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New species of *Goreopagurus* (Decapoda: Anomura: Paguridae) from Tasmania and reevaluation of sexual tubes in hermit crab systematics

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Abstract Lemaitre, R. and McLaughlin, P.A. 2003. New species of *Goreopagurus* (Decapoda: Anomura: Paguridae) from Tasmania and reevaluation of sexual tubes in hermit crab systematics. *Memoirs of Museum Victoria* 60(2): 221–227. A new, deep-water species is assigned to the hermit crab genus *Goreopagurus* McLaughlin, 1988, previously known only from western Atlantic and eastern Pacific waters. The assignment is made because of the unusual and sexually dimorphic expansion of the right cheliped characteristic of species of this genus. However, in contrast to its congeners, *Goreopagurus poorei* sp. nov. has distally quadriserial gills and exhibits no male sexual tube development. The latter condition has made it necessary to reevaluate the emphasis placed on sexual tubes in paguroid systematics. *Goreopagurus* has been emended to accommodate this species.

Keywords Crustacea, Anomura, Paguroidea, Paguridae, Goreopagurus, taxonomy

Introduction

McLaughlin (1988) proposed the genus Goreopagurus for a small hermit crab, Pagurus piercei Wass, 1963. Wass' (1963) original description of P. piercei was based on a single male from off Port Aransas, Texas, USA., and while the species was found in substantial numbers in the Middle Atlantic Bight (Wenner and Boesch, 1979), it was not until it was collected off the east Florida continental shelf that a critical morphological examination was conducted. McLaughlin (1988) found that adult females of P. piercei were provided with paired and modified first pleopods; mature males were found to have a short sexual tube produced from the gonopore on the right fifth coxa, and frequently a very short tube or papilla was produced from the left gonopore. At that time, only species of Nematopagurus A. Milne-Edwards and Bouvier, 1892, and "Pagurodes" limatulus Henderson, 1888 (subsequently reassigned to Michelopagurus McLaughlin, 1997) were known to have sexual modifications in both sexes. McLaughlin (1988) reasoned that Pagurus piercei could not be assigned to Nematopagurus because of the structure of the male sexual tube, which was long and distally filiform, rather than short and "stubby". Although Pagurus piercei and Pagurodes limatulus agreed in the form of the sexual tube and the female paired first pleopods, McLaughlin (1988) considered them not to be congeneric because the gills of Pagurus piercei were biserial, the chelipeds

were grossly unequal and the ambulatory dactyls relatively short. In contrast, the gills of *Pagurodes limatulus* were quadriserial, the chelipeds were subequal and the ambulatory dactyls relatively long.

In addition to the chelipeds being grossly unequal in *Goreopagurus piercei*, the right cheliped was distinctively sexually dimorphic. The carpus in small males and females was somewhat broader than the elongate chela, but with increased size, the male carpus developed a marked flare of the dorsomesial margin, the dorsal surface doubled or tripled in breadth, the lateral face became appreciably produced ventrally and the ventral surface became noticeably concave. The chela became correspondingly more elongate, while surface and marginal spination was reduced.

McLaughlin and Haig (1995) described a second species from the eastern Pacific. Although paired first pleopods were present in females, the male right sexual tube was distinctly shorter in *G. garthi* McLaughlin and Haig, 1995, and the left tube, if developed at all, was even shorter. Despite this difference in sexual tube development, McLaughlin and Haig had no difficulty in assigning their new species to *Goreopagurus*, because the dimorphic right cheliped, while not identical to that of *G. piercei*, was morphologically very similar and showed comparable changes in the carpus and chela in large males. Mature males of the Tasmanian species, *Goreopagurus poorei* Shield length is measured from the tip of the rostrum to the midpoint of the posterior margin of the shield. The ratio of corneal diameter to ocular peduncle length was obtained by measuring the length of the left ultimate peduncular segment, including the cornea along the lateral surface; corneal diameter was the maximum measured width of the left cornea. Sexual tube lengths are based on the criterion proposed by McLaughlin (2003). The holotype and most paratypes are deposited in Museum Victoria, Melbourne, Australia (NMV); three paratypes have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Goreopagurus McLaughlin, 1988

Emended diagnosis. Eleven pairs of biserial or distally quadriserial phyllobranchiate gills. Ocular acicles triangular, with prominent submarginal spine, separated basally by basal width or more of 1 acicle. Antennal peduncle with supernumerary segmentation. Maxillule with internal lobe moderately well developed and provided with 1 or 2 stiff distal bristles; external lobe produced, not recurved. Third maxilliped with well developed crista dentata and prominent accessory tooth; merus with or without dorsodistal and ventral marginal spines. Sternite of third maxillipeds with or without small spine on either side of midline.

