

Descriptions of megalopa and juveniles of *Sympagurus dimorphus* (Studer, 1883), with an account of the Parapaguridae (Crustacea: Anomura: Paguroidea) from Antarctic and Subantarctic waters

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Four species and a megalopa of the hermit crab family Parapaguridae were obtained during cruises of the USNS *Eltanin* (1962-8) and *Hero* (1971) to Antarctic and Subantarctic waters. Adults, numerous juveniles, and the presumed megalopal larvae of *Sympagurus dimorphus* (Studer, 1883), are reported. Morphological variations and pleopod development in juveniles, and the megalopa of this species, are described and illustrated. *Sympagurus haigae* (De Saint Laurent, 1972), and *Parapagurus latimanus* Henderson, 1888, previously were either poorly defined or known from only a few localities; they are diagnosed or their descriptions amended, and illustrated. *Parapagurus bouvieri* Stebbing, 1910, was found off the coast of New Zealand, extending its range across the Indian Ocean. It is postulated that, at least in some species of *Sympagurus*, megalopal development is more variable than previously assumed.

KEYWORDS: Hermit crabs, Parapaguridae, *Parapagurus*, *Sympagurus*, juvenile morphology, pleopod development, megalopa, Antarctic, Subantarctic.

Introduction

A collection containing four hermit crab species of the family Parapaguridae was obtained during cruises of the USNS *Eltanin* (1962-8) and *Hero* (1971), as part of the US Antarctic Research Program of the National Science Foundation. Most important in this collection are the numerous specimens of a morphologically highly variable species, *Sympagurus dimorphus* (Studer, 1883), including an unusually large series of juveniles. Availability of these juveniles has made possible the detailed description of morphological variations as well as pleopod and telson development during the early growth stages of this species. This information is of importance because juvenile developmental variations in species of this family have not been described, and appear to differ from those of other families. The only information available on variation in parapagurid juveniles was based on a few specimens included by Lemaitre (1989) in a study of western Atlantic species of *Parapagurus* and *Sympagurus*, and by Wolff (1961) for the highly specialized *Probeebei mirabilis* Boone.

In addition, the USNS *Eltanin* material contains a number of megalopal stage individuals also believed to represent *Sympagurus dimorphus*. The capture of these postlarvae is of considerable interest because the rearing of larvae for any species of this

family has not been successfully achieved beyond the second zoeal stage (Williamson and von Levetzow, 1967; Provenzano, unpublished). The early larval stages of parapagurids are still known based only on zoeae obtained from plankton samples (De Saint Laurent-Dechancé, 1964), and the species identifications are questionable (Lemaitre, 1989). De Saint Laurent-Dechancé (1964) considered that the megalopae (cited as *Glaucothoe* spp.) reported by several carcinologists (Bouvier, 1891, 1905, 1922; A. Milne Edwards and Bouvier, 1900; Whitelegge, 1900; Gurney, 1924; Hale, 1941, Barnard, 1950; Thompson, 1943; Lebour, 1954), actually represented species of *Parapagurus* (*sensu lato*, see Lemaitre, 1989). However, by current standards this stage has not been adequately described. A description of the USNS *Eltanin* megalopae, as well as illustrations, is included.

Two species, *Sympagurus haigae* (De Saint Laurent, 1972) and *Parapagurus latimanus* Henderson, 1888, were either poorly defined or were known from only a few localities; these species are diagnosed or their descriptions amended, and illustrated. Specimens of *Parapagurus bouvieri* Stebbing, 1910, a species previously known only from the southeastern Atlantic and southwestern Indian Ocean, were found off the eastern coast of New Zealand. *Parapagurus bouvieri* is excluded from the systematic account because it has been sufficiently discussed by Lemaitre (1990).

Materials and methods

To supplement the material obtained during the cruises of the USNS *Eltanin* and *Hero*, it has been necessary to examine specimens from other expeditions or sampling programmes. This supplemental material has been used to complete observations, clarify identities, or update the distributions of the species. Data on USNS *Eltanin* and *Hero* stations where Parapaguridae were obtained are included in the Appendix, and those from other expeditions or sampling programmes are included for each species under 'Additional material'. The USNS *Eltanin* and *Hero* material was sorted at the Smithsonian Oceanographic Sorting Center, and is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). The supplemental material has been returned to the Natural History Museum, London (BMNH) (formerly the British Museum (Natural History)), the Australian Museum, Sydney (AMS), and the University of Cape Town, Cape Town (UCT). The following abbreviations are used: SL, shield length, measured to the nearest 0.1 mm, from the tip of the rostrum to the midpoint of the posterior margin of the shield; CL, carapace length, measured from the rostral tip to the posterior midpoint of the carapace; TL total length of the megalopa, measured from the tip of the rostrum to the midpoint of the telson, excluding the telsonal setae; stn, station; ovigs, ovigerous; and LGL Ecological Research Associates, Bryan, Texas. Institutional abbreviations used follow the standards proposed by Leviton *et al.* (1985). In the figure legends, station numbers correspond to USNS *Eltanin* cruises, unless otherwise stated.

The term juvenile, used for *Sympagurus dimorphus*, is applied to individuals with incompletely developed pleopods (all with a SL \leq 4 mm in the material studied). Even though all these juveniles were found to have clearly open gonopores, it is uncertain whether they were sexually mature. Larval terminology used follows McLaughlin *et al.* (1989), and that of adults follows McLaughlin (1974, 1980), and Lemaitre (1989). Serrate and plumose setae mentioned in the text are visible only under higher magnification, are not shown as such in the illustrations, and do not necessarily agree with the terminology applied by Drach and Jacques (1977), Pohle and Telford (1981),

or Ingle (1990). Sex of juveniles was determined by location of the gonopores. The term adult is used for specimens with fully developed pleopods (all SL \geq 4 mm in the material studied). The division of specimens into size intervals is arbitrary, for convenience in describing morphological variations, and does not necessarily indicate crab instars. Illustrations were prepared using a Wild M-8 scope with a *camera lucida*.

Family PARAPAGURIDAE Smith, 1882

Sympagurus dimorphus (Studer, 1883)

(Figs 1–5, Tables 1 and 2)

?*Eupagurus modicellus* Stebbing, 1914: 255, 277, pl. 26, fig. D (see Remarks).

Sympagurus dimorphus. Lemaitre, 1989: 71, figs 36–38, 40E–H; 1990: 229.

?*Sympagurus dimorphus*. Manning and Chace, 1990: 40, fig. 22 (see Remarks).

Material examined. USNS *Eltanin*: 2♂ (SL 7.9–9.4 mm), 7♀ (SL 9.1–10.4 mm), 3♀♀ ovigs (SL 8.9–10.0 mm), stn 740, USNM. 2♂ (SL 3.4–3.9 mm), 6♀ (SL 3.6–9.7 mm), stn 326, USNM. 1♂ (SL 12.9 mm), 2♀ (SL 5.2–11.5 mm), 2♀♀ ovigs (SL 11.0–11.1 mm), stn 970, USNM. 2♂ (SL 5.1–6.6 mm), 2♀ (SL 5.5–5.7 mm), 2♀♀ ovigs (SL 6.9–7.5 mm), stn 1283, USNM 155043. 1♀ (SL 13.4 mm), stn 1346, USNM. 2♂ (SL 5.9–14.6 mm), 3♀ (SL 2.7–6.6 mm), stn 1398, USNM. 46♂ (SL 3.8–9.8 mm), 42♀ (SL 3.0–8.4 mm), 15♀♀ ovigs (SL 3.9–6.0 mm), stn 1403, USNM. 14♂ (SL 7.7–15.9 mm), 3♀ (SL 5.9–10.8 mm), stn 1411, USNM. 2♂ (SL 9.8–11.3 mm), 2♀ (SL 6.7–8.3 mm), stn 1417, USNM. 1♂ (SL 12.1 mm), 2♀ (SL 8.2–8.3 mm), stn 1712, USNM. 45♂ (SL 2.8–10.8 mm), 45♀ (SL 2.4–5.2 mm), 5♀♀ ovigs (SL 4.2–5.4 mm), stn 1851, USNM. 2♂ (SL 5.1–5.7 mm), 5♀ (SL 6.6–7.2 mm), 5♀♀ ovigs (SL 7.3–7.5 mm), stn 1974, USNM. 5♂ (SL 5.5–6.2 mm), 1♀ (SL 4.6 mm), 3♀♀ ovigs (SL 5.5–5.8 mm), stn 1981, USNM. 2♂ (SL 4.3–12.0 mm), stn 1989, USNM. 1♀ ovigs (SL 7.5 mm), stn 2215, USNM. *Hero*: 5♀ (SL 10.1–11.2 mm), 1♀ ovigs (SL 10.1 mm), stn 895.

Additional material. 2♂ (SL 2.2–2.5 mm), 5♀ (SL 2.2–4.2 mm), stn MAD 17W.1, 46°41'S, 37°49'E, Marion and Prince Edward Islands, southwestern Indian Ocean, 355–375 m, 24 May 1985, UCT.

Description of juveniles. Shield weakly calcified in medial region. Iridescence usually present (preserved specimens) on more heavily calcified regions, such as shield, antennal peduncles, chelipeds, second and third pereopods, sixth abdominal somite, and uropods. Ocular peduncles stout (Fig. 1 a, b). Antennal acicles not reaching distal margin of corneae, with 2–7 strong spines on mesial margin, often terminating in bifid tip (Fig. 1 a, b). Antennal flagellum with articles bearing 2–4 long setae; setae about 3 or 4 flagellar articles in length. Right cheliped generally similar in both sexes, well calcified. Left cheliped well calcified; dorsal margin of carpus (Fig. 2 a) with 1–6 small spines or tubercles, often with scattered to dense stiff bristles. Second and third pereopods more slender than those of adults (Fig. 2 d–g); carpus of right second pereopod armed with dorsodistal spine and 1–6 spines on dorsal margin (Fig. 2 h–j). Propodal rasp of fourth pereopod with 1 or 2 rows of ovate scales (Fig. 3 a–c). Telson with left posterior lobe armed with 3–10 corneous spines on distal margin, spines increasing in number with growth (Fig. 3 f–h, j–l). Males with paired first pleopods absent or incompletely developed (Fig. 4 a–d), paired second pleopods (Fig. 4 f–j), and paired (SL < 3 mm) or unpaired (SL \geq 3 mm) third (Fig. 4 l–n) to fifth pleopods. Females lacking first pleopods, with paired asymmetrical second pleopods (Fig. 5 b–f), and paired (SL < 3 mm) or unpaired (SL \geq 3 mm) third (Fig. 5 g–i) to fifth pleopod (rami of left not crossed).

