

***Leontocaris vanderlandi*, a new species of hippolytid shrimp  
(Crustacea: Decapoda: Caridea) from the Seychelles, with an  
analysis of phylogenetic relations within the genus**

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A new species of hippolytid shrimp, *Leontocaris vanderlandi* spec. nov. is described from deep water off the Seychelles. A comparison with the four other species in the genus is made, and a key to their identification is provided. A phylogenetic analysis of the species within the genus is presented.

### Introduction

So far, the hippolytid genus *Leontocaris* Stebbing, 1905 was known to contain four species, viz.: *L. amplectipes* Bruce, 1990; *L. lar*, Kemp, 1906; *L. pacificus* Zarenkov, 1976; *L. paulsoni* Stebbing, 1905. *Leontocaris paulsoni* Stebbing, 1905, is based on a single male specimen collected at a depth of 240-249 m, off Lion Head, South Africa. Several specimens of this species were later recorded by Barnard (1950) from the Cape Peninsula and off Saldanha Bay in depths between 240 and 265 m. *Leontocaris lar* Kemp, 1906, was described from the north-east Atlantic Ocean, off Ireland, on the basis of three specimens. *Leontocaris pacificus* Zarenkov, 1976, from Chile caught at a depth between 680 and 700 m. *Leontocaris amplectipes* Bruce, 1990, from a depth of 1000 m, south of Point Hicks, Victoria, Australia.

During the Seychelles Expedition, carried out as part of the Netherlands Indian Ocean Programme (NIOP), 1992-1993 (van der Land, 1994; Fransen, 1994), only few stations were sampled at greater depths. In one of the few successful hauls at 600 m, a yet unknown species of the hippolytid genus *Leontocaris* was collected which is here described.

Abbreviations: RMNH = Rijksmuseum van Natuurlijke Historie; pocl. = postorbital carapace length.

***Leontocaris* Stebbing, 1905**  
***Leontocaris vanderlandi* spec. nov.**  
(Figs. 1-26)

Material examined.— Holotype, ovigerous female, pocl. 4.38 mm (RMNH D 42663): NIOP-E, Sta. SEY.795; Seychelles, N of Platte Island atoll, 05°48'S 55°22'E; coral rubble with calcareous rocks and sand; depth 600 m; rectangular dredge; 7.i.1993.

Description of holotype.— Body form slender. Carapace smooth, with well developed, slender, compressed rostrum, broken off just beyond basal antennular segment;



Figs. 1. *Leontocaris vanderlandi* spec. nov., holotype, ovigerous female, pochl. 4.38 mm (RMNH D 42663), lateral aspect of whole animal.

dorsal margin with 7 teeth at regular intervals, without setae in between, with suture on anterior base of each tooth, proximal 2 teeth postorbital; dorsal carina in anterior 1/3 of carapace; lower margin with one tooth, without setae; lateral carinae expanded at level of eyestalks; inferior orbital margin strongly produced, rounded; antennal spine strong, acute, marginal, just overreaching inferior orbital angle; anterolateral angle of carapace slightly produced, angular, without branchiostegal spine; supraorbital and hepatic spines absent.

Abdomen smooth; pleura of segments 1-5 rounded, third segment feebly produced postero-dorsally, without posterodorsal tooth, sixth segment twice as long as fifth segment and twice as long as deep, compressed, postero-lateral angle acute, postero-ventral angle blunt. Telson with 2 pairs of acute, marginal dorsal spines at 0.58 and 0.81 of telson length; distal margin broad, 1/4 of telson length, almost straight, with pair of short marginal spines and 5 pairs of spines in between, twice as long as marginal spines. Uropods slightly longer than telson, with protopodite typical for the genus, unarmed, exopod with row of 11-13 teeth in distal 2/3 of outer margin and acute, mobile disto-lateral spine at diaeresis.

Antennal peduncle with ventro-medial carina in proximal half of slender basal segment, about 4 times as long as distal width, with disto-lateral angle rounded, with medial margin setose; statocyst obsolete; stylocerite acute, reaching 3/4 of basal antennular segment, lateral margin strongly convex; intermediate segment subcylindrical, slightly longer than wide, unarmed, medially setose; distal segment subcylindrical, about as long as wide, unarmed, medially setose; upper flagellum uniramous,

about 1.6 times length of peduncle, with 15 segments, of which proximal 10 segments broad, with aesthetascs, distal 5 slender; lower flagellum subequal to upper flagellum, with 18 segments.

Antenna with basicerite robust, with rounded ventro-lateral margin; ischiocerite and merocerite with angular distal margins, carpocerite slender, subcylindrical, about 4 times as long as wide, almost reaching middle of scaphocerite; flagellum broken; scaphocerite well developed, about 2.6 times as long as central width, lateral margin with row of 13 teeth in distal 3/5, slightly convex, disto-lateral tooth not extending beyond oblique distal border of lamina.

Eye well developed; cornea globular, pigmented, without accessory pigment spot; eye-stalk about as long as wide, slightly broadening distally.

Epistome and labrum typical for the genus. Paragnath well developed, alae with transverse triangular distal lobes, and with more or less triangular submedian ventral lobes; corpus rather short, broad, with 2 longitudinal submedian carinae in anterior part, distally produced into distinct knob.

Thoracic sternites rather narrow anteriorly, broadening posteriorly, fourth rather long, unarmed, fifth with median hemispherical eminence, sixth and seventh with larger hemispherical eminence and small postero-lateral lobes, eighth unarmed.

Mandible (left) with two-segmented palp; distal segment of palp cylindrical, about 1/3 length of basal segment, about twice as long as wide, with two long, plumose, apical setae and one plumose lateral seta, basal segment broadening distally; molar process normal, distally excavate, with 2 blunt teeth, with dense mass of marginal setae, short, simple slender proximally, larger, stouter distally, with numerous blunt denticles distally; incisor process normal, obliquely truncate distally, with 5 acute teeth, lateral teeth largest.

Maxillula with slender, bilobed palp, both lobes rounded, each with single, long, plumose seta; upper lacinia broadened centrally, distal border with double row of about 13 short, stout, simple spines and numerous simple setae; lower lacinia slender, tapering distally, with numerous simple setae.

Maxilla with short, slender palp, medially emarginate, with one long, plumose, distal seta and one short, plumose distal seta; basal endite bilobed, distal lobe slightly broader than proximal lobe, both with numerous simple setae distally; coxal endite less developed, indistinctly bilobed, distal lobe very small, proximal lobe rounded, with several long, plumose setae; scaphognathite about three times as long as broad, posterior lobe slender, slightly expanding distally, anterior lobe broad.