Right cheliped with elongate, slender chela; propodal-carpal articulation generally perpendicular. Carpus tending to be strongly produced ventrally, at least in large males, dorsomesial margin slightly to prominently expanded. Left cheliped appreciably shorter than right; chela slender, triangular in crosssection; propodal-carpal articulation perpendicular. Sternite of third pereopods with anterior lobe variable in shape. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl with or without preungual process. Fifth pereopods chelate. Sternite of fifth pereopods consisting of 2 ovate or subcircular lobes.

Mature males with coxae of fifth pereopods generally symmetrical; gonopore of right without or with vas deferens produced as short sexual tube; gonopore of left without or with vas deferens produced as very short tube or papilla; 3 unpaired uniramous or weakly biramous pleopods developed on left side of abdominal somites 3–5, very rarely vestigial pleopod on somite 2. Females with paired gonopores; well developed, paired and modified first pleopods; 4 unpaired pleopods, second to fourth unequally biramous, fifth with endopod rudimentary or absent.

Abdomen flexed. Uropods asymmetrical. Telson with transverse indentations; posterior lobes symmetrical or slightly asymmetrical; separated by small median cleft; terminal margins oblique or straight, each armed with few to several small spines; lateral margins frequently delimited by narrow chitinous plate. Goreopagurus poorei sp. nov.

Figures 1-3

Michelopagurus n. sp.—Koslow and Gowlett-Holmes, 1998: 32. *Michelopagurus* sp.—Poore et al., 1998: 71.

Material examined. Holotype. Australia, Tasmania, 84 km SSE of SE Cape, "J1" seamount, 44°16.2'S, 147°19.8'E, 1300 m, 27 Jan 1997 (CSIRO stn SS01/97 37), NMV J44757 (male, 5.2 mm).

Paratypes. Australia, Tasmania, off Freycinet Peninsula, 41°58.6'S, 148°38.9'E, 500 m, 27 Jul 1986 (stn SLOPE 47), NMV J17433 (2 males, 3.6, 4.2 mm). 85.4 km SSE of SE Cape, "Main Pedra" seamount, 44°15.6'S, 147°06.0'E, 741 m, 21 Jan 1997 (CSIRO stn SS01/97 03), NMV J44807 (5 males, 2.9-3.6 mm); NMV J44767 (2 ovigerous females, 2.4, 2.7 mm). 83.8 km SSE of SE Cape, "J1" seamount, 44°16.2'S, 147°19.8'E, 987 m, 27 Jan 1997 (stn SS01/97 36), NMV J448051 (male, 2.4 mm; ovigerous female, 2.6 mm); USNM 1007889 (female, 3.7 mm). 84.0 km SSE of SE Cape "J1" seamount, 44°16.2'S, 147°19.8'E, 1300 m, 27 Jan 1997 (stn SS01/97 37), NMV J52355 (3 males, 3.3-4.9 mm; ovigerous female, 3.2 mm). 85.8 km SSE of Cape, "B1" seamount, 44°18.6'S, 147°16.2'E, 1150 m, 28 Jan 1997 (stn SS01/97 43), NMV J448021 (male, 3.0 mm). 69.7 km SSE of SE Cape, "Mackas" seamount, 44°12.6'S, 147°02.4'E, 640 m, 29 Jan 1997 (stn SS01/97 50), NMV J44808 (male, 3.0 mm). 65.5 km SSE of Cape, SE "Andys" seamount, 44°10.8'S, 147°00.0'E, 800 m, 29 Jan 1997 (stn SS01/97 56), NMV J44804 (5 males, 2.9-4.7 mm), USNM 1007890 (2 males, 2.6, 3.9 mm). 65.1 km SSE of Cape, SE "Andys" seamount 44°10.8'S, 146°59.4'E, 900 m, 29 Jan 1997 (stn SS01/97 57), NMV J44809 (male, 3.0 mm).