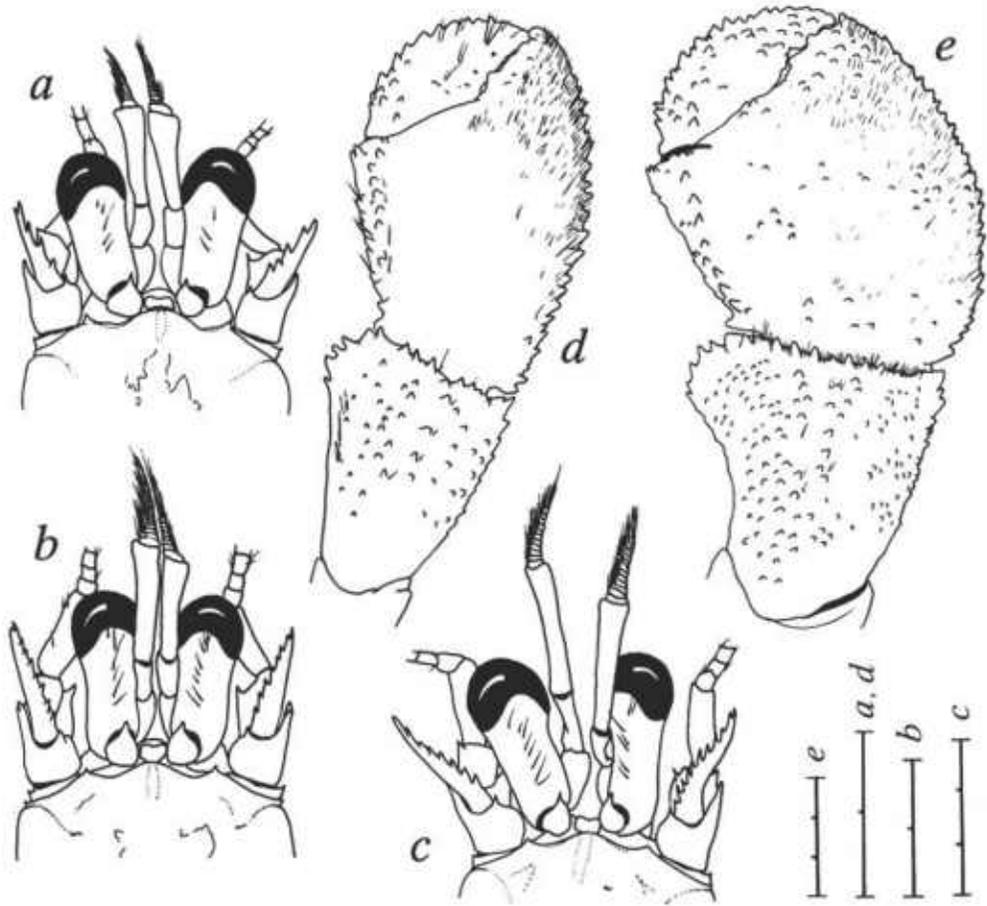


FIG. 1. *Sympagurus dimorphus* (Studer, 1883). Specimens from stn 1851. a–c, Anterior portion of shield and cephalic appendages: a, ♀ SL 2.9 mm; b, ♂ SL 3.9 mm; c, ♂ SL 4.8 mm. d, e, Propodus and chela of right cheliped: d, SL 2.9 mm; e, ♂ SL 5.8 mm. Scales equal 3 mm (e, c), and 2 mm (a, b, d).

Symbiotic associations. Juveniles are found in gastropod shells often with one or more small polyps of an undetermined anthozoan species attached to the shell.

Distribution. Southern hemisphere from 22 to 57°S, but possibly as far north as 9°, at Ascension Island (see Remarks). Depth range: 110–1995 m.

Remarks. The distribution cited for this species by Lemaitre (1989, 1990), was based partly on the literature. With the study of the USNS *Eltanin* and *Hero* material, as well as numerous lots examined from the Australian and New Zealand regions (Lemaitre, unpublished), the wide distribution of this species in the southern hemisphere can now be confirmed. Previously known from depths to 603 m, its bathymetric distribution is here extended to 1995 m, on the lower continental slope region.

Manning and Chace (1990) recently listed *Sympagurus dimorphus* as occurring in Ascension Island, in the South Atlantic. Their opinion was based on a specimen (apparently lost, SL 2.5 mm) previously identified by Stebbing (1914) in his description

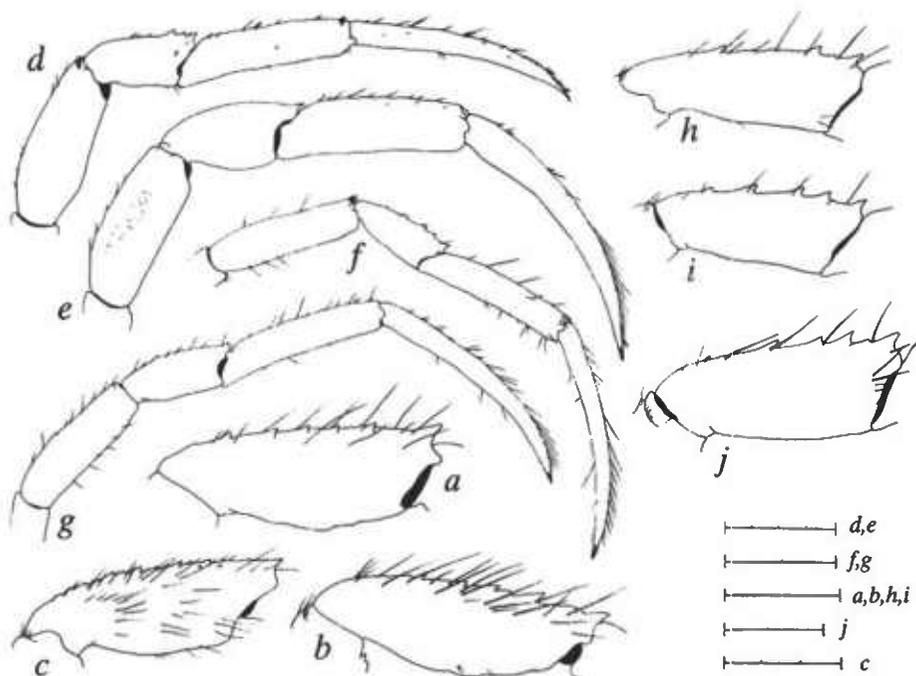


FIG. 2. *Sympagurus dimorphus* (Studer, 1883). Specimens from stn 1851. a-c, Carpus of left cheliped, mesial view: a, ♀ SL 2.9 mm; b, ♂ SL 4.8 mm; c, ♂ SL 6.1 mm. d-j, Right pereopods, lateral view: d, second, ♂ SL 5.8 mm; e, third, same ♂; f, second, ♂ SL 2.9 mm; g, third, same ♂; h, carpus of second, ♂ SL 2.8 mm; i, carpus of second, ♀ SL 2.9 mm; j, carpus of second, ♂ SL 3.9 mm. Scales equal 4 mm (d, e), 3 mm (c), 2 mm (f, g), and 1 mm (a, b, h-j).

of *Eupagurus modicellus*, and which they believed to actually represent a juvenile of *S. dimorphus*. Except for the eyestalks described by Stebbing as long and slender, and the unarmed antennal acicles depicted in his somewhat diagrammatic figure (pl. 26, fig. D), the specimen could be *S. dimorphus*. However, some doubt still remains about its identity. The large series of juveniles studied from the USNS *Eltanin* and *Hero* collections indicate that small individuals (such as Stebbing's) of *S. dimorphus* have short, stout eyestalks not exceeding the antennal peduncles and armed antennal acicles (Fig. 1 a, b). Unfortunately, Stebbing's specimen is not available and his description lacks the necessary information on other characters that could help ascertain its identity. Although Ascension Island is located considerably north of the known range of *S. dimorphus*, its presence there is possible given the counterclockwise circulation system of the South Atlantic, which could transport larvae from off southeastern Africa, where this species does occur, to Ascension Island. Additional material is needed to confirm the presence of this species in Ascension Island.

Variations in juveniles of *Sympagurus dimorphus*

(Figs 1-3, Table 1)

Antennal acicle (Fig. 1 a, b). Strength of the spines on the mesial margin of the antennal acicle is greater in small specimens (SL < 3.0 mm), the spines increasing in number with growth. The acicle is straight, not curved as in adults, and does not exceed the distal margin of the cornea.

Epistomial spine. Present in 95% of the juveniles examined.

Right cheliped (Fig. 1 d). The proportions and armature are similar in both sexes. The dorsal surface of the palm is generally smooth or with scattered small tubercles. The palm is about 1.25 times broader than long.

Carpus of left cheliped (Fig. 2 a). The dorsal armature consist of small spines or sharp tubercles which can often be numerous in adults (Fig. 2 b,c).

Second and third pereopods (Fig. 2 d-j). The proportions of the meri, carpi, and propodi change with growth. The segments are slender in small specimens (SL < 3.0 mm), but become broader and stronger with increasing size (Fig. 2 d-g). The number of spines on the dorsal margins of the carpi usually increases with growth (Fig. 2 h-j).

