granulosa were collected in the Beagle Channel (about 54°54’S, 67°12’W), Tierra del Fuego, Argentina, at 10–50 m depth, from 1996 to 1998 (for further sampling details, see Roccatagliata and Lovrich 1999).

Only 78 specimens of P. granulosa were infested by B. callosus, with one (occasionally two) rhizocephalan externae under their abdomens. The externae were removed from the crab, fixed in 5% formalin and dissected under a stereomicroscope for stages of isopod hyperparasites. In 31 of the 85 externae dissected, one or more stages of a cryptoniscid isopod, Liriopsis pygmaea, were recovered. All the dissected externae and the recovered isopods were preserved in 70% ethanol.

Almost all of the cryptoniscus larvae and all of the early subadult females were found inside the mantle cavity of the externae. On the other hand, a few cryptonisci, all the advanced subadult females (excepting one aberrant female that was found within the mantle), and all of the adult females were attached to the outer wall of the externae. A few epicaridium larvae taken from the brood pouch of a female, collected on 23 March 1997, were used for the description of this larval stage.
Cryptoniscus larvae and functional males are not distinguishable by their external features, both retain the typical isopod morphology. The term ‘cryptoniscus larva’ is used in this survey to refer to both stages.

Appendages were dissected and stained with a saturated solution in 70% ethanol of Chlorazole Black E. Drawings were made with the help of a camera lucida. Material for SEM was cleaned with a diluted solution of Triton® X-100 detergent and exposed to ultrasonic treatment for a few seconds.

The total length of the epicaridium and cryptoniscus larvae was measured along the midline from the anterior edge of the cephalon to the tip of the pleotelson.

Most of the material studied has been deposited in the Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ (MACN-In No. 35970).

The abbreviation ‘Cr’ refers to the cryptoniscus larva, ‘SA♀₁’ to the early subadult female, ‘SA♀₂’ to the advanced subadult female and ‘A♀’ to the adult female.

*Liriopsis pygmaea* (Rathke, 1843)

(Figures 1–6)

*Liriopsis* Rathke 1843: 60–63, pl. 1, Figures 8–12; Steenstrup 1855: 25; Lilljeborg 1859: 6–14, pl. 1, Figures 1–23; Lilljeborg 1860: 73–74, pl. 6, Figures 1, 2.

*Liriopsis* Rathke [pygmaea]: Schultze in Müller 1859: 310 (footnote).

*Cryptothiria* Rathke 1843: 60–63, pl. 1, Figures 8–12; Steenstrup 1855: 25; Lilljeborg 1859: 6–14, pl. 1, Figures 1–23; Lilljeborg 1860: 73–74, pl. 6, Figures 1, 2.

*Cryptothiria pygmaea*: Bate and Westwood 1868: 261–266 [partim]; ?Czerniavsky 1868: 78–79 (doubtful identification of a single male from the Black Sea).

*Cryptoniscus pygmaeus*: Müller 1871: 72; Fraisse 1878: 287.

*Liriopsis pygmaea* Rathke 1843: 60–63, pl. 1, Figures 8–12; Steenstrup 1855: 25; Lilljeborg 1859: 6–14, pl. 1, Figures 1–23; Lilljeborg 1860: 73–74, pl. 6, Figures 1, 2.

*Liriopsis* Rathke 1843: 60–63, pl. 1, Figures 8–12; Steenstrup 1855: 25; Lilljeborg 1859: 6–14, pl. 1, Figures 1–23; Lilljeborg 1860: 73–74, pl. 6, Figures 1, 2.

Figure 1. *Liriopsis pygmaea*. SEM photographs of the epicaridium larva. (a) Ventral habitus; (b) ventral view of abdomen; (c) detail of anal tube. All photographs belong to the same specimen.
Nielsen and Stro¨mberg 1965: 54; Bourdon 1967: 281, 284 (Table 1); George and Stro¨mberg 1968: 251; Nielsen and Stro¨mberg 1973: 77–92, Figures 1, 6, 7, 29, 36, 37; Altes 1981: 27; Grygier and Bowman 1990: 27–28; Grygier 1993: 186; Warrenchuk and Shirley 2000: 971–976, Figure 1.