Other material. Australia, Tasmania. 66.5 km SSE of Cape, SE "Andys" seamount, 44°11.4'S, 148°57.0'E, 620 m, 29 Jan 1997 (stn SS01/97 55), NMV J44806 (2 males, 2.9, 3.4 mm). 65.6 km SSE of Cape, SE "Andys" seamount, 44°10.8'S, 147°00.0'E, 800 m, 29 Jan 1997 (stn SS01/97 56), NMV J44764 (ovigerous female, 2.6 mm). Exact locality not recorded (CSIRO cruise 1/97), NMV J44810 (male, 2.4 mm; 3 ovigerous females, 2.4–3.3 mm).

Description. Gill lamellae distally quadriserial (Fig. 1a). Shield (Fig. 1b) as broad or broader than long; anterior margins between rostrum and lateral projections weakly concave; anterolateral margins sloping or slightly terraced; posterior margin roundly truncate, frequently with slight median concavity; dorsal surface with few sparse tufts of setae. Rostrum (Fig. 1b–d) acutely or obtusely triangular, with or without small terminal spine or spinule, sometimes also with 1 small spine or spinule laterally on one side. Lateral projections obtusely triangular, each with small submarginal spine.

Ocular peduncles 0.4–0.6 length of shield, moderately stout and with distinct medial constriction; dorsomesial surface with 2 or 3 short, transverse rows of stiff setae in distal half, 1 sparse tuft of setae on dorsal surface; corneal diameter 0.4–0.5 of peduncular length. Ocular acicles narrowly and acutely triangular, with strong submarginal spine; separated basally by at least basal length of 1 acicle.

Antennular peduncles overreaching distal margins of corneas by at least entire length of ultimate segments. Ultimate segment with row of long, stiff setae at dorsodistal margin and additional few scattered, short setae. Penultimate segment with few scattered setae. Basal segment with slender spine on lateral margin of statocyst lobe.

Antennal peduncles overreaching distal corneal margins by

New Tasmanian hermit crab and reevaluation of sexual tubes



Figure 1. *Goreopagurus poorei* sp. nov.: paratypes: a–c, f, male (3.9 mm), USNM 1007889; d, male (sl =2.6 mm), USNM 1007890; e, female (3.7 mm), USNM 1007889. a, gill lamella; b, shield and cephalic appendages, dorsal view; c, d, rostrum, dorsal view; e, female coxae, eight thoracic sternite, and first abdominal somite with paired pleopods, ventral view; f, telson, dorsal view.

0.7 to entire length of ultimate segments. Fifth segment with several sparse tufts of setae. Fourth segment with few scattered setae. Third segment with prominent, acute spine at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, mesial margin with 3–7 small spines or spinules (occasionally only weakly apparent) and usually with 1 prominent spine on lateral margin in distal half; dorsomesial distal angle with well developed spine. First segment usually with small spine on dorsolateral distal margin and 1 spine on ventrolateral margin distally. Antennal acicle long, reaching beyond midlength of ultimate peduncular segment, arcuate, terminating in small spine; mesial surface with row of tufts of stiff setae. Antennal flagella long, but usually not overreaching tip of outstretched right cheliped; articles each usually with 2 or 3 short (< length of 1 article) setae.

Third maxilliped with 2 or 3 spines on basis; ischium with accessory tooth on well developed crista dentata; merus with 1 spine on ventral margin and 1 spine at dorsodistal margin. Sternite of third maxillipeds with tiny spinule on either side of midline.

Right cheliped (Fig. 2a–e) of large males very elongate, somewhat shorter in females and small males; palm, fixed finger and dactyl slender, dorsoventrally compressed. Dactyl 0.7–0.9 length of palm; cutting edge with 1 moderately prominent calcareous tooth at midlength, 3 or 4 smaller calcareous teeth proximally and row of very small corneous teeth in distal 0.3, terminating in small corneous claw, but often worn; dorsomesial margin with row of very small spines, spinules or spinulose tubercles, dorsal surface somewhat elevated in midline, occasionally unarmed but usually with single or double row of very small spinules, tubercles or protuberances. Palm slightly shorter than carpus; dorsomesial margin not distinctly delimited, rounded mesial face with irregular rows of very small tubercles, granules or spinules; dorsolateral margin with row of very small spinules, dorsal surface with covering of very small spinules or granules and very short setae, most prominent in females and small males, occasionally additional short row of slightly larger spinules or granules adjacent to dorsolateral margin proximally, dorsal midline with 1 or short, longitudinal row of 2-4 small spines proximally; cutting edge of fixed finger with entire calcareous margin in proximal half, usually few individual calcareous teeth distally, terminating in corneous claw, often worn. Carpus (Fig. 2b, c, e) longer than merus, produced ventrally, particularly in large males; dorsomesial margin weakly to notably expanded, armed with row of prominent, blunt or acute spines, dorsodistal margin with 1 or 2 spines mesially, dorsal surface usually with numerous very small tubercles, granules or low protuberances and scattered setae, dorsolateral margin usually delimited at least distally by row of small granules or spinules; mesial face usually sloping, often