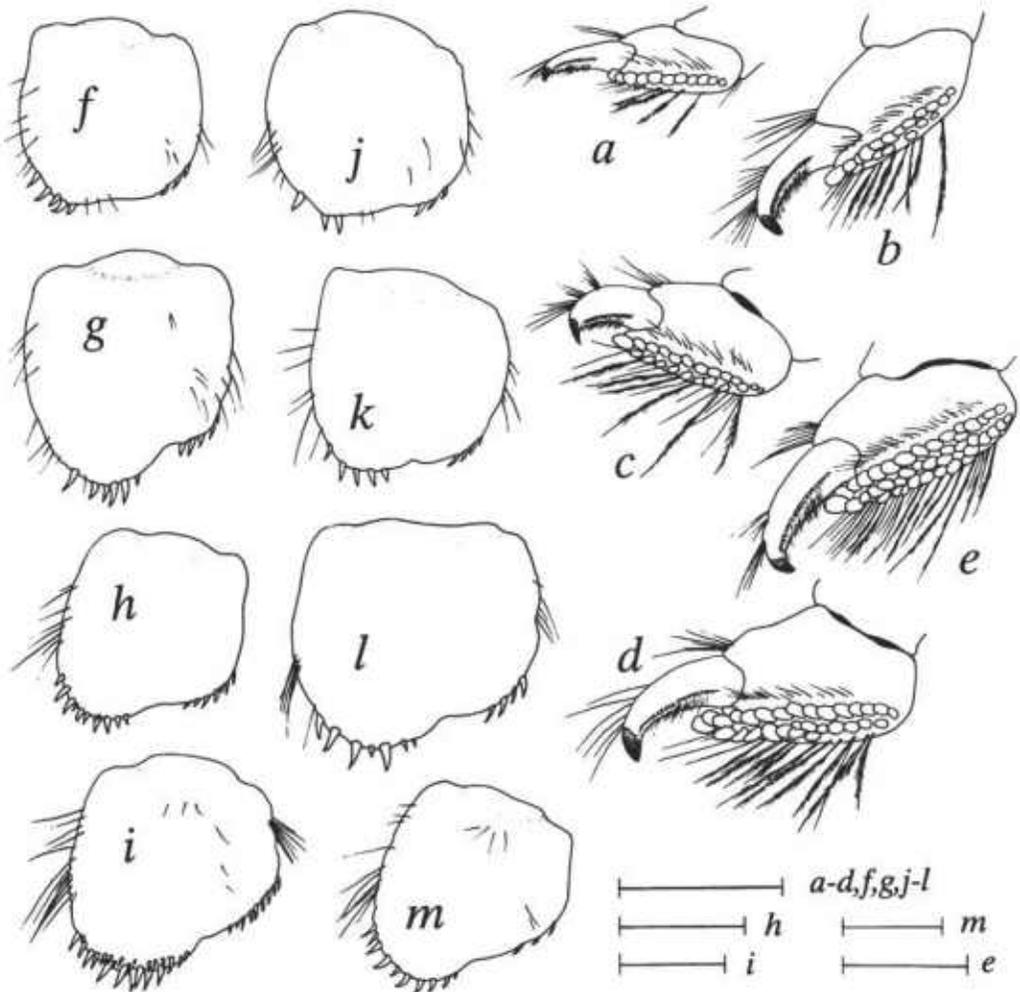


FIG. 3. *Sympagurus dimorphus* (Studer, 1883). Specimens from stn 1851. a-e, Propodus and dactyl of left fourth pereopod, ventrolateral view: a, ♀ SL 2.9 mm; b, ♂ SL 3.9 mm; c, ♂ SL 3.7 mm; d, ♂ SL 4.8 mm; e, ♂ SL 6.1 mm. f-m, Telson, dorsal view: f, ♀ SL 2.4 mm; g, ♀ SL 3.1 mm; h, ♀ SL 3.7 mm; i, ♀ SL 4.8 mm; j, ♂ SL 2.9 mm; k, ♂ SL 3.1 mm; l, ♂ SL 3.9 mm; m, ♂ SL 4.8 mm. Scales equal 1 mm.

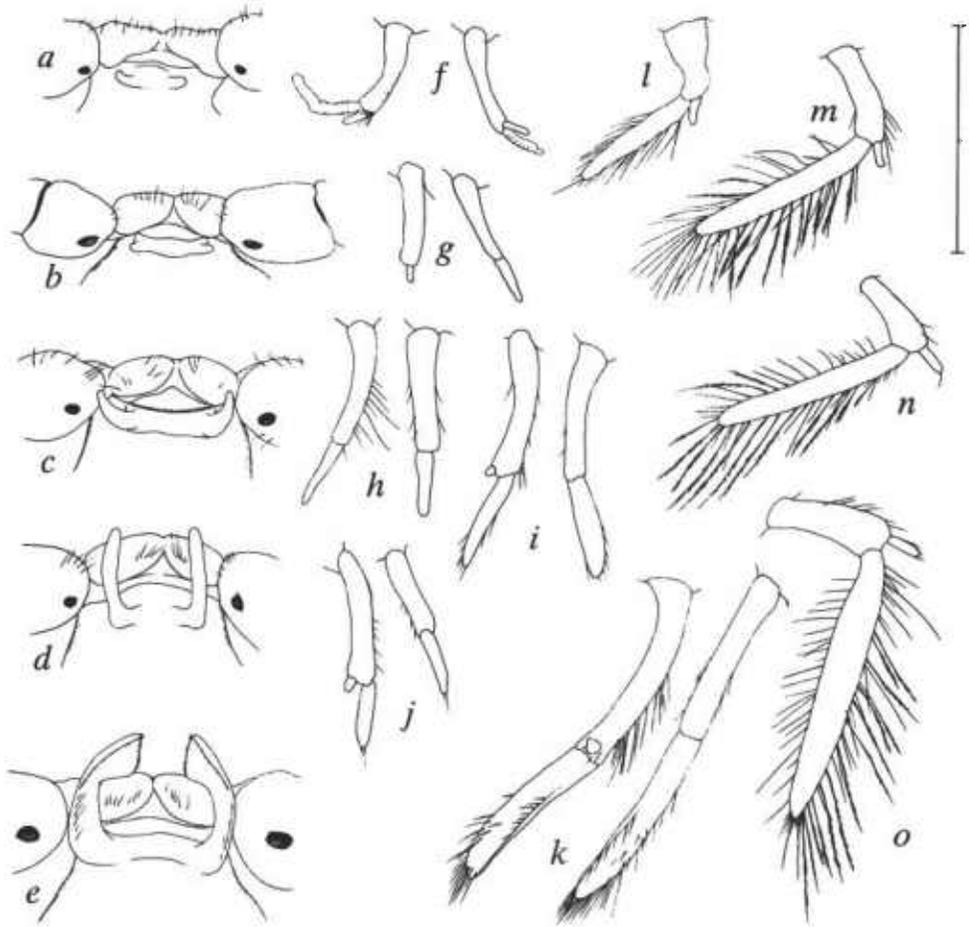


FIG. 4. *Sympagurus dimorphus* (Studer, 1883). Males from stn 1851. a-e, First pair of pleopods and coxae of fifth pereopods, posteroventral view: a, SL 2.9 mm; b, SL 3.1 mm; c, SL 3.9 mm; d, SL 3.7 mm; e, SL 4.8 mm. f-k, Second pair of pleopods, posterior view (right on right, left on left): f, SL 2.9 mm; g, SL 3.1 mm; h, SL 3.7 mm; i, SL 3.7 mm; j, SL 3.9 mm; k, SL 4.8 mm. l-o, Left third pleopod, lateral view: l, SL 2.9 mm; m, SL 3.7 mm; n, SL 3.9 mm; o, SL 4.9 mm. Scale equals 2 mm.

Fourth pereopod (Fig. 3 a-c). The number of rows of scales on the propodal rasp varies from 1 to 2. Juveniles often have a well-defined row of scales and a few additional scales forming an incomplete second row proximally (Fig. 3 b).

Telson (Fig. 3 f-h, j-l). In the smallest juveniles examined, the posterior margin of the telson is straight or slightly concave and the terminal margin of each future lobe is armed with a few spinules. The armature of the terminal margin of the left posterior lobe becomes more complex (more so in females) as individuals grow. At approximately SL 4.0 mm, the spines on the distal margin of the lobe are arranged in a single row in both sexes. However, adult females invariably develop several additional irregular rows of smaller spines often numerous (up to 43 spines) on the dorsodistal and ventrodistal margin of the lobe (Fig. 3 i, Table 1). Males generally retain a single row of spines on the lobe, although the spines become more numerous (Fig. 3 m).