First maxilliped with short subcylindrical palp, with plumose distal seta and several simple setae over entire length of palp; basal endite broad, distally rounded, medially straight with many simple short setae; coxal endite much smaller than basal endite, rounded, with few long simple setae; exopod with large broad caridean lobe, flagellum feebly developed, short, with vestigial setation; epipod large, deeply bilobed.

Second maxilliped with endopod normal; dactylar segment short, broad, more or less triangular, obliquely articulating with propodal segment, 1.8 times as broad as long, densely setose medially with simple or denticulate setae; propodal segment about 2.5 times as long as wide, medial margin with long, distally denticulate, spini-form setae, and some simple long setae on antero-medial margin; carpal and meral

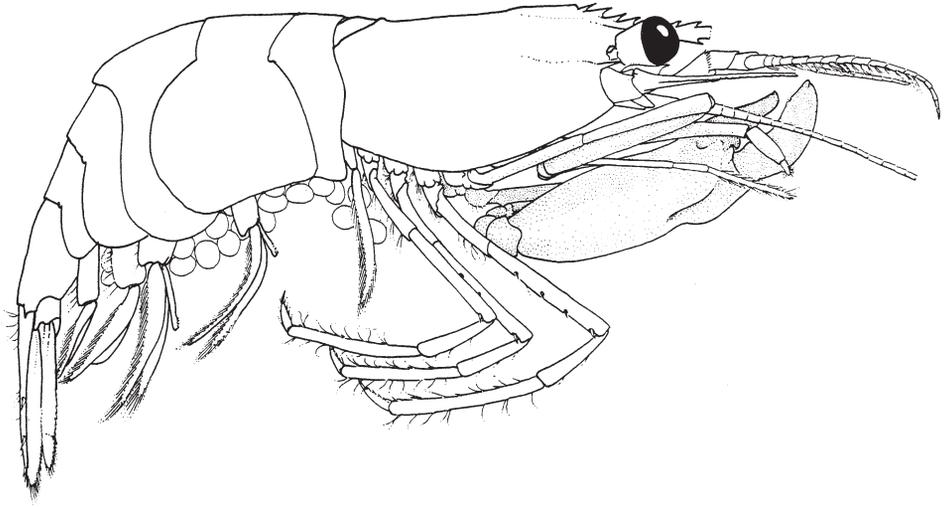


Fig. 2. *Leontocaris vanderlandi* spec. nov., holotype, lateral aspect whole animal.

segments normal; basis and ischium fused, with few simple long setae along medial margin, ischial segment medially excavate, lateral margin with long plumose setae; coxal segment medially produced, without setae; exopod with slender flagellum with long plumose terminal and preterminal setae and few simple setae proximally; epipod simple, with podobranch.

Third maxilliped slender, extending to distal margin of scaphocerite, exceeding antennular peduncle; basal segment distinctly separated from ischiomer segment medially by deep slit, medial margin of basis expanded, rounded, with several rows of long simple setae, in particular along slit between basis and ischiomerus, without exopod; ischiomerus about 7.5 times longer than proximal width, broadly expanded proximally, slender and subcylindrical distally, with few simple setae proxio-medially; penultimate segment subcylindrical, about 4.0 times as long as wide, 0.23 of ischiomer length; distal segment subcylindrical, about 10 times as long as wide, tapering distally, about 0.55 of ischiomer segment, with numerous groups of serrate setae distoventrally and few feeble setae distally; coxal segment broad, with long simple setae on medially developed margin, without epipod or lateral plate, with small arthrobranch and large pleurobranch.

First pereopods similar, small, slender, almost reaching distal margin of scaphocerite; chela small, with palm subcylindrical, 1.8 times finger length, about 2.2 times as long as deep; dactylus stout, ventrally concave, with small, acute, hooked tip and dense arc of short simple disto-dorsal setae, cutting edge entire; fixed finger rather slender, subcylindrical, with small, acute, hooked tip and cutting edge entire; carpus about 1.8 times chela length, subcylindrical, unarmed, about 7 times as long as distal width, tapering proximally; merus about 0.77 times as long as carpus, about 6 times as long as central width, unarmed; ischium about 0.5 carpal length, 4 times longer than distal width, slightly compressed; coxa without epipod; without arthrobranch.

Second pereiopods very unequal, dissimilar. Major pereiopod (left) exceeding basal antennular segment by carpus and chela; chela with palm smooth, glabrous, about twice as long as central width, subcylindrical with well-developed open ventral flange, with deep narrow submarginal fissure along central medial half in which several rows of membranous papillae; dactylus strongly compressed, laminar, far exceeding fixed finger, about 2.5 times longer than central depth, lateral margin rounded, indistinctly lobular, far overreaching small blunt distal tooth, curved laterally, cutting edge curved medially, with large acute recurved proximal tooth; fixed finger stout, 1.5 times as long as deep, moderately compressed, distally blunt with small hook-like tip, triangular tooth at midlength, separated by deep notch from irregularly denticulate broad proximal tooth, groups of simple setae medially as well as distally; carpus long and slender, 4-segmented, with proximal segment about as long as palm and as ischium and merus together, with ventral, lateral and dorsal longitudinal carinae, medially excavate; ventral carina with row of 12 short acute teeth, with robust distal tooth on flexor margin; distal three carpal segments short, robust, subequal, quadrate, irregular, about  $0.1 \times$  proximal segment, with large dorso-lateral plates; merus about  $0.6 \times$  proximal carpal segment, about  $3 \times$  distal width, expanded distally, medially excavate, with distinct proximo-medial flange with row of about seven shallow lobes with short denticulate robust setae; ischium about  $0.6$  length of merus, about  $5 \times$  distal width, medially excavate, with ventro-medial flange bearing 6 long stout curved setae; basis and coxa normal, without special features; exopod, epi-pod and arthrobranch lacking.