Rafael Lemaitre and Patsy A. McLaughlin



Figure 2. *Goreopagurus poorei* sp. nov.: a–c, f, paratype male (3.9 mm), USNM 1007890; d, e, holotype male (5.2 mm), J44757. a, merus, carpus and chela of right cheliped, dorsal view; b, carpus of same, lateral view; c, same, mesial view; d, carpus and chela of right cheliped, dorsal view; e, carpus of same, ventromesial view; f, merus, carpus and chela of left cheliped, dorsal view.



Figure 3. *Goreopagurus poorei* sp. nov.: paratype male (3.9 mm), USNM 1007890. a, second right pereopod, lateral view; b, dactyl of same, mesial view; c, third right pereopod, lateral view; d, dactyl of same, mesial view; e, anterior lobe of sternite of third pereopods, ventral view; f, propodus and dactyl of left fourth pereopod, lateral view.

New Tasmanian hermit crab and reevaluation of sexual tubes

appearing somewhat concave, ventromesial margin unarmed; ventrolateral margin with row of granules, tubercles or spines. Merus subtriangular; dorsodistal margin sometimes with 1 spine, dorsal surface with few low protuberances and setae; ventromesial and ventrolateral margins each with row of spines, ventral surface usually with few scattered spines and sparse, moderately long setae. Ischium with row of small spinules on ventromesial margin, at least proximally, and scattered moderately long setae.

Left cheliped (Fig. 2f) long and slender, but not reaching much beyond proximal margin of palm of right in large males; dactyl and fixed finger weakly arched ventrally. Dactyl 1.5-2.0 length of palm; cutting edge with row of tiny corneous teeth, terminating in small corneous claw; dorsal surface elevated in midline and with sparse row of setae; dorsomesial margin with irregular row of small spinules or tubercles, at least in proximal half. Palm 0.4-0.6 length of carpus; dorsomesial margin with irregular row of small spines or tubercles, dorsal surface usually with covering of very short setae, midline prominently elevated and armed with row of small spines, extending onto fixed finger but usually not to tip, dorsolateral margin with row of small spinules or granules, adjacent dorsal surface granular; ventral surface with scattered tufts of long setae; cutting edge of fixed finger with row of very small calcareous teeth, interspersed distally with corneous teeth. Carpus slightly shorter to slightly longer than merus; dorsal surface somewhat flattened, dorsomesial and dorsolateral margins each with row of spines, strongest distally; mesial face with numerous protuberances and setae, distomesial margin with few spinules ventrally, sometimes extending onto ventromesial margin; ventral surface with few spinules or low protuberances and scattered, moderately long setae; lateral face unarmed, ventrolateral margin with row of spines. Merus subtriangular; dorsal surface with few low protuberances and sparse setae; ventromesial and ventrolateral margins each with row of spines and moderate to long setae, ventral surface frequently with moderately dense covering of short setae. Ischium with row of small spines or spinules on ventromesial margin and scattered moderately long setae.

Ambulatory legs (Fig. 3a-d) similar from left to right. Dactyls 1.2-1.4 length of propodi; dorsal margins each with sparse row of short stiff setae; ventral margins each with row of 10-13 corneous spines; lateral faces each with weak longitudinal sulcus; mesial faces each with row of corneous spinules dorsally. Propodi 1.3-1.7 length of carpi; each with 1 or 2 corneous spinules at ventrodistal angle and row of widely-spaced, small corneous spinules on ventral margin, dorsal surfaces each with low protuberances and sparse stiff setae or bristles. Carpi each with small spine at dorsodistal margin, few stiff setae arising from low protuberances on dorsal surface, 1 or 2 stiff setae on ventral margin distally and occasionally also medially. Meri with low protuberances and sparse tufts of setae on dorsal surfaces, tufts of stiff setae and occasionally 1 to few, often spinulose, protuberances or small spinules on ventral surfaces, distal angles of second percopods occasionally each with acute spine (not present in holotype). Ischia unarmed but with few stiff setae or bristles. Anterior lobe of sternite of third pereopods (Fig. 3e) subsemicircular with stiff bristles on anterior margin.