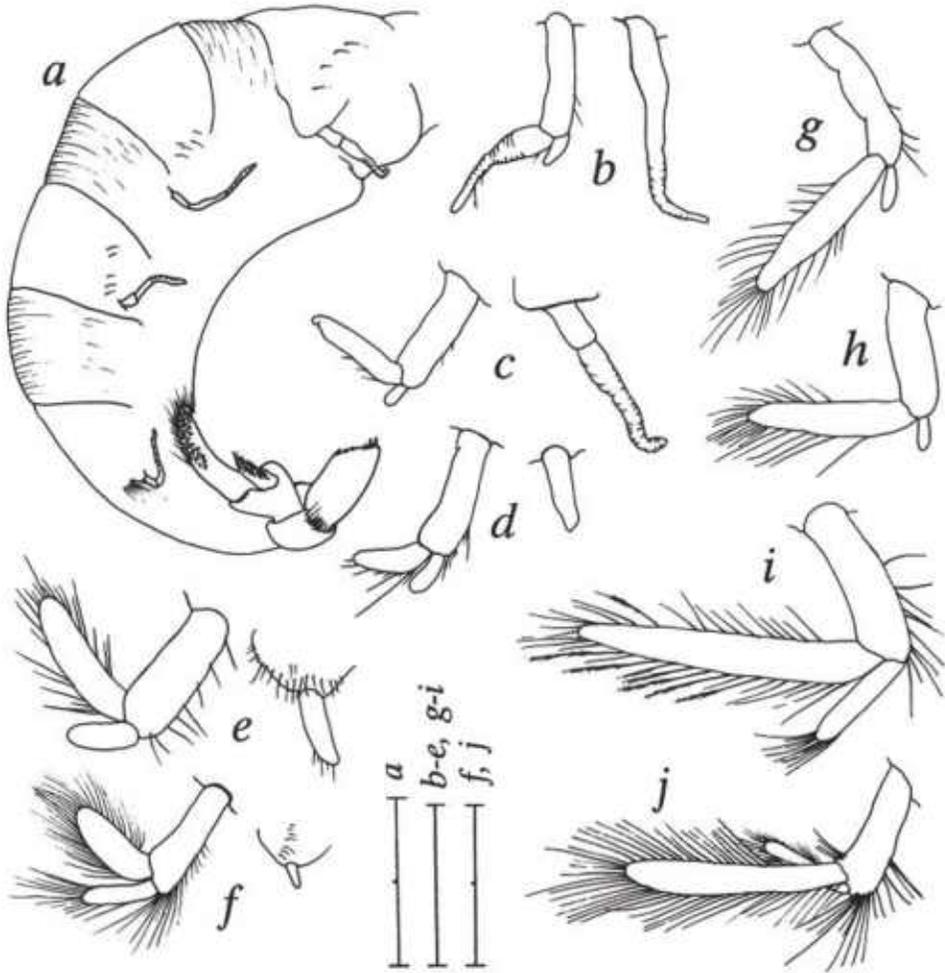


FIG. 5. *Sympagurus dimorphus* (Studer, 1883). Females from stn 1851. a, Right side of abdomen showing second to fifth pleopods, ♀ SL 2.9 mm. b-f, Second pair of pleopods, posterior view (right on right, left on left): b, SL 2.4 mm; c, SL 2.9 mm; d, SL 3.1 mm; e, SL 3.7 mm; f, SL 4.0 mm; g-j, Third left pleopod, lateral view: g, SL 2.4 mm; h, SL 2.9 mm; i, SL 3.7 mm; j, SL 4.0 mm. Scales equal 2 mm (a, f, j), and 1 mm (b-e, g-i).

Table 1. Range of variation of selected characters by SL size intervals in *Sympagurus dimorphus* (Studer).

SL interval (mm)	Character				
	No. spines antennal acicle	No. spines carpus left cheliped	No. spines carpus right P2	No. rows scales propodal rasp P4	No. spines left lobe of telson
2 to <3 mm	2-7	2-6	1-6	1-1.5 ^a	3-7
3 to <4 mm	5-8	2-6	1-6	1-2	5-10
≥4 mm	6-15	6-22	3-10	2-5	6-31 ^b

^a 1.5 meaning incomplete second row, as seen in Fig. 3 b.

^b Large females often with up to 74 spines, including smaller ones on dorsodistal and ventrodistal margin.

Table 2. Development of pleopods by SL size intervals and sex in *Sympagurus dimorphus* (Studer).

	SL 2-<3 mm			SL 3-<4 mm			SL \geq 4 mm
	Male	Female	Male	Female	Male	Female	Female
Pl 1	Absent or present as pair of short uniramous, subequal buds (Fig. 4 a)	Absent	Paired, subequal, uniramous, incompletely developed (Figs 4 b-d)	Absent	Paired, subequal, uniramous, fully developed (Fig. 4 e)	Absent	Absent
Pl 2	Paired, biramous, subequal; endopod short; exopod rudimentary, curled and wrinkled (Fig. 4 f)	Paired, asymmetrical. Left biramous, with short endopod; exopod long, rudimentary, wrinkled distally (Figs 5 b, c). Right uniramous, rudimentary, wrinkled (Figs 5 a-c)	Paired, slightly asymmetrical, uniramous. Left often with vestigial endopod (Figs 4 g-j)	Paired, asymmetrical. Left with rami incompletely developed, not crossed. Right reduced or vestigial (Figs 5 d-f)	Paired, subequal, fully developed. Left often with vestigial endopod (Fig. 4 k)	Paired, asymmetrical. Left biramous, rami crossed. Right vestigial.	
Pl 3	Paired, asymmetrical. Left biramous, with short endopod (Fig. 4 l). Right uniramous, rudimentary, wrinkled	Paired, similar to male Pl 3 (Fig. 5 g)	Unpaired (left only) with short endopod (Figs 4 m, n)	Unpaired (left only), similar to male Pl 3 (Fig. 5 i), rami not crossed	Unpaired (left only), with short endopod (Fig. 4 o)	Unpaired (left only), biramous, rami crossed (Fig. 5 j)	
Pl 4	Paired, asymmetrical. Similar to Pl 3	Paired, similar to male Pl 4	Unpaired (left only), similar to Pl 3	Unpaired, (left only), similar to Pl 3	Unpaired (left only), similar to Pl 3	Unpaired (left only), similar to Pl 3	
Pl 5	Paired, asymmetrical. Similar to Pl 3, 4	Paired, similar to male Pl 5	Unpaired (left only), similar to Pl 3, 4, but with shorter rami	Unpaired (left only), similar to Pl 3, 4, but with shorter rami	Unpaired (left only), similar to Pl 3, 4, but with shorter rami	Unpaired (left only), rami not crossed, similar to male Pl 5	

Pl = pleopod.

Development of pleopods in juveniles of *Sympagurus dimorphus*

(Figs 4, 5 and Table 2)

Juveniles SL 2 to <3 mm. In males, pleopod development consists of two distinct processes: (1) a reduction in the ambulatory function of the megalopal pleopods, and (2) the development of paired, sexually modified pleopods typical of the adult. In these small juveniles, both sexes have paired second to fifth pleopods; however, those of the males retain symmetrical, unequally biramous, albeit reduced, second pleopods (Fig. 4f), and generally well-developed paired third through fifth pleopods, whereas in females those of the right are already showing noticeable reduction (Fig. 5a). Frequently buds of the future paired first pleopods are visible (Fig. 4a).

Juveniles SL 3–<4 mm. Differences between the sexes become more evident. In males, the buds of the first pair of pleopods increase appreciably in size (Fig. 4 b–d). The second pair of pleopods undergo slight reduction in size, often accompanied by the total loss of the endopods (Fig. 4 g, h); an increase in exopod size follows. However, not uncommonly a vestigial endopod is retained on one side (Fig. 4 i, j). In females there is no indication of pleopod development on the first abdominal somite. On the second somite, reduction in the right pleopod continues, whereas development in both size and setation has begun in the left (Fig. 5 d–f). The left third pleopod also shows continued development of both rami (Fig. 5 i), culminating in the crossing of the rami (a character unique to females of the Parapaguridae) at about SL 4 mm (Fig. 5 j).

Adults. Pleopods are fully developed at a size of about SL 4 mm. Adult males have paired, symmetrical first and second pleopods modified as gonopods (see Lemaitre 1989: 72, Fig. 36 K, L), and unpaired left third to fifth pleopods, each with a well-developed exopod and a very short endopod (Fig. 4 o). Adult females lack first pleopods, and have paired, asymmetrical second pleopods (right vestigial, left with crossed rami); and unpaired left third to fifth pleopods, the third and fourth similar and with crossed rami (Fig. 5 j), and the fifth with well-developed exopod and a short endopod (rami not crossed).

Megalopa of *Sympagurus dimorphus*

(Figs 6 and 7)

USNS Eltanin material. 21 specimens (CL 2.9–4.1 mm, TL 10.0–16.1 mm), stn 1851, USNM.

Carapace (Fig. 6 a). Shield distinctly more than 1/2 carapace length, about as broad as long. Rostrum obtusely subtriangular, terminally rounded and often with inconspicuous granule. Anterior margins straight or weakly concave. Anterolateral margins sloping. Lateral margins with median constriction. Cervical groove deep. Sulci on posterior carapace weakly defined except for well-marked *linea anomurica*. Ocular peduncles stout, constricted medially, distal half broadened distally; cornea strongly dilated, pigmented. Ocular acicles absent.

Abdomen (Fig. 6 a, b). Symmetrical, segmentation well defined, somites naked and weakly convex dorsally. Somite 1 lacking pleopods; somites 2–5 with paired, biramous pleopods. Pleura of somites 2–5 terminating posteroventrally in strong hook-like process directed anteriorly. Pleopods long, similar except for slight reduction in size from anterior posterior; exopod with approximately 20 long setae subequal to exopodal length; endopod about one-third as long as exopod, appendix interna of 3 or 4 minute corneous, hook-like processes.

Tail fan (Fig. 6 a, b, e, f). Telson with anterior half broad and rounded laterally; anterior half with few setae on dorsal surface near posterolateral margins; posterior half much narrower than anterior half, subtriangular, with about 30 long marginal setae. Uropods each with 2 rows of ovate corneous scales on anterior margins of exopod and endopod; exopod elongate.