Material examined

Beagle Channel (about 54°54’S, 67°12’W), 10–50 m. Infesting the rhizocephalan Briarosaccus callosus. 24 July 1996: 14 Cr, 13 A♀, 1 SA♀2; 10 September 1996: 8 Cr; 2 October 1996: 80 Cr; 2 November 1996: 5 Cr; 20 December 1996: 14 Cr, 1 SA♀2; 28

Figure 2. Liriopsis pygmaea. Epicaridium larva. (a) Second antenna; (b) sixth pereopod; (c) fourth pleopod; (d) uropods. Scale bars: 0.05 mm.
January 1997: 9 Cr, 6 SA♀; 23 March 1997: 45 Cr, 3 SA♀, 4 A♀ (one of them carrying epicaridia); 10 June 1997: 28 Cr; 6 October 1997: 6 Cr.

**Epicaridium larva**

*Total length.* Approximately 0.26 mm.

*Cephalon (Figure 1a).* Cephalon rounded anteriorly; body gradually narrowing posteriorly. Dorsal segmentation distinct. Pleotelson (Figure 2d) projecting dorsally as rounded translucent lamella, extending somewhat beyond distal end of anal tube (hardly noticeable...
Figure 4. *Liriopsis pygmaea*. Cryptoniscus larva. (a) Dorsal habitus; (b) first antenna; (c) second antenna; (d) first pereopod, with detail of distal process of propodus. Scale bars: 0.5 mm (a); 0.1 mm (b–d).
Liriopsis pygmaea from the Beagle Channel

Figure 5. *Liriopsis pygmaea*. Cryptoniscus larva. (a) Third pereopod; (b) sixth pereopod; (c) seventh pereopod, merus and carpus only; (d) first pleopod, (e) uropods. Scale bars: 0.1 mm (b and c, same scale).
Figure 6. *Liriopsis pygmaea*. (a, b) Habitus of early subadult female; (c) ventral habitus of advanced subadult female; (d, e) dorsal and ventral habitus of adult female; (f, g) adult female, details of anterior and posterior ends of the slit. Scale bars: 5 mm (a–c); 0.5 mm (f); 1 mm (g).
under light microscopy). Anal tube (Figures 1c, 2d) approximately as long as uropod peduncle, consisting of rolled laminae with margins in contact at dorsal mid-line, margins slightly fringed.

First antenna. Peduncle with two articles, basal article with three plumose setae. Rami with two and three distal setae, respectively (articulation with peduncle observed for one ramus only), two aesthetascs arising between rami.

Second antenna (Figure 2a). Peduncle with three articles; distal article longest, with three plumose and one small simple setae, distally. Flagellum with three articles gradually decreasing in length distally, third article with three long lamellae (only one drawn) and five setae (at least some of them plumose), largest seta as long as antenna.

Pereopods. First five pereopods alike, subchelate, becoming slightly longer posteriorly. Sixth pereopod (Figure 2b) elongated, ending in bristle-like dactylus. Merus with one feeble seta proximally and two thicker ones distally. Carpus and propodus apparently coalesced, together fusiform. Dactylus slightly longer than basis.

Pleopods (Figure 2c). All five alike, becoming slightly shorter posteriorly; exo- and endopod with three and two distal plumose setae, respectively.

Uropod (Figures 1b, 2d). Uropod widely covered dorsally by pleotelson lamella. Peduncle with one long plumose seta on outer distal angle. Exopod placed dorsally and anteriorly to endopod; distal end with two plumose setae. Endopod slightly shorter than exopod, with two large setae curved downwards and one small straight seta.

Cryptoniscus larva

Total length. 1.40–1.52 mm.