Minor second pereiopod with proximal carpal segment extending to just beyond scaphocerite; chela small; palm subcylindrical,  $1.6$  times as long as fingers, as long as

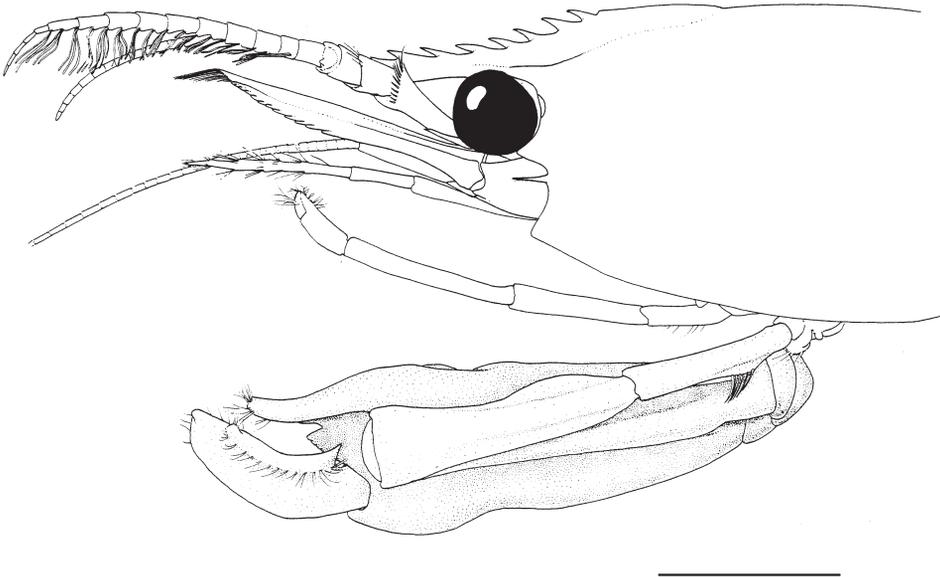
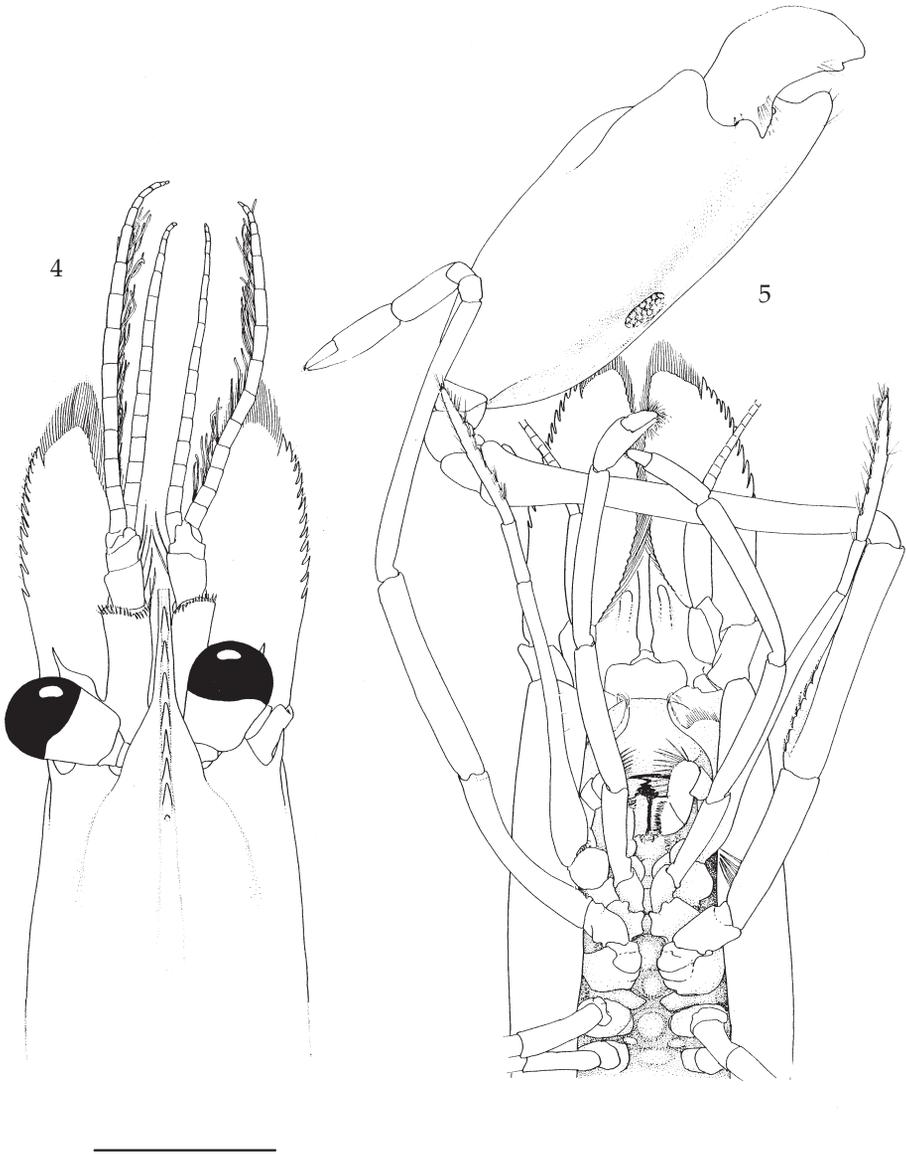
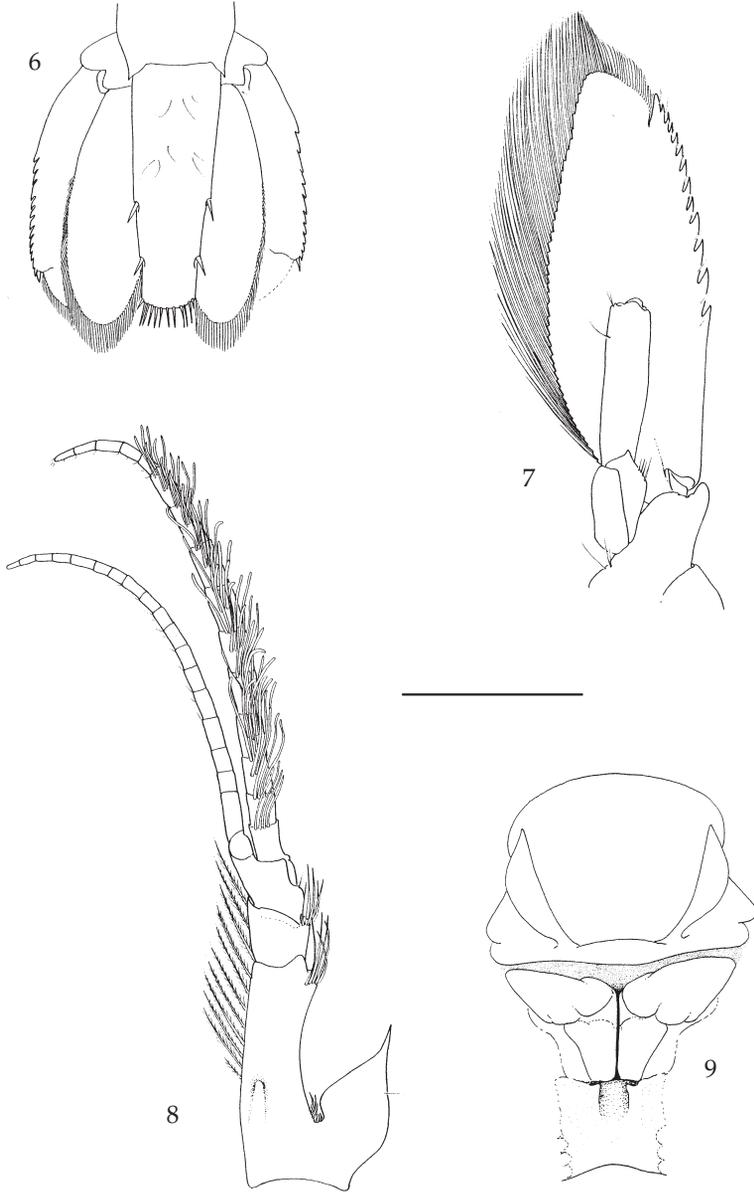