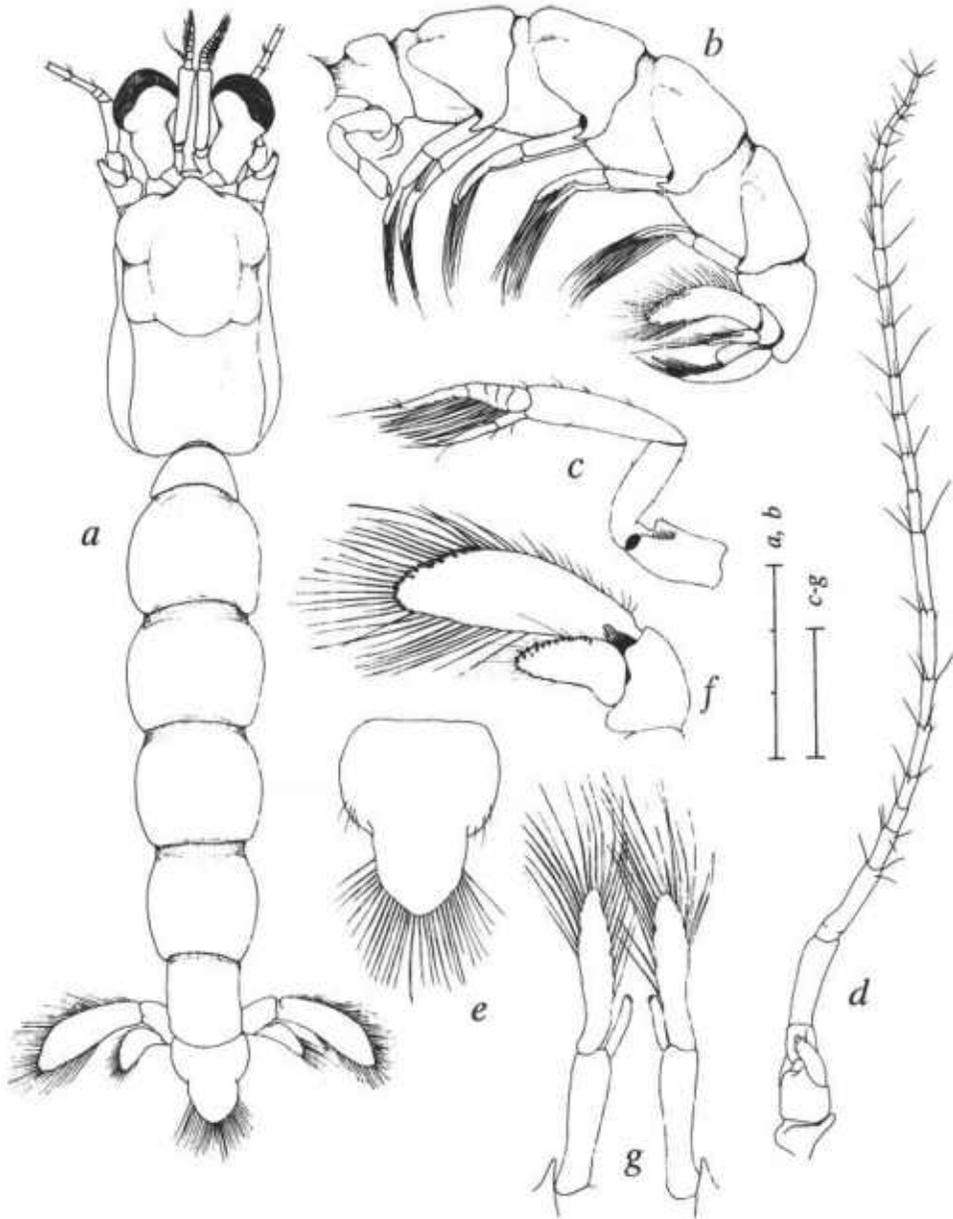


FIG. 6. Megalopa of *Sympagurus dimorphus* (Studer, 1883). a, Carapace, cephalic appendages and abdomen, dorsal view; b, left side of abdomen; c, left antennules, lateral view; d, left antenna, lateral view; e, telson, dorsal view; f, left uropod, dorsal view; g, second pair of pleopods, posterior view. Scales equal 3 mm (a, b), and 1 mm (c-g).

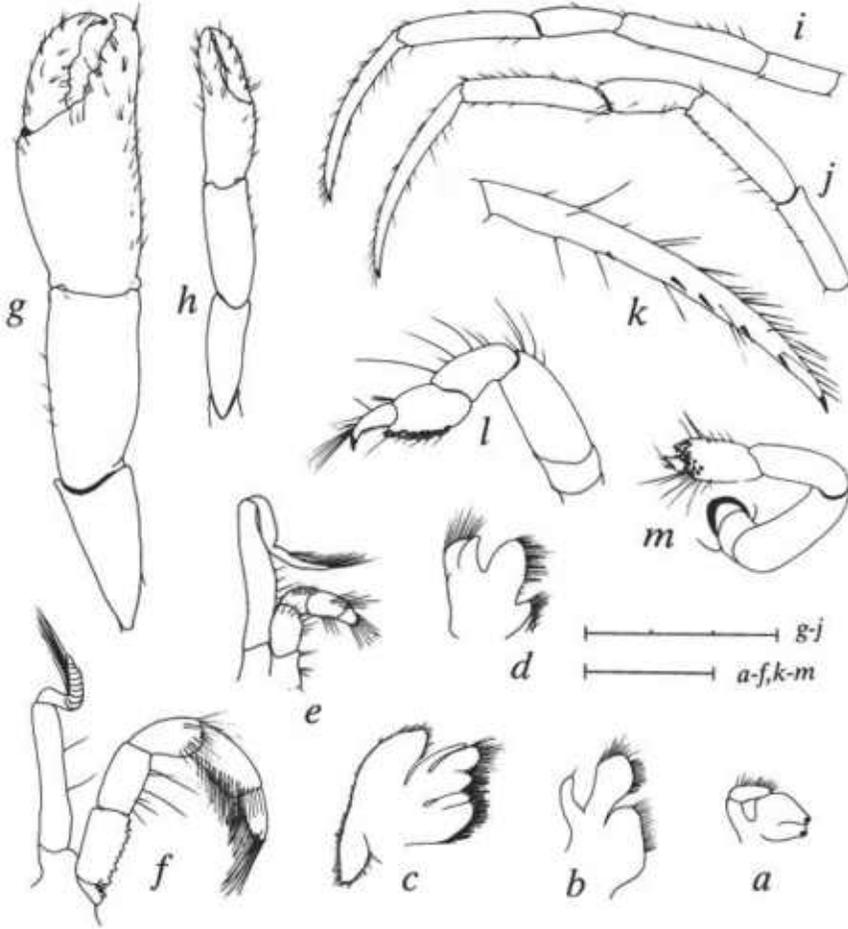


FIG. 7. Megalopa of *Sympagurus dimorphus* (Studer, 1883). a–f, Left mouthparts, internal view: a, mandible; b, maxillule; c, maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped. g, Right cheliped; h, left cheliped; i, second left pereopod, lateral view; j, third left pereopod, lateral view; k, dactyl of same, mesial view; l, fourth left pereopod, lateral view; m, fifth left pereopod, lateral view. Scales equal 3 mm (g–j), and 1 mm (a–f, k–m).

Antennule (Fig. 6c). Biramous; 3-segmented peduncle exceeding distal margin of cornea by slightly less than length of ultimate segment; ultimate and penultimate segments with scattered setae; basal segment with row of stiff bristles. Exopod (upper ramus) with 5 segments clearly delineated, setae progressing distally 0, 8, 6, 7, 6 (including long terminal seta); endopod (lower ramus) with 2 or 3 articles delineated, setae (average) progressing distally in specimens with 2 articles: 3, 6 (including 2 terminal setae).

Antenna (Fig. 6d). Peduncle slightly shorter than eyestalks (including corneae), supernumerary segment apparent. Second segment with spine at distolateral angle, remaining segments unarmed. Acicle bifid terminally, with 3 or 4 short setae. Flagellum with 21–25 articles, each article having 3 or 4 setae.

Mandible (Fig. 7a). Incisor and molar processes each with small rounded, corneous tooth on distomesial angle. Palp 2-segmented, with 15 marginal setae on distal segment.

Maxillule (Fig. 7 b). Endopod rounded distally, with long terminal seta. Coxal endite with 16–18 plumose setae. Basial endite with about 10 long setae and 15 short, stiff setae.

Maxilla (Fig. 7 c). Endopod elongate, narrow basally, not exceeding distal margin of basal endite. Coxal and basal endites bilobed, setal formula (average) from distal to proximal: 18, 17, 12, 37. Scaphognathite with marginal setae; posterior lobe well separated from protopod.

Maxilliped 2 (Fig. 7 e). Exopod 2-segmented, with 11 plumose setae terminally; basal segment with 5 long simple setae on mesial margin. Endopod 4-segmented, basal fifth segment obscurely delineated from protopod. Ultimate and penultimate segments with plumose setae on dorsal and ventral faces and some serrate setae terminally on ultimate and on mesial face of penultimate segments.

Maxilliped 3 (Fig. 7 f). Exopod 2-segmented, flagellum with 8 plumose setae; basal segment with 2 simple setae. Endopod 6-segmented, with ischium and basis clearly distinct; dactyl and propodus with serrate and plumose setae; ischium with crista dentata developed as series of 10 or 11 blunt teeth; basis with 1 tooth and 4 short, thick corneous spinules.

Gills. Consisting of 11 or, in some specimens, 12 pairs as follows:

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	—	—	—	—	—	—	1 ^a	1 ^b
Arthrobranchs	—	—	2	2 ^a	2 ^a	2 ^a	2 ^a	—

^a Consisting of series of undivided lamellae.

^b Vestigial, present as 12th pair in some specimens.

Chelipeds (Fig. 7 g, h). Markedly unequal, smooth, unarmed; right about 1.5 times longer than left. Fingers with cutting edges each consisting of unequal (right) or subequal (left) calcareous teeth, and terminating in corneous claws curved inwardly.

Pereopods (Fig. 7 i–m). Ambulatory legs (Fig. 7 i–k) slender, with scattered setae on ischium to propodus; dactyl broadly curved, terminating in sharp corneous claw, with dorsodistal row of long setae, few long setae on ventral margin, and ventromesial row of 5 corneous spinules. Fourth pereopod (Fig. 7 l) with single row of ovate scales on propodal rasp. Fifth pereopod (Fig. 7 m) with propodal rasp of ovate scales occupying subtriangular area less than half the length of propodus.

Remarks. We assign these megalopae to *Sympagurus dimorphus* for two reasons: (1) the presence in these of a vestigial pleurobranch on the last thoracic somite, a characteristic of *S. dimorphus* that is lacking in any of the other parapagurid species known from Antarctic and Subantarctic waters; and (2) the larvae were found along with numerous juveniles of *S. dimorphus* at station 1851, where no other parapagurids were found.

H. Milne Edwards (1830) erected the genus *Glaucothoe* (as *Glaucothoë*) for an apparently pelagic, symmetrical crustacean, *G. peronii* H. Milne Edwards, that appeared to be morphologically somewhere between the Paguridea and the Thalassinidea. During the following 40 years, carcinologists debated whether *Glaucothoe* constituted a distinct genus of the Thalassinidea or Paguridea (e.g. Dana, 1852; Henderson, 1888) or a developmental stage in the Paguridea (Rathke, 1840; Bell, 1853;

Bate, 1868). Bouvier (1891) reviewed the arguments of all earlier carcinologists, as well as actual specimens of three presumed species that had by then assigned to *Glaucothoe*, and concluded that the taxa of *Glaucothoe* were simply developmental stages of particular pagurid genera, *G. peronii*, for example, belonging to a species of the genus *Sympagurus*.