Fourth percopods (Fig. 3f) with small preungual process at base of claw.

Males without sexual tube on either coxa of fifth pereopods; unpaired left pleopods 3–5 with endopods rudimentary, very rarely with vestigial second pleopod present. Females with paired and modified first pleopods (Fig. 1e); second to fourth unpaired left pleopods with endopods stout, egg-bearing, exopods long, slender and usually non egg-bearing; fifth pleopod as in males. Uropods markedly asymmetrical. Telson (Fig. 1f) with transverse indentation; posterior lobes separated by moderately shallow median cleft, terminal margins slightly oblique to nearly horizontal, each with 3–5 small spines, lateral margins sometimes delimited by narrow chitinous band.

Colour (in preservative). Cephalothorax, carpi and meri of chelipeds and entire ambulatory legs with tint of reddishorange; chelas dirty-white. Ocular peduncles dull red.

Distribution. Tasmania, off Freycinet Peninsula and seamounts SSE of Southeast Cape: "Andys", "B1", "J1", "Main Pedra", and "Mackas" seamounts; 500–1300 m depth.

Etymology. For Gary C. B. Poore, Curator of Crustacea at Museum Victoria, Melbourne, Australia, in recognition of his major contributions to crustacean systematics.

Remarks. On the basis of a few individuals, this species was tentatively but incorrectly assigned to *Michelopagurus* by P.A. McLaughlin in correspondence to Koslow and Gowlett-Holmes (1998).

Individuals of Gorepagurus poorei are significantly larger than those of G. piercei and G. garthi. Specimens range in shield length from 2.4 to 5.2 mm, whereas the specimens of G. piercei and G. garthi, all sexually mature and including some ovigerous females recorded by McLaughlin (1988) and McLaughlin and Haig (1995) range from 0.5 to 1.8 mm, and 1.3 to 2.3 mm, respectively. McLaughliin (1988) and McLaughlin and Haig (1995) attributed variation of the right cheliped, particularly the carpus, of G. piercei and to some extent also G. garthi, to sexual dimorphism. Although specimens of G. poorei as small as those of G. piercei and G. garthi are not known, it appears that in G. poorei variations of the carpus are related to allometric growth rather than sexual dimorphism. The dorsomesial margin of the carpus in large specimens of G. poorei develop a more marked flare (Fig. 2a-d) than in smaller specimens; the strength and sharpness of the spines on the dorsomesial and ventrolateral margins of the carpus diminish with increased size.

Not only is *G. poorei* immediately distinguishable from *P. piercei* and *P. garthi* by the absence of male sexual tubes, the gill lamellae are distally quadriserial rather than biserial. Although uniformity in gill structure is usual in most genera, *Goreopagurus* is not the only genus in which both biserial and distally quadriserial gills are found. A similar condition exists in the parapagurid genus *Sympagurus* (Lemaitre, in press: fig. 1) and the pagurid *Xylopagurus* A. Milne-Edwards, 1880 (pers. obs.). McLaughlin and de Saint Laurent (1998) reported that gill lamellae vary from deeply quadriserial to only distally so within a single species or even within a single individual. De Saint Laurent-Dechancé (1966) considered quadriserial gills

more primitive than biserial gills, thus one might envision the evolution of the gill lamellae from completely divided to distally divided to entire (biserial). In the case of the three species of *Goreopagurus*, the most primitive species then would be *G. poorei*. Support for this hypothesis is also apparent in the transition from no sexual tubes in *G. poorei* to very short tubes in *G. garthi* to short tubes in *G. piercei*.