Fig. 3. *Leontocaris vanderlandi* spec. nov., holotype, lateral aspect anterior region. Scale = 2 mm.



Figs. 4-5. *Leontocaris vanderlandi* spec. nov., holotype. 4, dorsal aspect anterior region; 5, ventral aspect anterior region. Scale = 2 mm.

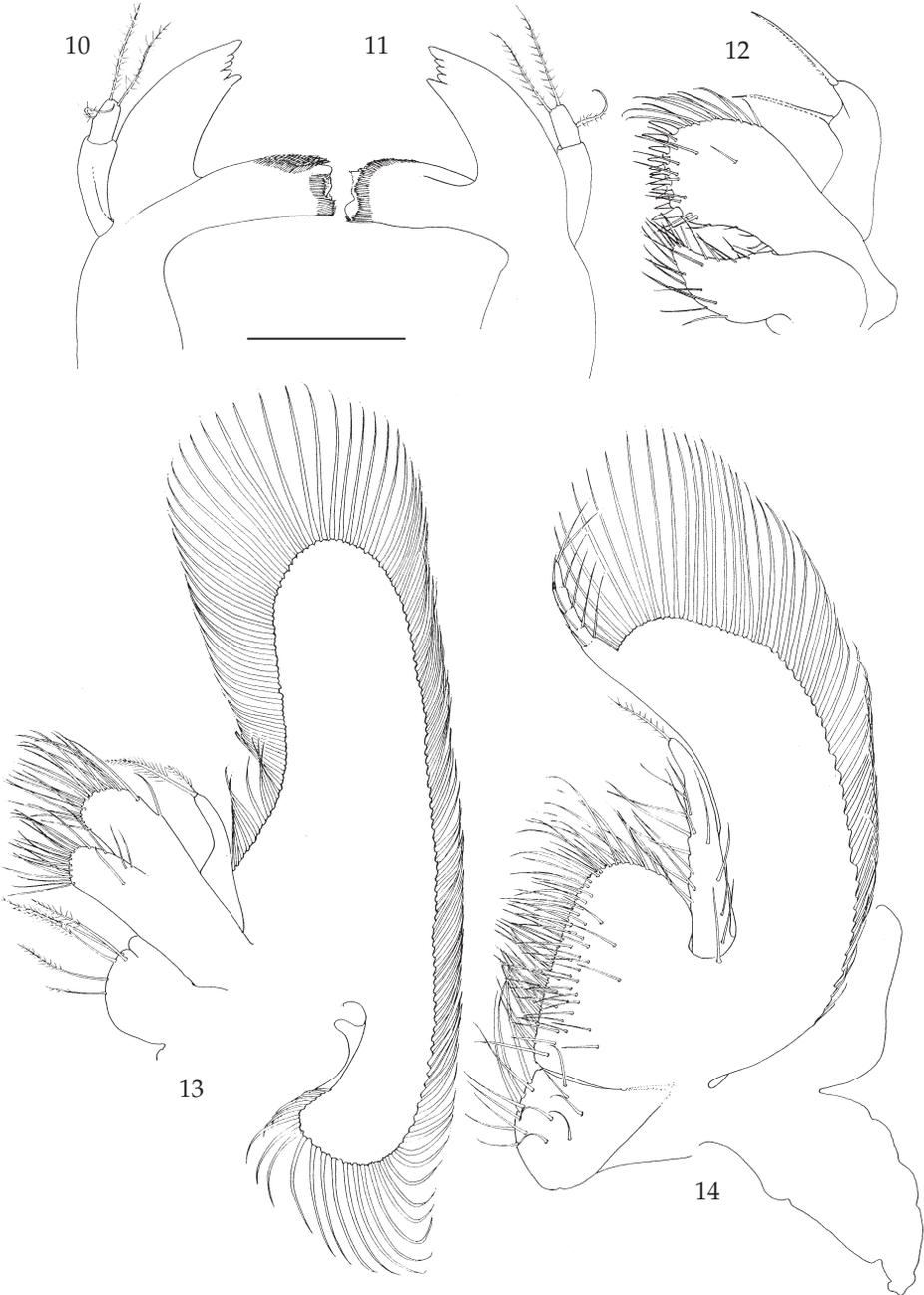
distal carpal segment, 3 times as long as deep; fingers subcylindrical, feebly spathulate and tapering distally, both with small distal hook and many small distal simple setae, cutting edges entire; carpus four-segmented, distal segment robust, unarmed, two central segments short, stout, 0.3 of palm length, unarmed, proximal segment elongate, 2.3 times as long as chela, 13 times as long as distal width; merus 0.73 times as long as proximal carpal segment, about  $8 \times$  distal width, unarmed; ischium curved