Body (Figures 3a, b, 4a). Body flattened dorsoventrally, gradually narrowing posteriorly, dorsal surface with faint (visible only under high magnification) transverse striations (not drawn). Cephalon slightly longer than half its width, frontal edge almost semicircular. Eyes very distinct, consisting of a single lens encircled by reddish pigment. All pereonites with a couple of minute setae dorsally; third and fourth pereonites slightly shorter than remaining ones. Pleon (including pleotelson) somewhat longer than the first five pereonites together; first to fourth pleonites with mid-ventral lobe between pleopods, becoming gradually less developed from first (Figure 3e) to fourth and disappearing on fifth. Pleotelson with posterior margin rounded and entire, slightly exceeding peduncles of uropods.

First antenna (Figure 4b). Peduncle with three articles. First article posteriorly expanded; caudal end rounded, with three setae (one plumose, two simple); anterior end projected medially into large spur-like tooth (either exposed, Figure 3d, or partially covered by median plate, Figure 3c), and laterally with three setae (one plumose, two simple). Second peduncular article, ornamented with delicate ridges bounding polygonal areas (Figure 3d); small tooth halfway along its anterior margin (Figure 3d); distal end with row of four setae (two plumose, two simple) anteriorly and two setae (one plumose, one simple) posteriorly. Third peduncular article partly hidden by second one; anterior margin with long simple seta; distal margin with numerous aesthetascs (only most ventral ones drawn). Ventral
flagellum with three long distal setae, dorsal flagellum with four long distal setae and two basal aesthetascs.

**Second antenna (Figure 4c).** Second antenna scarcely extending beyond fourth pereonite (including distal setae). Peduncle with four articles, first two articles with fine striae. First article largest and unarmed, remaining ones gradually increasing in length and with setae, namely second article with one simple, third article with two plumose and one simple, and fourth article with four plumose (only ventral ones shown) and one simple setae. Flagellum with five articles, approximately 0.70 times as long as peduncle, with 2-1-2-1 short simple setae on first four articles (only ventral ones shown); fifth article with four unequal distal setae.

**Oral cone.** Oral cone directed anteriorly (Figure 3c).

**Pereopods.** First pereopod (Figure 4d): basis with strong distal condyle flanked by two transparent lamellae. Ischium 0.65–0.73 times as long as basis. Merus with seta-like projection anteriorly and two feeble simple setae posteriorly. Carpus, armed on posterior margin with distal tiny spine between two unequal setae, proximal one hardly noticeable. Propodus slightly shorter than basis, broadly articulated with carpus, postero-distal angle with a depressed area limited proximally by a blunt process bearing two unequal spines (see detail). Dactylus fitting into depressed area of propodus, anterior margin slightly serrated, with one stout spine and one delicate seta distally.

Second pereopod similar in shape to first, but slightly larger.

Third (Figure 5a) to fifth pereopods alike, but slightly increasing in length posteriorly. Basis length roughly equal to that of propodus. Ischium 0.76–0.81 times as long as propodus, biceps-like, distally with two transparent lamellae flanking merus. Merus with one thick and one feeble setae, distally. Carpus with strong spine on distal-posterior angle. Propodus with three spines in distal depressed area, posterior margin with fringe of minute setae. Dactylus apparently fused with distal spine (no articulation discernible at high magnification), both together approximately half as long as propodus, posterior margin with fringe of minute setae, distal end bifid.

Sixth pereopod (Figures 3e, 5b): ischium approximately half as long as basis. Merus with one thick and one feeble setae, distally. Carpus approximately as long as merus. Propodus almost globular, approximately 0.75 times as long as ischium. Dactylus (probably the dactylus itself plus a completely fused distal spine) extremely large and styliform, almost twice as long as basis. Seventh pereopod (Figures 3e, 5c) as sixth except for: shorter thick seta on merus (only the thicker basal part of this seta remains).