In a subsequent report, Bouvier (1905) amended his hypothesis. While acknowledging the 'glaucothoé' (megalopa) as a normal postzoeal stage in hermit crab development, he was convinced that the large (>7 mm) taxa of *Glaucothoe* represented abnormal larvae of species arrested in their development, and that, while continuing to moult and grow, did so without a change to the asymmetrical body form. A similar conclusion appears to have been arrived at independently by Alcock (1905). Bouvier's hypothesis (1905) was challenged by Gurney (1924), who believed that these large taxa of *Glaucothoe* were no more abnormal than the smaller postlarval stage of typical pagurids such as the ones described by Thompson (1903). Gurney's viewpoint (1924) was strongly supported by Dechancé and Forest (1958).

In a preliminary study of *Parapagurus*, De Saint Laurent-Dechancé (1964) expressed the opinion that postlarvae (megalopae) referred to *Glaucothoe peronii* by A. Milne Edwards and Bouvier (1900), Bouvier (1905, 1922), Gurney (1924), and others, were correctly assigned to *Parapagurus* (*sensu lato* see Lemaitre, 1989). In this same report, De Saint Laurent-Dechancé (1964) described the zoeal stages of several parapagurid species collected from plankton samples, but was not able to refer any to particular species. Although a subsequent study dealing with megalopae was indicated, this was not published.

Anomuran crabs exhibit a distinct single postlarval moult prior to the juvenile mode, although there possibly may be exceptions (Gore, 1985). The distinction between zoeal and megalopal stages is seen most succinctly in the change in locomotor function from the maxillipeds to the pleopods. In terms of carapace and cephalic appendage structure, pereopod and frequently even gill development, the megalopal stage is quite reminiscent of the adult body form, albeit more feebly developed. Perhaps the most distinguishing characters of the megalopa are seen in the retention of the elongate, symmetrical, visibly 6-segmented abdomen, development of functional paired pleopods on the second through fifth abdominal somites and the tail-fan-like configuration of the uropods and telson, which are used in harmony to propel the organism through the water. It has been presumed that the reduction in the pleopods and transformation of the uropods is accomplished at the time of the moult to the first juvenile (crab stage) and coincides with the young hermit crab seeking out and occupying a gastropod shell (Thompson, 1903; Gurney, 1942). However, as pointed out by McLaughlin *et al.* (1989), in the few studies of juvenile development that have been reported, pleopod changes do not occur uniformly among hermit crab genera, yet in all other respects the megalopal moult appears truly to be to the juvenile mode. In those species where marked reductions in the pleopods of the right side do not accompany the megalopal moult (e.g. *Dardanus pectinatus* (Ortmann) (c.f. Forest, 1954); *Paguristes sericeus* A. Milne Edwards (c.f. Provenzano and Rice, 1966); *P. ortmanni* Miyake (c.f. Quintana and Iwata, 1987); *Clibanarius sclopetarius* (Herbst) (c.f. Bossi-Garcia, 1987); *C. vittatus* (Bosc) (c.f. Bossi-Garcia, 1988); *Anapagurus chiroacanthus* (Lilljeborg) (c.f. Ingle, 1990); and *A. petiti* (Dechancé and Forest) (c.f. Pike and Williamson, 1960, as species N.1)], there is reduction either in the size and setation of the pleopods of the right side, or at least reduction in the size of the endopods with the moult to the first juvenile stage, except in *Anapagurus*. In *A. chiroacanthus* the fifth abdominal somite of

the megalopa carries only a pair of pleopodal buds. However, the first crab stage has fully developed pleopodal exopods on this somite, although endopods are lacking on all pleopods. In *A. petiti*, Pike and Williamson (1960) report three pairs of symmetrical pleopods still present in crab stage 2. A change in the structure of the telson occurs with the moult to the first crab stage in all species described to date.

The megalopal stage described in this study bears considerable similarities to the earlier descriptions of *G. peronii*; however, none of these descriptions is sufficiently detailed to permit precise comparison. H. Milne Edwards (1830: pl. 8, fig. 3) and Gurney (1924: fig. 72) illustrated the mandible with a 3-segmented palp, and Thompson (1943: fig. 3) depicts the palp as 4-segmented. The palp in our specimens is 2-segmented. Gurney also illustrated the basis of the third maxilliped of *G. peronii* as distinctly separated from the ischium, but not from the protopodal base of the exopod. Our specimens have the basis clearly delineated. Dechancé and Forest (1958) state that the crista dentata on the ischium of the third maxilliped consists of only a few tubercles in the megalopal stage, whereas nearly 20 are present in the first juvenile crab. Our specimens have a crista dentata of approximately 10 or 11 teeth. The branchial formula is reported by Bouvier (1891) and A. Milne Edwards and Bouvier (1900) as consisting of 11 branchiae on each side as follows: two arthrobranchs on the third maxilliped, two arthrobranchs on each of pereopods 1-4, and one pleurobranch on pereopod 4. Gurney (1924) reported a similar formula (except for the inclusion of an epipod on the third maxilliped), and noted that the branchiae on pereopods 2-4 were phyllobranchs, while the remaining were rudimentary. The branchial formula of our specimens differs from those reported by these authors in that some have 12 branchiae on each side, the additional one being a clearly visible vestigial pleurobranch on the last thoracic somite.

A characteristic emphasized for all taxa assigned to *Glaucothoe* was the absence of ocular acicles (ophthalmic scales) (e.g. Henderson, 1888; Bouvier, 1891; Gurney, 1924). Our specimens of *Sympagurus dimorphus* also lack ocular acicles. In contrast, one lot of juveniles of the western Atlantic species *S. pictus* Smith, from the Gulf of Mexico (LGL stn WC3 5503, 27°35'13"N, 92°22'40"W, 781 m, 9 June 1985) that we have recently examined, included one specimen (SL 3.6 mm, CL 5.7 mm, TL 15.2 mm) that still had paired, biramous pleopods with well-developed exopods and endopods complete with appendix internae on abdominal somites 2-5, uropods and convexly rounded telson forming a generally symmetrical tail-fan, and well-developed ocular acicles. The basis of the third maxilliped was clearly delineated and the crista dentata was composed of 10 teeth. In an additional lot of this same species from the University of Miami collections (R/V *Gerda* stn 503, 26°31'N, 78°51'W, 336 m, 4 February 1965), we found a juvenile (SL 2.5 mm) accompanied by its moult from the preceding stage. The pleopods of the moult were paired, with typical well-developed exopods, endopods with appendix internae; the uropods and convexly rounded telson formed a nearly symmetrical tail-fan; the abdomen showed distinct segmentation of the six somites; the dactyls of the fourth and fifth pereopods were well defined; the crista dentata was moderately well developed with nine teeth and the basis was distinctly separated from the protopod. Regrettably, the ocular peduncles were missing from the moult, thus no determination of the presence of ocular acicles could be made; however, the acicles of the juvenile were very well developed, each with a prominent submarginal spine; pleopod development was similar to that described for early juvenile females of *S. dimorphus*. The telson in this juvenile shows faint indications of a transverse suture; the posterior portion was weakly bilobed and the terminal margin of each lobe was armed with a few spines. It would appear that development of ocular acicles in the megalopae

of parapagurids is more variable than previously presumed. Alternatively, one might hypothesize that, at least in some species of *Sympagurus*, more than one megalopal moult occurs prior to the juvenile phase of development.

Sympagurus haigae (De Saint Laurent, 1972)

(Fig. 8)

Parapagurus haigae De Saint Laurent, 1972: 115, figs 9, 17; Wicksten, 1987: 55; 1989: 314.

Sympagurus haigae. Lemaitre, 1989: 37.

USNS Eltanin material. 1♂ (SL 4.2 mm), stn 71, USNM.

Additional material. *Albatross*: paratypes, 1♂ (SL 3.5 mm), 2♀♀ ovigs (SL 2.8–3.0 mm), stn 4110, Santa Catalina Island, S. of Long Point, 320–333 m, 11 April 1904, USNM 168318; paratype, 1♂ (SL 2.1 mm), stn 4412, Santa Catalina Island, S. of Bird Rock, 477–493 m, 11 April 1904, USNM 168319; 35♂ (SL 3.6–4.1 mm), 1♀ ovigs (SL 3.0 mm), stn 2935, 32°44'30"N, 117°23'W, off southern California, 223 m, 4 February 1889, USNM 216289. *R/V Velero IV*: 3♂ (SL 3.0–3.6 mm), 1♀ ovigs (SL 3.0 mm), stn 24471, 33°31'N, 118°42'W, off southern California, 302–348 m, 8 March 1976, AMS P.26903; 1♂ (SL 3.6 mm), 1♀ ovigs (SL 3.1 mm), stn 24813, 33°57'N, 120°29'W, San Miguel Island, 4 miles SW of Point Bennett, 301–333 m, 24 April 1976, coll. M. K. Wicksten, USNM 170396.

Description (amended from De Saint Laurent, 1972). Shield weakly calcified on dorsomedial region; ventrolateral margin usually with minute spine. Rostrum with dorsal ridge. Distal margin of cornea reaching to about $\frac{2}{3}$ of fifth antennal segment, and to about midlength of penultimate antennular segment. Antennal peduncle with flagellum reaching to tip of right cheliped, with numerous setae <1 to 3 flagellar articles in length; fourth segment bearing small spine on dorsolateral distal angle; second segment with dorsolateral distal angle produced into strong spine (rarely bifid or multifid) reaching to approximately midlength or more of antennal acicle; acicle exceeding eye by about $\frac{1}{3}$ to $\frac{1}{2}$ length of acicle. Epistomial spine upwardly curved. Sternite of third maxilliped with small spine on each side of midline.

Right cheliped considerably variable in proportions depending on size, large specimens with carpus and chela much longer than broad (Fig. 8d, f). Chela with iridescent areas (preserved specimens) on dorsal surface; lateral margin well delimited by row of sharp to blunt spines; dorsomesial margin well defined by row of small spines, mesial face nearly perpendicular to dorsal face. Left cheliped with carpus weakly calcified on lateral face; palm with dorsomesial row of 4–6 small tubercles or spines.

Anterior lobe of sternite of third pereopods unarmed, subtriangular, setose. Fourth pereopod with propodal rasp bearing single row of rounded scales at least on distal $\frac{4}{5}$ (occasionally with 2 or 3 rows on proximal $\frac{1}{5}$; Fig. 8i). Fifth pereopod with propodal rasp subtriangular, extending to midlength of propodus.