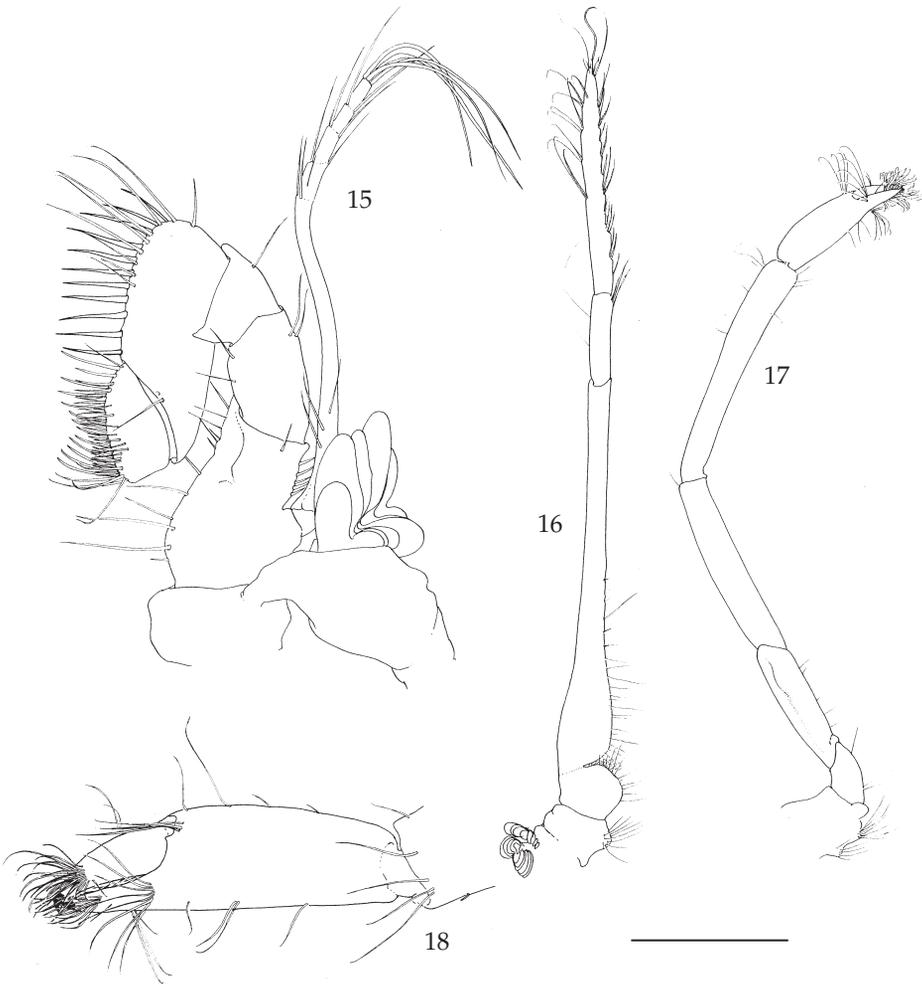
Figs. 6-9. *Leontocaris vanderlandi* spec. nov., holotype. 6, telson and uropods, dorsal aspect; 7, left antennular peduncle, ventral aspect; 8, left antennal peduncle, ventral aspect; 9, paragnath, ventral aspect. Scale : 6 = 2 mm; 7, 8 = 1.5 mm; 9 = 1 mm.

inward, 0.9 of merus length, about 7 × proximal width, unarmed; basis and coxa short, stout, without special features.

Ambulatory pereiopods moderately slender. Third pereiopod with carpus reaching to about distal antennular peduncle; dactylus robust, slightly compressed,

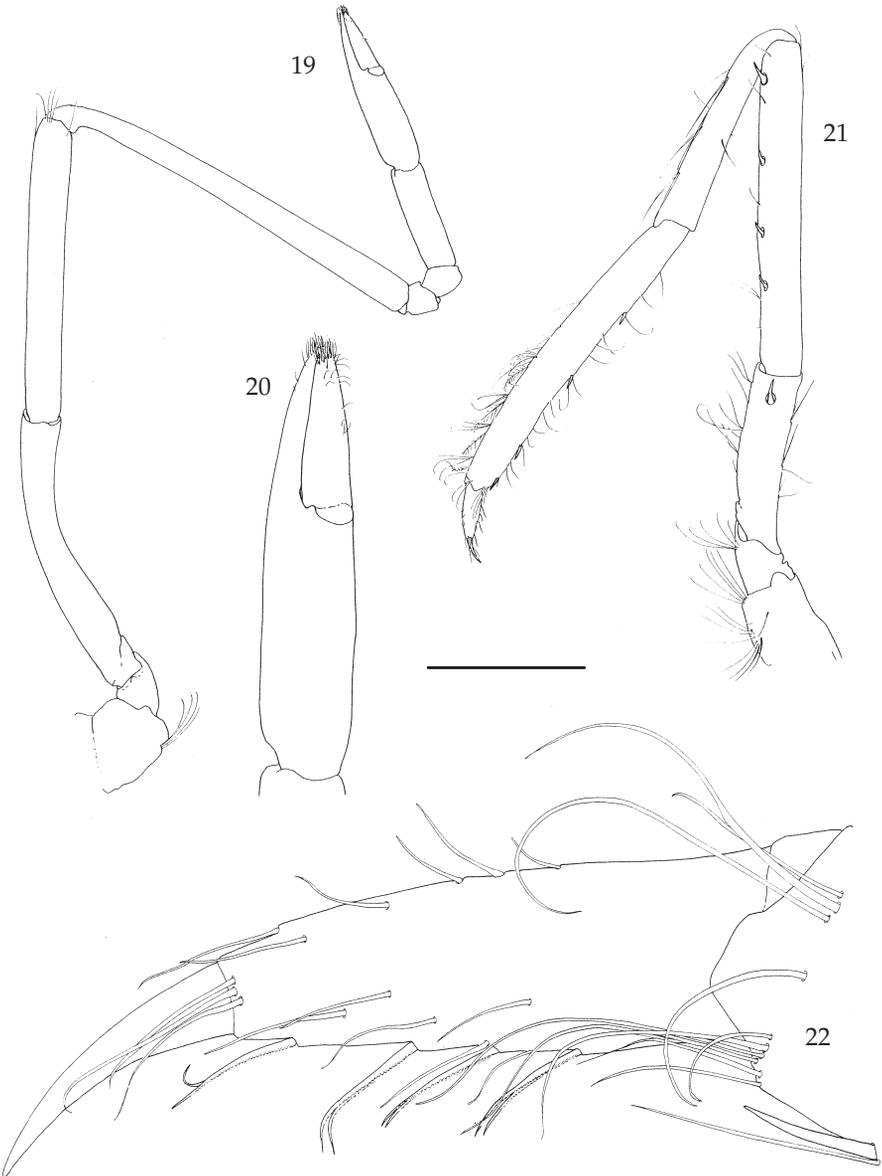


Figs. 10-14. *Leontocaris vanderlandi* spec. nov., holotype. 10, left mandible, ventral aspect; 11, left mandible, dorsal aspect; 12, left maxillula, ventral spect; 13, left maxilla, ventral aspect; 14, left first maxilliped, ventral aspect. Scale = 0.6 mm.