**Coxal plates.** Coxal plates (epimeres) with fine cuticular striations and without marginal teeth (Figure 3e).

**Pleopods.** All five pleopods alike (Figure 5d). Basal segment with two coupling setae on inner margin, these slightly longer than endopod. In first four pleopods both rami with five plumose setae distally, outermost setae of exopods clearly shorter than remaining ones. Fifth pleopod as previous ones, except endopod with only three distal setae.

**Uropod (Figure 5e).** Peduncle and endopod combined approximately as long as pleotelson. Peduncle widely covered by pleotelson, outer margin with two unequal simple setae distally, longer one reaching end of exopod. Exopod approximately 0.80 times as long as
endopod. Endopod with six delicate plumose setae proximally on dorsal surface, inner margin with fringe of minute setae, distal end with five plumose and three simple setae, two of latter longer than others, 1.5 and twice as long as article, respectively. Exopod, with five simple setae at distal end, longest seta approximately three times as long as article.

Early subadult female

Total length. 6.0–8.2 mm.

Whole isopod inside mantle cavity of rhizocephalan externa. Body (Figure 6a, b) orange-reddish (same colour as rhizocephalan ovary), consisting of large sac with small flat disc tilted over it. Appendages absent. Sac with five or six lateral lobes and pyriform vesicle (heart?) visible through cuticle. Disc with irregular concentric folds, detached from sac on one side but continuous with it on the other. Apparently, sac develops as internal anchor and disc becomes external brood sac in latter stages.

Advanced subadult female

Total length. 8.0–9.7 mm.

Anterior part of isopod protruding from mantle cavity of rhizocephalan externa. Body (Figure 6c) divided by constriction into two parts: rhomboidal caudal anchor, immersed in mantle cavity, and a freely exposed anterior subspherical sac. In some specimens developing adult visible beneath subadult cuticle. These developing adults with incipient brood pouch on ventral surface, visible as elongated area bounded by two folds and with rudiments of anterior finger-like processes and caudal digitations at its extremities.

Adult female

Total length. 3.3–9.3 mm.

Anchor with definitive form and sac exhibiting long ventral slit, through which the epicaridium larvae are expelled. Body (Figure 6d, e) divided by narrow neck into anchor deeply embedded in host’s body and subspherical part (brood pouch) protruding from host’s mantle wall. Anchor part: dorsal surface convex, with three parallel hollow bars; ventral surface concave, with tiny central papilla (called ‘vésicule rectale’ by Caullery, 1908, in his description of Liriopsis monophthalma). Heart visible through translucent cuticle as rounded sac below this papilla. Brood pouch: dorsal surface circumvallated by four lines, with five bunches of longitudinal muscles between them (muscles only evident in spent females). Ventral surface with longitudinal mid-line groove in ovigerous females (visible as slit in spent females). Mid-line furrow (slit): anterior end with finger-shaped process fitting between thick margins (Figure 6f); posterior end with six internal digitations, only visible by stretching pouch and peering through slit (Figure 6g).

Discussion

The genus Liriopsis contains two nominal species: L. pygmaea and L. monophthalma (see Grygier 1993). Rathke (1843) described Liriope pygmaea, the type species by monotypy of the genus, based on a few cryptoniscus larvae. In his description, Rathke mentioned that the last (seventh) pair of pereopods of the larva was shorter and thinner than the previous ones and ended in a stylet-like article (see also his Figure 11 in pl. I). Sars (1899) presented a more
detailed description with illustrations of the cryptoniscus larva; he noticed that the last two pairs of pereopods were very small, with the propodus almost globular and the dactylus straight and styliform. More recently, Nielsen and Strömberg (1973) published SEM photographs of the two pereopods (see their Figures 36, 37) confirming Sars’ description.