Sexual tube development and its role in systematics of Paguroidea

H. Milne Edwards (1837) described specialised tubular structures found on the coxae of the fifth percopods in a species of the semiterrestrial hermit crab genus Coenobita Latreille, 1829. De Haan (1849) described an apparently similar structure in the pagurid, Pagurus spiriger De Haan, 1849, a species subsequently transferred to the genus Spiropagurus Stimpson, 1858. Although these tubular structures on the coxae of male pagurids and coenobitids were recognised by early carcinologists (e.g., Stimpson, 1858; Miers, 1881; Henderson, 1888; A. Milne-Edwards and Bouvier, 1892, 1893; Borradaile, 1903; Alcock, 1905), it was de Saint Laurent-Dechancé (1966) and de Saint Laurent (1968, 1970a, 1970b) in particular who discussed their role in the systematics of Paguridae. Importantly, she pointed out that early classifications had placed species in genera on the basis of tube position, without consideration of other characters, and as a result, species with disparate morphologies often were assigned to the same genus. At that time, only eight genera had been described with male sexual tubes. There are now many more (McLaughlin, 2003) and the number has increased dramatically in the past 35 years.

Two types of sexual tubes can be differentiated, although most descriptions make no distinction. Those in several, but not all, species of *Coenobita* represent prolongations of the coxae that are heavily calcified, and are diagnostic at the specific level (Nakasone, 1988). In contrast, sexual tubes in Paguridae are diverse and may be coxal prolongations or external prolongations of the vas deferens that may be calcified, chitinous or membranous. Their development and form have had a major, although not always informed, impact on classification at the generic level. McLaughlin's (2003) key to genera emphasises the length and direction of sexual tubes but there are many instances where intrageneric variation requires alternative pathways. Her figures 7h–t illustrate the varibility.

De Saint Laurent (1968, 1970a, 1970b) was of the opinion that just the presence or position of tubes was not indicative of close phylogenetic relationships. McLaughlin and Lemaitre (2001), and Lemaitre and McLaughlin (2003) emended the diagnoses of *Pylopagurus* A. Milne-Edwards and Bouvier, 1891, *Enallopaguropsis* McLaughlin, 1981, and *Enallopagurus* McLaughlin, 1981, to indicate minor sexual tube development in some species. Their rationale was that members of each genus shared suites of other morphological characters. In contrast, Komai (1998, 1999) transferred four species from *Pagurus* to *Parapagurodes* McLaughlin and Haig, 1973 simply because males were found to have very short sexual tubes. As a result, the presence of a right sexual tube is the only commonly shared character among these species currently assigned to *Parapagurodes*. On the basis of cheliped morphology and other attributes, *P. gracilipes* (Stimpson, 1858) and *P. nipponensis* Yokoya, 1933 appear most closely related to McLaughlin's (1974) "*bernhardus*" group of *Pagurus*. Similarly *Parapagurodes imalli* (Yokoya, 1939) and *P. constans* (Stimpson, 1858), while not immediately identifiable with specific groups within *Pagurus*, are not phylogenetically related to the species for which the genus *Parapagurodes* was proposed. This view is also supported by the larval data of Hong and Kim (2002) for *P. constans*.

Correspondingly, Asakura (2001: 827) transferred Catapagurus doederleini Doflein, 1902 to Parapagurodes, stating that Doflein's (1902) species agreed in all diagnostic characters with McLaughlin and Haig's (1973) genus. Yet Asakura (2001: 888) pointed out how the structure of the ambulatory legs of P. doederleini differed from all species presently included in Parapagurodes. Additionally, there are marked differences in telson structure of P. doederleini and all of the other assigned species. The only shared character of any potentially phylogenetic significance is the presence in P. doederleini, as in the other species, of a very short right sexual tube and a slight protrusion of the vas deferens from the left gonopore. We concur with Asakura's conclusion that Doflein's (1902) species is not assignable to Catapagurus or Hemipagurus as redefined; however, its inclusion in Parapagurodes is equally inappropriate.

Our only precise information on the structure and function of hermit crab sexual tubes is the recent study by Tudge and Lemaitre (2003) of *Micropagurus acantholepis* (Stimpson, 1858), a species with a moderate to long (> 2 coxal lengths) left sexual tube. These authors demonstrated that a well developed sexual tube is used in the transport of spermatophores and described the ultrastructure. Sexual tube structure is just one of a number of morphological characters that should be considered when making generic evaluations.

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New Tasmanian hermit crab and reevaluation of sexual tubes

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