Figs. 15-18. *Leontocaris vanderlandi* spec. nov., holotype. 15, left second maxilliped, ventral aspect; 16, left third maxilliped, ventral aspect; 17, left first pereopod, ventral aspect; 18, same, detail of chela. Scale 16, 19 = 0.6 mm; 17, 18 = 1.5 mm.

about 0.24 length of propodus, tapering distally, slightly concave flexor margin with 4 pairs of denticulate setae and several simple setae on corpus, unguis slightly curved, long, acute, conical, about 0.5 length of corpus; propodus about 8 × central width, with 4 spines and many long simple setae along ventral margin, dorsal margin with simple and plumose setae; carpus 0.7 × propodus length, unarmed, with several long simple setae along dorsal margin; merus as long as propodus, with 4 movable spines along ventro-mesial margin, distal-most spine strongest, subdistal; ischium 0.5 of merus length, with subdistal mesial spine; basis and coxa normal, without special features; without exopod, epipod or arthrobranch. Fourth and fifth pereopods generally similar; merus of fourth with 3 movable spines along ventro-



Figs. 19-22. *Leontocaris vanderlandi* spec. nov., holotype. 19, minor, right second pereiopod, ventral aspect; 20, same, detail of chela; 21, third left pereiopod; 22, same, detail of dactylus. Scale 19, 21 = 1.5 mm; 20 = 0.6 mm; 22 = 0.15 mm.

mesial margin, fifth only with one subdistal ventro-mesial movable spine.

Branchial formula:

	maxilliped			pereiopod				
	I	II	III	I	II	III	IV	V
Arthrobranch	-	-	+	-	-	-	-	-
Pleurobranch	-	-	+	+	+	+	+	+
Podobranch	-	+	-	-	-	-	-	-
Epipod	+	+	-	-	-	-	-	-
Exopod	+	+	-	-	-	-	-	-

The third maxilliped bears a small distally placed and a larger proximally placed gill. The distal gill is here regarded an arthrobranch, the proximal one a pleurobranch. This is more an indication of their relative position than that they have been identified as being an arthrobranch and pleurobranch according to their position on the body.

Pleopods typical for the genus.

Eggs rather large, 0.45 mm in diameter.

Etymology.— I take great pleasure in dedicating this species to my colleague, Jacob van der Land, chief-scientist on board of the R.V. *Tyro*, when cruising through the Seychelles.

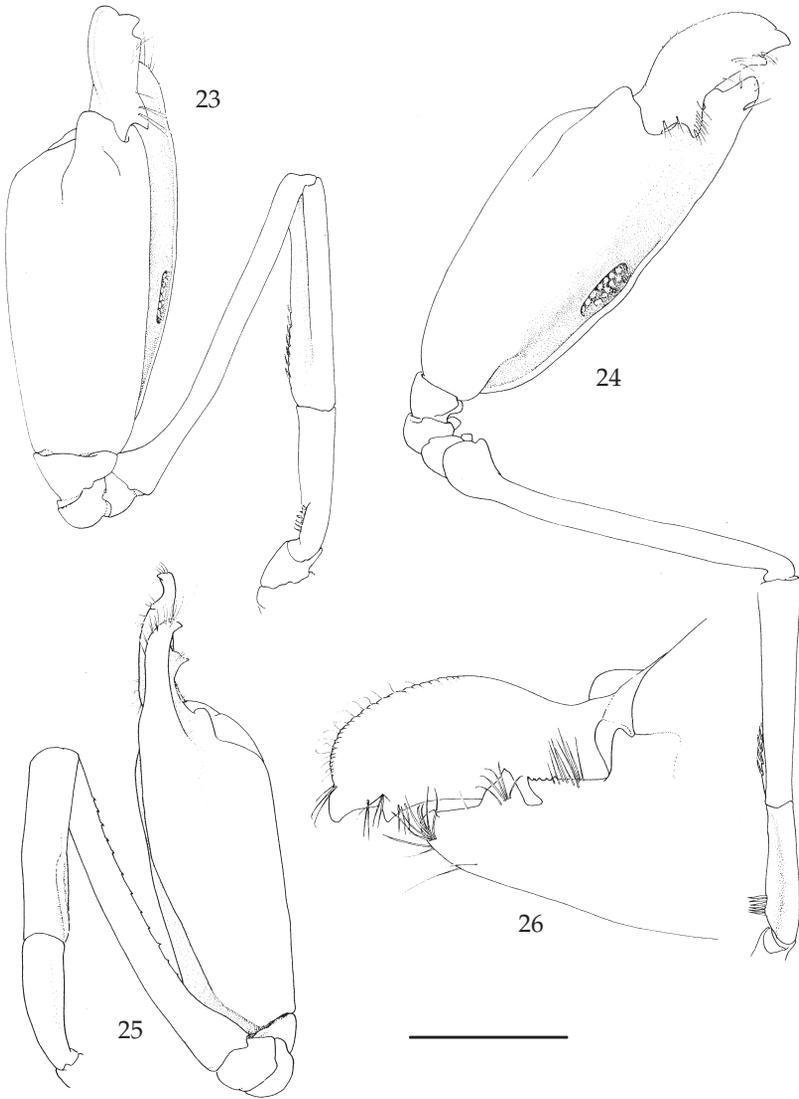
Associated fauna.— The dredge was completely filled with coral rubble and calcareous rocks among which were found: corals, zoantharians, serpulids, echinoderms and molluscs.

Systematic position.— The descriptions of species of *Leontocaris* recognized at present are based on one or a few specimens per species. Infra-specific variation is therefore not well known. From the descriptions the species can be easily distinguished from each other, except for *Leontocaris pacificus* and *L. paulsoni*. These last-named two species differ by the number of ventral rostral teeth and the presence or absence of mobile, ventro-medial spines on the meri and ischia of the ambulatory pereiopods. These spines were not mentioned by Stebbing (1905) and Barnard (1950) for *L. paulsoni*, whereas Zarenkov (1976: 10-11, fig 3) described and figured them for *L. pacificus*.