Our cryptoniscus larva differs from previous descriptions of *L. pygmaea* in the following details: (1) Sars (1899) stated that the large, linguiform expansion of the first antennular article had no traces of setae or spines; however, these setae are present both in an SEM photographs presented by Nielsen and Strömberg (1973: Figure 6) and in our specimens (see Figure 4b). (2) Sars (1899) mentioned and illustrated (see his figure ‘1C.’ in pl. 100) two teeth on the frontal edge of the second article of the antennule, and Nielsen and Strömberg (1973: Figures 6, 7b) provided SEM photographs of these two teeth. In contrast, our larvae have only one tooth there (see Figures 3d, 4b). (3) Sars (1899) stated that the exopod of the uropod scarcely attains half the length of the endopod (see his ‘1Urs.’ in pl. 100), but in our specimens the exopod is approximately 80% as long as the endopod (see Figure 5e).

Fraisse (1878) described and illustrated the cryptoniscus larva of *Cryptoniscus monophthalmus*. Later, Bonnier (1900) transferred this species to the genus *Liriopsis*, where it has since remained. According to Fraisse (1878), this larva has only the last (seventh) pereopod different from the others, with a fusiform propodus, of about the same length as the dactylus (see his Figures 45 and 54a in pl. XV). On the other hand, Caullery (1908) noticed that the last two pairs of pereopods (sixth and seventh) of *L. monophthalma* were quite similar to those of *L. pygmaea*, i.e. both have a subglobular propodus and a sword-like dactylus (see his figures B10–11). Since these two available descriptions are inadequate and also contradictory, we cannot establish with certainty the differences between the cryptoniscus larvae of *L. monophthalma* and *L. pygmaea*.

Lilljeborg (1859) described the epicaridium of *L. pygmaea*. Our specimens mainly differ from that description in having a biramous antennule and an anal tube distally. For *L. monophthalma*, Fraisse (1878) reported a bifid antennule but he did not mention an anal tube. Caullery (1908) revealed that *L. monophthalma* had an anal tube but unfortunately he did not illustrate it. Epicaridium larvae are very small and some anatomical aspects are hardly visible even at high magnification, therefore, some structures could have been erroneously reported or omitted in earlier descriptions.

Caullery (1908) described several juvenile females of *L. monophthalma*, all of them free in the mantle cavity of their host. The earliest stage is similar to the male except for having only two pairs of appendages, the antennules and the second(?) pereopods; the following stages become gradually broader. Despite the fact that we have recovered hundreds of tiny cryptoniscus larvae from our dissected rhizocephalan externae, no juvenile females have been found.

The stage herein referred to as SA$_R^1$ resembles Caullery’s description of *L. monophthalma* (1908: figure G3). However, the anterior end of the early subadult female of *L. monophthalma* is more or less conical, whereas that of our SA$_R^1$ carries a flat apical disc. This disc, by increasing many-fold in size, is likely to become the large brood pouch of the A$_Q$. The developing A$_Q$ is sometimes visible through the cuticle of the SA$_R^2$, confirming that the latter effectively precedes the former.

The A$_Q$ of *L. pygmaea* was satisfactorily described by Lilljeborg (1859). In addition, Fraisse (1878) briefly described the A$_Q$ of *L. monophthalma*, but did not mention any feature distinguishing it from the female of *L. pygmaea*. Lilljeborg (1859) had the opportunity to observe living specimens of *L. pygmaea* showing pulsating movements of
the brood sac. As was suggested by Caullery (1908), these contractions seem to be generated by the dorsal bundles of muscles, which have been represented in Figure 6d of the present paper.

The differences between *L. pygmaea* and *L. monophthalma* are obscure. The latter species is apparently restricted to the Mediterranean Sea, whereas *L. pygmaea* appears to have a broader geographic distribution. Because of the lack of detailed descriptions of these two species, and in order to avoid future nomenclatural problems, we provisionally identify our specimens as *L. pygmaea*, the type species of the genus. It is hoped that the present descriptions, together with the study of other relevant material, will allow a thorough revision of this genus in the future.

**Acknowledgements**

The authors thank Dr Gustavo A. Lovrich (CADIC, Ushuaia) for supplying us with the material used in this study, which was collected in surveys funded by the International Foundation for Sciences, Sweden (grant IFS A-2507/1). Our thanks also go to Dr Mark J. Grygier (Lake Biwa Museum, Japan) for reviewing and offering critical comments on the manuscript, and to Dr Axel O. Bachmann for his help with the German literature. This paper was partially supported by the Universidad de Buenos Aires (grant X019) and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina).