Gills phyllobranchiate, with narrow lamellae.

Telson and uropods asymmetrical, left side largest. Left exopod of uropod elongate. Telson of males with left posterior lobe armed with 5 strong, often curved spines on distal margin (Fig. 8m); right lobe armed and distal margin with 4 spines smaller, less strong than those on right lobe. Telson of females with posterior lobes armed with several irregular rows of small corneous spines on dorsodistal margin (in addition to spines on distal margin; Fig. 8l).

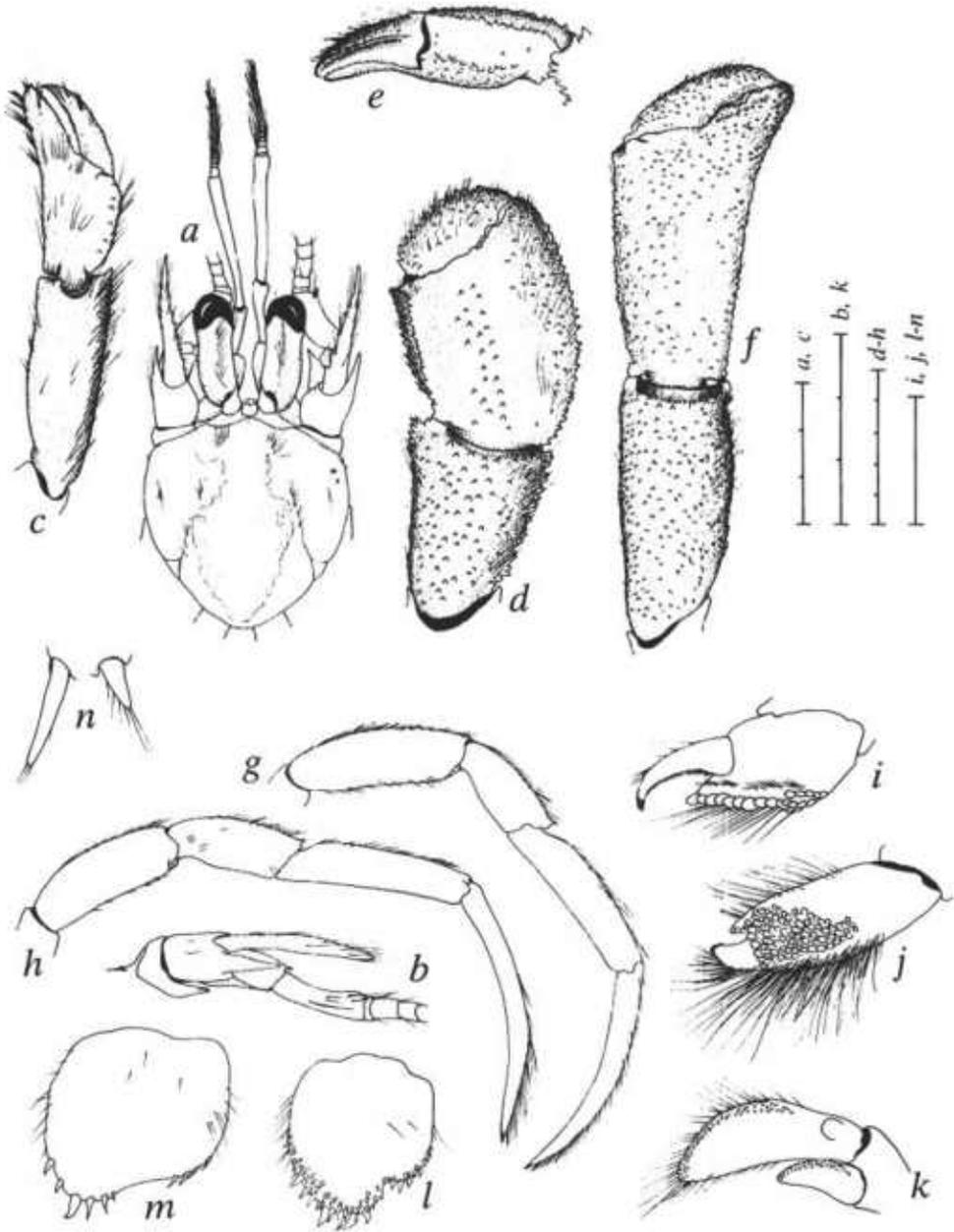


FIG. 8. *Sympagurus haigae* (De Saint Laurent, 1972). a-e, g-k, m, n, ♂ SL 4.2 mm, stn 71; f, ♂ SL 3.9 mm, *Albatross* stn 2935; l, ♀ SL 3.0 mm, *Albatross* stn 2935. a, Shield and cephalic appendages; b, right antennal peduncle, lateral view; c, left chela and carpus; d, right chela and carpus; e, same chela, mesial view; f, right chela and carpus; g, right second pereopod, lateral view; h, right third pereopod, lateral view; i, propodus and dactyl of left fourth pereopod, lateral view; j, propodus and dactyl of left fifth pereopod, lateral view; k, left uropod, dorsal view; l, telson of female, dorsal view; m, telson of male, dorsal view; n, second pair of pleopods of male (right on right, left on left). Scales equal 3 mm (a-c, k), 5 mm (d-h), and 1 mm (i, j, l-n).

Males lacking first pleopods; second pleopods asymmetrical, uniramous, each consisting of single segment (Fig. 8n). Females lacking first pleopods; with paired asymmetrical second pleopods, left biramous (rami crossed), right vestigial.

Symbiotic associations. The single specimen from USNS *Eltanin* station 71 was found without housing. Specimens from the northern range of this species, however, are frequently found living in gastropod shells with an actinian attached.

Distribution. Eastern Pacific, from off southern California (including the Gulf of California), to off Valparaiso, Chile. Depth range: 55–923 m.

Remarks. Previously, this species was known only as far south as the Gulf of Panama (De Saint Laurent, 1972; Wicksten, 1987, 1989). Thus, the discovery of *S. haigae* off Valparaiso represents a considerable extension (over 7600 km) of its range.

Parapagurus latimanus Henderson, 1888

(Fig. 9)

Parapagurus latimanus Henderson, 1888: 91, pl. 9, fig. 2. Lemaitre, 1986: 526; 1989: 11.

Parapagurus pilosimanus latimanus. De Saint Laurent, 1972: 103, pl. 1, fig. 5.

HOLOTYPE: 1♂ (SL 6.6 mm), *Challenger* stn 167A, New Zealand, 18 m? (see Remarks), 27 June 1874, BMNH 1883: 33.

USNS Eltanin material. 1♂ (SL 6.7 mm), stn 1712, USNM. 2♂ (SL 7.6–10.2 mm), 1♀ (SL 6.8 mm), 1♀ ovis (SL 10.0 mm), stn 2198, USNM.

Diagnosis. Shield about as broad as long, dorsal surface well calcified. Rostrum broadly subtriangular, with short dorsal ridge. Lateral projections broadly rounded. Lateroventral margin unarmed. Ocular peduncles less than half length of shield, inflated basally; width of cornea about same as distal width of ocular peduncle. Ocular acicles subtriangular, terminating in simple strong spine (rarely bifid on one side). Antennular peduncle exceeding eyes by nearly entire length of penultimate segment; lateral face of basal segment with subrectangular distal lobe armed with 2 spines, and 1 spine proximally. Antennal peduncle exceeding eyes by nearly entire length of fourth antennal segment; flagellum with numerous setae 1–4 flagellar articles in length; fourth segment unarmed; acicle straight or weakly curved outward in dorsal view, exceeding eyes by half length of acicle, with proximal half of mesial margin bearing 6 small blunt to sharp tubercles. Epistomial spine absent. Sternite of third maxillipeds with strong spine on each side of midline. Left cheliped well calcified, densely setose; carpus with irregular row of small tubercles on dorsal margin. Sternite of third pereopods subsemicircular, setose, armed with small tubercle or spine. Fourth pereopod with propodal rasp with 2 often irregular rows of lanceolate scales (Fig. 9g, h). Fifth pereopod with propodal rasp less than half length of propodus. Telson and uropods asymmetrical, left side largest; posterior lobes of telson armed with long, evenly spaced corneous spines on distal margins, spines on left lobe extending posteriorly nearly to midlength of lateral margin of telson; left exopod of uropod elongate. Males with well-developed paired first and second pleopods modified as gonopods (Fig. 9l, m). Females with unequally paired second pleopods, right vestigial.

Symbiotic associations. One specimen found living in a shelter formed by an undetermined zoanthid, probably a species of *Epizoanthus*.

Distribution. Off the eastern coast of New Zealand. Depth range: 909–1995 m (see Remarks).