*Leontocaris vanderlandi* spec. nov. differs from the other species in the genus in having a two-segmented mandibular palp, by the much shorter carpus of the ambulatory pereiopods in relation to the propodi, and by the telson having only two marginal dorsal pairs of spines and the straight distal margin.

Key to the species of *Leontocaris* Stebbing, 1905

1. Third abdominal segment with postero-dorsal tooth; epigastric teeth on middle of carapace, separated from dorsal rostral teeth; telson tapering distally, with 7 pairs of marginal dorsal spines ..... 2
- Third abdominal segment without postero-dorsal tooth; epigastric teeth in anterior part of carapace, at equal distance to dorsal rostral teeth; telson with posterior margin rounded or straight, with 2-5 pairs of marginal dorsal spines ..... 3
2. Rostrum with 6-8 teeth on ventral margin ..... *L. paulsoni*
- Rostrum with 12 teeth on ventral margin ..... *L. pacificus*



Figs. 23-26. *Leontocaris vanderlandi* spec. nov., holotype. 23, major, left second pereiopod, ventral aspect, folded; 24, same, dorsal aspect, folded; 25, same, ventral aspect, extended; 26, detail of fingers of chela. Scale 23-25 = 2 mm; 26 = 0.6 mm.

- 3. Exopods of uropods disto-laterally entire; dactyli of ambulatory pereiopods more than 0.5 of propodus length ..... *L. amplectipes*
- Exopods of uropods disto-laterally serrate; dactyli of ambulatory pereiopods less than 0.5 of propodus length ..... 4
- 4. Pleuron of fifth abdominal segment with small posterior tooth; telson with five pairs of marginal dorsal spines and three pairs of terminal spines; carpus of

- ambulatory pereopods about as long as propodus; mandibular palp one-segmented ..... *L. lar*
- Pleuron of fifth abdominal segment rounded; telson with two pairs of marginal dorsal spines and six pairs of terminal spines; carpus of ambulatory pereopods 0.7 of propodus length; mandibular palp two-segmented ..... *L. vanderlandi* nov. spec.

### Relation with the larval genus *Problemacaris*

In 1921, Stebbing established the monospecific genus *Problemacaris* for two remarkably spiny decapod larvae found near Table Mountain, South Africa, between 300 fms and the surface. He named the species *Problemacaris spinetum*. In 1924, he described and figured these specimens in full detail. Gordon (1964) re-examined Stebbing's specimens concluded that they represent the larval stages of a species of *Leontocaris*, most likely *L. paulsoni*, which is known from the same region. A feature the larvae and adults have in common is the presence of two epigastral spines on the carapace. *Problemacaris boschmai* Gordon, 1964, was described in the same article from several stations SW of Ireland and off the Bay of Biscay. As *Leontocaris lar* Kemp, 1906, was described from off Ireland, Gordon suggested that *Problemacaris boschmai* and *Leontocaris lar* might be conspecific. This view is supported by the fact that some of the specimens of *Problemacaris boschmai* figured by Gordon indeed show the distinctive features of *Leontocaris* in the major second pereopods, such as the 4-segmented carpus, the flange and locking mechanism on the lateral surface of the palm, and the distinctive features of the fingers. In addition, both forms share the presence of 3 epigastric spines on the carapace.

Another unidentified *Problemacaris* specimen was described by Gordon from a plankton haul near Tristan de Cunha, representing a young larva without a trace of pleopods. Although not far from the type-locality of *Leontocaris pacificus* Zarenkov, 1976, it is not likely to be conspecific with that species, as the larva has 3 epigastric spines on the carapace while *Leontocaris pacificus* has only 2.

A specimen taken from a depth of 340 m off Christchurch, New Zealand, was identified by Gordon (1964) as *Problemacaris spinetum*. The only difference she found between this specimen and the specimens described by Stebbing (1921; 1924) is the absence of a serrated lateral margin of the exopod of the uropod in the New Zealand specimens. This feature happens to be one of the distinguishing characters of *Leontocaris amplectipes* Bruce, 1990, described from South Australia. However, the New Zealand larva has only 2 epigastric spines on the carapace, while *Leontocaris amplectipes* has 3. Also in this case the conspecificity with a known adult of a species of *Leontocaris* remains unclear.

More definite conclusions on the conspecificity of species of *Leontocaris* and the larva-based genus *Problemacaris* can only be drawn when more larval stages (preferably reared in the laboratory) become available.

### Distribution

Both adult specimens of *Leontocaris* and larval *Problemacaris* specimens have thus far been found in temperate waters of the northern and southern hemisphere. Adult

specimens seem to be restricted to depths between 240 and 1000 m. The difficulty of sampling hard substrata along continental slopes at these depths might explain the scarce number of specimens found. The specimen of *Leontocaris vanderlandi* spec. nov. from 600 m depth in the Seychelles is the first record of a member of its genus in tropical waters.

### Biology

Kemp (1910) suggested an association with coelenterates (*Antipatharia* and the scleractinian coral *Lophohelia*) for *Leontocaris lar*, as the specimens were found in trawls together with large numbers of the above mentioned coelenterates. Bruce (1990) also suggested a commensal life-style with coelenterates for *Leontocaris amplexicus* on the basis of several morphological features of the species. *L. vanderlandi* was caught together with scleractinian corals and zoantharians which could be its host.

Bruce (1990) commented on the possible predatory function of the double folding major second chela with its locking mechanism similar to that of the raptorial claws in stomatopods.

### Position of *Leontocaris* in the Hippolytidae

The position of *Leontocaris* within the Hippolytidae is not clear. Christoffersen (1987) performed a manual cladistic analysis of the hippolytid genera. As a result *Leontocaris* was grouped together with *Thorella* Bruce, 1982, *Tozeuma* Stimpson, 1860, *Trachycaris* Calman, 1906, *Latreutes* Stimpson, 1860, *Paralatreutes* Kemp, 1925, *Gelastocaris* Bruce, 1990, *Hippolyte* Leach, 1814, and *Phycocaris* Kemp, 1916, into the family Hippolytidae sensu Christoffersen. The autapomorphic characters on which this family was based are: "97) the third maxilliped not overreaching the antennular peduncle; 98) the fourth and fifth pereopods lacking an exopod". In *Leontocaris* the third maxilliped is as long as, or longer than the antennular peduncle. This is also true for several other members of genera within the Hippolytidae sensu Christoffersen (1987), such as *Thorella*, *Latreutes* and *Gelastocaris*. The absence of an exopod on the fourth and fifth pereopod is a feature that counts for all 37 recognized genera of Hippolytidae sensu Chace (1997), as well as for many other non-hippolytid caridean genera. The synapomorphic characters leading to *Leontocaris* in the cladogram (Christoffersen, 1987: fig. 8) of the Hippolytidae are not always applicable to *Leontocaris*: "141) posteroventral angle of fifth abdominal somite rounded; 169) posterior margin of telson rounded in adult". Going down in the cladogram, one other character does not match with *Leontocaris*: "3) first pereopod more robust than second pereopod in post-larval stages" (autapomorphy for Crangonoidea and Alpheoidea sensu Christoffersen, 1987).