**References**

Altes J. 1981. Les Liriopsides. Bulletin de la Société d’Histoire naturelle de l’Afrique du Nord (Alger) 69, 3/4: 3–35.

Arnaud PM, Do-Chi T. 1977. Données biologiques et biométriques sur les lithodes *Lithodes murrayi* (Crustacea: Decapoda: Anomura) des îles Crozet (SW ocean Indien). Marine Biology 39:147–159.

Bate CS, Westwood JO. 1868. A History of the British Sessile-eyed Crustacea. Vol. II, London: John Van Voorst. 536 p.

Bonnier J. 1900. Contribution à l’étude des Épicarides: les Bopyridae. Travaux de la Station zoologique de Wimereux 8:1–478.

Boschma H. 1962. Rhizocephala. Discovery Reports 33:55–92.

Bourdon R. 1963. Épicarides et Rhizocéphales de Roscoff. Cahiers de Biologie Marine 4:415–434.

Bourdon R. 1967. Données complémentaires sur les Épicarides et les Rhizocéphales de Roscoff. Bulletin des Académie et Société Lorraines des Sciences 6:279–286.

Brinkmann A. 1936. Die Nordischen Munidaarten und ihre Rhizocephalen. Bergens Museums Skrifter 18:1–111.

Brinkmann A, Jr. 1984. Unpublished information concerning rhizocephalan and cryptoniscid parasites on decapod crustaceans collected by the late Professor August Brinkmann Sr. Sarsia 69:211–213.

Caullery M. 1908. Recherches sur les Liriopsidés, Épicarides cryptonisciens parasites des Rhizocéphales. Mitteilungen aus der Zoologischen Station zu Neapel 18:583–643.

Czerniavsky V. 1868. Materialia ad zoographiam Ponticam comparatam. Transactions of the First Meeting of the Russian Naturalists in Saint Petersburg 1868, 19–136 (in Russian).

Fraisse P. 1878. DieGattung Cryptoniscus Fr. Müller (*Liriope Rathke*). Arbeiten aus dem Zoologisch-Zootomisch Institut in Würzburg 4:239–296.

George RY, Strömborg JO. 1968. Some new species and new records of marine isopods from San Juan Archipelago, Washington, USA. Crustaceana 14:225–254.

Giard A, Bonnier J. 1890. Prodrome d’une monographie des Épicarides du golfe de Naples. Bulletin scientifique de la France et de la Belgique, Série 2 22:367–391.

Grygier MJ. 1993. Cryptoniscidae s. s. (Isopoda: Epicaridea): nomenclatural history and recommendations. Publications of the Seto Marine Biological Laboratory 36:185–195.

Grygier MJ, Bowman T. 1990. The correct family-level name for the ‘cryptoniscid’ isopods (Epicaridea). Crustaceana 58:27–32.

Høeg J, Lützen J. 1985. Crustacea Rhizocephala. Marine Invertebrates of Scandinavia. No. 6, Oslo: Norwegarian University Press. 90 p.
Lange S. 1999. Rhizocephala (Crustacea, Cirripedia) of the Faroe Islands. Sarsia 84:79–93.

Lilljeborg W. 1859. Les genres Liriopè et Peltogaster, H. Rathke. Nova Acta Regiae Societatis Scientiarum Upsaliensis 3:1–35.

Lilljeborg W. 1860. Supplément au mémoire sur les genres Liriopè et Peltogaster, H. Rathke. Nova Acta Regiae Societatis Scientiarum Upsaliensis 3:73–102.

Müller F. 1859. Polypen und Quallen von Santa Catharina: die Formwandlung der Liriopè cathariensis n. sp. Archiv für Naturgeschichte 25:310–321.