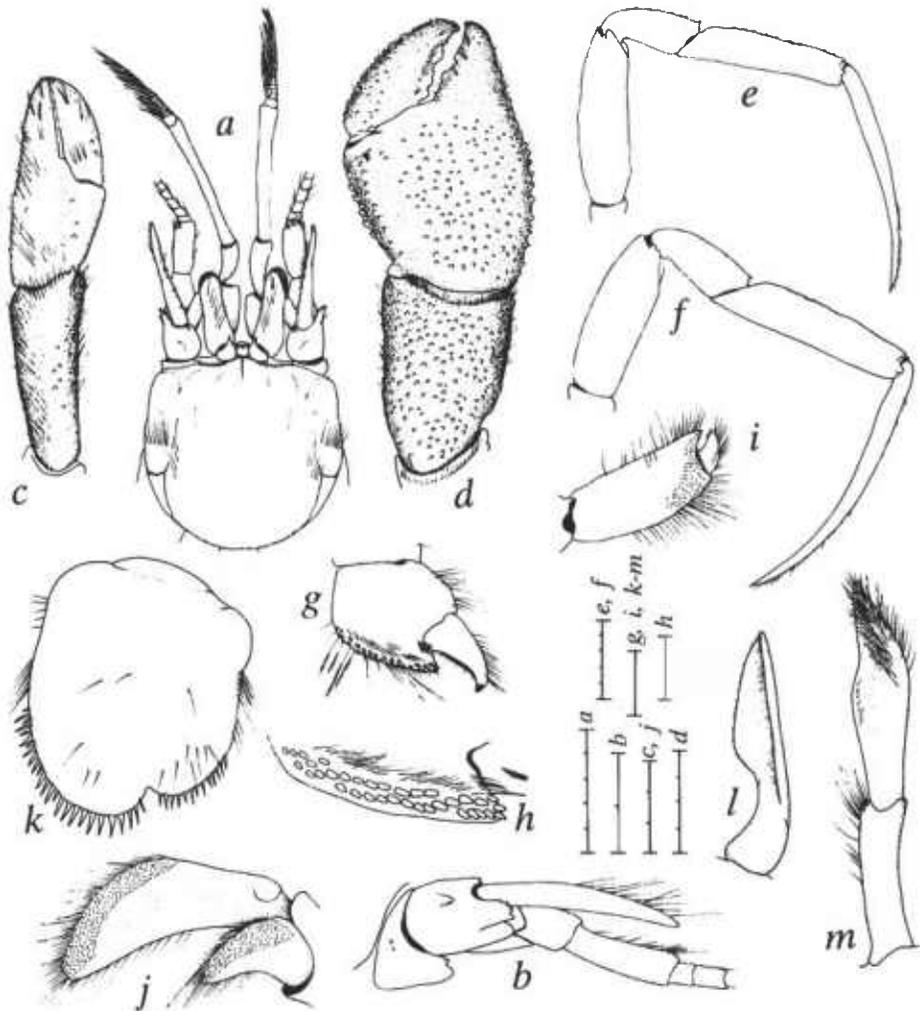


FIG. 9. *Parapagurus latimanus* Henderson, 1888. a-i, l, m, ♂ SL 7.5 mm, stn 2198; j, k, ♂ SL 9.5 mm, stn 2198. a, shield and cephalic appendages; b, right antennal peduncle, lateral view; c, left chela and carpus; d, right chela and carpus; e, right second pereopod, lateral view; f, right third pereopod, lateral view; g, propodus and dactyl of right fourth pereopod, lateral view; h, propodal rasp of same, ventrolateral view; i, propodus and dactyl of right fifth pereopod, lateral view; j, left uropod, dorsal view; k, telson, dorsal view; l, male left first pleopod, mesial view; m, male left second pleopod, anterior view. Scales equal 5 mm (a, e, f), 2 mm (b), 3 mm (c, j), 4 mm (d), 1 mm (g, i, k-m), and 0.5 mm (h).

Remarks. Based on the literature, Lemaitre (1986, 1989) elevated De Saint Laurent's subspecies *Parapagurus pilosimanus latimanus* (1972) to specific rank, and tentatively retained this taxon in *Parapagurus* Smith, 1879. Examination of the material from the USNS *Eltanin* has shown that indeed *P. latimanus* belongs in the genus *Parapagurus* as redefined by Lemaitre (1989).

Parapagurus latimanus closely resembles *P. andreui* Macpherson, 1984, from the southeastern Atlantic and southwestern Indian Ocean (see Lemaitre, 1990). The two species can best be differentiated by the armature of the antennal acicle (armed in

P. latimanus, unarmed in *P. andreui*), and the shape of the scales of the propodal rasp of the fourth pereopod (lanceolate in *P. latimanus*, conical in *P. andreui*). However, because some degree of inter-specific overlap was observed even in these characters, more material is needed to properly evaluate the differences between the two species.

Henderson (1888) listed the holotype of *P. latimanus* as from *Challenger* station 167A, in a depth of 18 m (10 fathoms). The depth reported for the holotype appears to be an error because species of *Parapagurus* are normally found on the continental slope region (~350–3000 m). The shallowest record for a species of this genus is 102 m, cited by Lemaitre (1989) for *Parapagurus pilosimanus*; however, this is a very rare occurrence. In Murray's (1895) summary of the *Challenger* expedition, he indicates that many invertebrate specimens were brought up while dredging at station 167, in 270 m (150 fathoms), taken just previous to station 167A. Although impossible to confirm, it is conceivable that the holotype was obtained instead at the deeper station 167.

Discussion

The study of presumed megalopae and juveniles of *Sympagurus dimorphus* from the USNS *Eltanin* and *Hero* material has provided insight into early morphological variations in this species, as well as the patterns of pleopod and telson development that might typically occur in species of the Parapaguridae. In juveniles of *S. dimorphus* those morphological characters that change most drastically during the transition from juvenile to adult are the antennal acicle, the second and third pereopods, the propodal rasp of the fourth pereopod, and the pleopods. As previously mentioned, the development and variations of these structures differs from that of other hermit crab families and, if not considered, can lead to taxonomic errors similar to the ones cited by Provenzano and Rice (1966). Although it was not possible to determine whether the juvenile material used in this study included all juvenile crab instars that might actually occur in *S. dimorphus*, some observations can be made.

The development of pleopods in juvenile hermit crabs has been described in detail for only a few species of the families Diogenidae (five: *Clibanarius scolopetarius*, *C. misanthropus*, *Paguristes sericeus*, *P. ortmanni*, and *Dardanus pectinatus*), and Paguridae (six: *Pagurus bernhardus*, *P. samuelis*, *P. annulipes*, *P. kenneryi*, *Anapagurus chiroacanchus*, and *A. petiti*). When compared with other hermit crab species, the pattern of juvenile pleopod development observed in *Sympagurus dimorphus* is most similar to that of species of the Diogenidae. The right pleopods in *S. dimorphus* apparently are lost relatively late during juvenile development. In the Diogenidae the right pleopods disappear at the second to fourth crab instars (Forest, 1954; Dechancé, 1958; Provenzano and Rice, 1966; Brossi-García, 1987, 1988), although considerable variability was noted in *Paguristes ortmanni* by Quintana and Iwata (1987); and in the Paguridae, the right pleopods disappear at the first to third crab instars (e.g. Thompson, 1903; Coffin, 1960; Kurata, 1968; Carvacho, 1988; McLaughlin *et al.*, 1989). According to these authors, in species of these two families the right pleopods disappear before the appearance of the gonopores. In *S. dimorphus*, rudimentary right pleopods are still present in specimens of 3 mm shield length, and gonopores are already present in all specimens examined of shield length < 3 mm. Although the number of instars necessary for this species to reach a shield length of 3 mm could not be determined from the samples studied, it appears that in *S. dimorphus* either the right pleopods are retained longer during juvenile development, or the gonopores appear earlier than in other hermit crab families.

As previously mentioned, megalopae of all hermit crabs lack first pleopods. In *Sympagurus dimorphus*, like in other hermit crab species in which adults have gonopods, these appendages develop during the early crab stages, and gradually acquire the adult form. Some carcinologists believe that the first and second pleopods arise as new structures and not from pre-existing pleopods (Provenzano and Rice, 1966). This condition appears to apply for *S. dimorphus* only for the first pair of gonopods of the males, but not for the second pair, as these are present in the megalopa described herein, and do not undergo any substantive reduction prior to transition to adult gonopod structure.

Carcinologists (e.g. De Saint Laurent-Dechancé, 1964; Williamson and von Levetzow, 1967) have noted the similarity between the zoeal stages assigned to species of the Parapaguridae and those of the Diogenidae, in particular with those in species of *Dardanus*. Although the megalopa of *Sympagurus dimorphus* bears some resemblance to that of species of *Dardanus* (see Provenzano, 1963a, b), we have found more similarity with that of species of another diogenid genus, *Aniculus* (see Forest, 1984). The similarity of these megalopae is most marked in the shape of the cephalic shield, the shape and proportions of the abdominal somites, and the abdominal pleura of somites 2–5. In *S. dimorphus* and *Aniculus*, the lateral margin of the shield is constricted medially by a well-defined groove; the width of abdominal somites 2–5 (viewed dorsally) decreases only slightly from anterior to posterior, giving the abdomen a more robust appearance than in *Dardanus*; and the pleura of the abdominal somites 2–5 each have a strong hook-like process that is very uncommon in hermit crabs. The megalopa of *S. dimorphus*, however, differs from both *Dardanus* and *Aniculus* in the spination of the ventral margins of the dactyls of the ambulatory legs. The telson of the megalopa of *S. dimorphus* is distinct from other described megalopae in having the posterior half constricted (Fig. 6e).

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Appendix

List of stations from USNS *Eltanin* and *Hero* cruises where specimens of Parapaguridae were collected. Species or larva found at each station are indicated by number in the last column: 1, *Parapagurus latimanus*; 2, *P. bouvieri*; 3, *Sympagurus haigae*; 4, *S. dimorphus*; 5, megalopa of *S. dimorphus*.

Station	Cruise	Position	Depth (m)	Date	Species
USNS <i>Eltanin</i>					
71	3	31°05'S, 71°44'W	187	24 June 1962	3
740	9	56°06'S, 66°19'W	494	18 September 1963	4
970	11	54°59'S, 64°53'W	641	11 February 1964	4
1283	14	43°14'S, 97°41'W	178	13 September 1964	4
1346	15	54°49'S, 129°48'W	603	7 November 1964	4
1398	15	44°00'S, 178°06'W	430	29 November 1964	4
1403	16	41°42'S, 175°29'E	951	31 January 1965	4
1411	16	51°00'S, 162°01'E	371	8 February 1965	4
1417	16	54°24'S, 159°01'E	93	17 May 1965	4
1712	23	38°24'S, 178°53'E	1995	28 May 1966	1, 4
1718	24	38°27'S, 168°07'W	659	12 July 1966	2
326	25	46°04'S, 83°55'W	298	9 October 1966	4
1851	27	49°40'S, 178°53'E	540	3 January 1967	4, 5
1974	27	54°30'S, 158°59'E	124	15 February 1967	4
1981	27	47°21'S, 147°52'E	915	24 February 1967	4
1989	32	53°29'S, 169°48'E	594	1 January 1968	4
2198	33	43°48'S, 174°24'W	909	12 May 1968	1, 2
2215	34	54°31'S, 159°00'E	110	18 June 1968	4
<i>Hero</i>					
895	715	54°59.9'S, 64°50'W	548	3 November 1971	4