Müller F. 1871. Bruchstücke zur Naturgeschichte der Bopyriden. Jenaische Zeitschrift für Medizin und Naturwissenschaften 6:53–73.

Nielsen S-O, Strömberg J-O. 1965. A new parasite of Cirolana borealis Lilljeborg belonging to the Cryptoniscinae (Crustacea Epicaridea). Sarsia 18:37–62.

Nielsen S-O, Strömberg J-O. 1973. Morphological characteristics of taxonomical importance in Cryptoniscina (Isopoda Epicaridea). A scanning electron microscopic study of cryptoniscus larvae. Sarsia 52:75–96.

Nierstrasz HF, Brender à Brandis GA. 1926. X. e. Isopoda: I. Epicaridea. In: Grimpe G, Wagler E, editors. Tierwelt der Nord- und Ostsee. Vol. X, Leipzig Akademische Verlagsgesellschaft: p 1–56.

Otto RS, MacIntosh RA. 1996. Observations on the biology of the lithodid crab Paralomis spinosissima from the Southern Ocean near South Georgia. High Latitude Crabs: Biology, Management, and Economics. Alaska Sea Grant Program Report 96-02, Fairbanks: University of Alaska. p 627–647.

Pérez C. 1929. Notes sur les Épicarides et les Rhizocephales des côtes de France (V). Non spécificité du parasitisme du Liriopis pygmaeae. Bulletin de la Société zoologique de France 54:607–608.

Pérez C. 1931. Notes sur les Épicarides et les Rhizocephales des côtes de France (VII). Peltogaster et Liriopis. Bulletin de la Société zoologique de France 56:509–512.

Pike RB. 1961. Observations on Epicaridea obtained from hermit-crabs in British waters, with notes on the longevity of the host-species. Annals and Magazine of Natural History, Series 13 4:225–240.

Pohle GW. 1992a. First Canadian record of Paralomis bouvieri Hansen, 1908 (Decapoda: Anomura: Lithodidae), infected by the rhizocephalan Briarosaccus callosus (Cirripedia: Peltogastridae) and carrying a hyperparasitic cryptoniscinid (Epicaridea). Canadian Journal of Zoology 70:1625–1629.

Pohle GW. 1992b. First record of the rhizocephalan Briarosaccus callosus (Cirripedia, Peltogastridae) infecting the Atlantic porcupine stone crab Neolithodes grimaldii (Decapoda, Anomura, Lithodidae). Crustaceana 62:133–136.

Rathke H. 1843. Beiträge zur Fauna Norwegens. Nova Acta Academiae Caesareo-Leopoldinae Naturae Curiosorum 20:1–264.

Roccatagliata D, Lovrich GA. 1999. Infestation of the false king crab Paralomis granulosa (Decapoda: Lithodidae) by Pseudione tuberculata (Isopoda: Bopyridae) in the Beagle Channel, Argentina. Journal of Crustacean Biology 19:720–729.

Sars GO. 1899. An Account of the Crustacea of Norway. Vol. 2, Isopoda, Bergen: Bergen Museum, 270 p.

Shino SM. 1952. On the genus Danalia Giard found in Japan. Annotationes Zoologicae Japonenses 25:329–336.

Steenstrup J. 1855. Bemerkungen über die Gattungen Pachybdella Dies. und Peltogaster Rathke, zweier auf dem Hinteleibe von Krabben und Krebsen schmarotsenden Thierformen. Archiv für Naturgeschichte 21:15–29, addendum.

Warrenchuk JJ, Shirley TC. 2000. Parasitism by the rhizocephalan Peltogaster paguri Rathke, 1842 and hyperparasitism by the bopyrid isopod Liriopis pygmaeae (Rathke, 1843) on Pagurus hirsutiusculus (Dana, 1851) in southeastern Alaska. Crustaceana 73:971–977.

Watters G. 1998. Prevalences of parasitized and hyperparasitized crabs near South Georgia. Marine Ecology Progress Series 170:215–229.