In his checklist of the genera and species of Hippolytidae, Chace (1997: 40) indicated the problematic position of *Leontocaris* when writing: "A 107-character non-cladistic analysis of the 40 genera originally assigned to the family [Hippolytidae] seemed to support the concept of a reasonably homogeneous group, with possible exception of *Leontocaris*....." In the diagnosis of the family Hippolytidae, Chace (1997:

39) further states that the first pair of pereopods is more robust than the second pair. This character does not apply for *Leontocaris*.

To keep the genus into the Hippolytidae sensu Chace (1997), the family definition should be broadened. The diagnostic feature of the first pereopods being more robust than the second should be deleted. The set of diagnostic characters used by Chace to define the Hippolytidae does not contain an autapomorphy for the group. It is likely that the Hippolytidae sensu Chace are not a monophyletic group. The seemingly high level of homoplasy in the cladogram by Christoffersen (1987) with regards to the position of *Leontocaris*, does not support its present position in the Hippolytidae sensu Christoffersen (1987) either. It is therefore not clear which taxon forms the sistergroup of *Leontocaris*.

### Phylogenetic analysis of *Leontocaris*

Synapomorphies for the species in the genus *Leontocaris* in relation to other Caridea are: 1) scaphocerite with serrate lateral margins; 2) major second pereopod folding and locking mechanism; 3) third maxilliped with medial slit separating the ischiomeral segment from the basis. These autapomorphies support the hypothesis that the genus *Leontocaris* is a monophyletic group. As the phylogenetic relations within the Hippolytidae are unclear, two outgroup species were used to give direction to the characters used in the analysis.

As the most distantly related outgroup, *Procaris ascensionis* Chace & Manning, 1972, belonging to the Procarididea, is used. The autapomorphy of the Procarididea is, according to Kensley & Williams (1986: fig. 8), the absence of chelae on first and second pereopods. The Procarididea are regarded the sistergroup of the Caridea (Abele & Felgenhauer, 1986; Kensley & Williams, 1986; Schram, 1986; Christoffersen, 1988). From within the Hippolytidae, the type-species of the type-genus, *Hippolyte varians* Leach, 1814, was added.

The list of the characters used and the distribution of the characters across the species are given in table 1 and 2, respectively.

Results.— The data set was analysed with PAUP 3.1.1 with all characters weighted equally, with characters 4 and 18 ordered, the others unordered, and with exhaustive search. It resulted in one most parsimonious tree (fig. 27a) with length = 26, CI = 0.885 (CI excluding uninformative characters = 0.833), RI 0.812 and RC = 0.719. There was one tree with length = 27 (fig. 27b).

When character 4 and 18 were treated irreversible the analysis resulted in two most parsimonious trees with length = 27, CI = 0.852 (CI excluding uninformative characters = 0.789), RI = 0.840 and RC = 0.716. These trees have the same topology as in fig. 27a and b. The consensus tree (both strict and 50 % majority rule) (Fig. 27c) shows a trichotomy at the base of the *Leontocaris* group.

Discussion.— Character 1. This character was coded missing for *Procaris ascensionis* and *Hippolyte varians* as homologous structures are not recognized in these species. Because of this, the apomorphic or plesiomorphic state of the character could not be indicated.

Character 2. A serrate lateral margin is an autapomorphy for *Leontocaris*. Serrate lateral margins are known for several other caridean species like *Psaliopus* (Psali-

dopodidae), *Thalassocaris* (Pandalidae), *Pontophilus* (Crangonidae), which seem all phylogenetically distant from *Leontocaris* and are likely non-homologous structures derived through parallel evolution. *Gelastocaris*, a genus of Hippolytidae (sensu Chace, 1997), also shows serrate lateral margins of the scaphocerite. Here the teeth are articulating and therefore most likely the result of parallel evolution too.

Character 3. The two apomorphous states are not placed in a transformation series as there are no hypothesis to support one or the other state to be more derived. As no large series of specimens of each species is available, the variation in this character cannot be measured. The character might turn out to be less informative when more material becomes available.

Character 4. It is assumed that a three-segmented palp is the plesiomorphous character-state in caridean shrimps. The reduction of the number of segments has occurred independently in several groups.

Character 5-9. These provide synapomorphies for *Hippolyte* together with *Leontocaris*.

Table 1. List of 18 characters with their states.

1. Carapace; posteriormost epigastral teeth	10. Major second pereiopod; proximal segment carpus
0. mid-dorsal	0. unarmed
1. in anterior third	1. with row of spines along ventral carina
2. Scaphocerite; lateral margin	11. Minor second pereiopod; cutting edge chela
0. entire	0. distally denticulate
1. serrate	1. entire
3. Scaphocerite; number of teeth lateral margin	12. Ambulatory pereiopods; dactylus
0. 0	0. less than 0.3 of propodus length
1. 11-13	1. 0.5 of propodus length
2. 17-19	13. Ambulatory pereiopods; carpus
4. Mandibular palp	0. much less than 0.7 of propodus length
0. three-segmented	1. about as long as propodus
1. two-segmented	14. Third abdominal segment; posterodorsal tooth
2. one-segmented	0. absent
3. absent	1. present
5. Third maxilliped; number of segments	15. Fifth abdominal segment; posterior margin pleura
0. 7	0. without tooth
1. 5	1. with tooth
6. Pereiopod 1-5; exopods	16. Exopod of uropod
0. present	0. entire
1. absent	1. serrate
7. Pereiopods 1-4; epipods	17. Telson; distal margin
0. present	0. with several pairs of spines
1. absent	1. bifurcated
8. Chela or subchela pereiopods 1 and/or 2	18. Telson; marginal dorsal spines
0. absent	0. 2
1. present	1. 4 or 5
9. Second pereiopod; carpus	2. 7
0. entire	
1. 3-segmented	
2. 4-segmented	

Table 2. Matrix of *Leontocaris* species and the states of the the characters as listed in table 1; - = missing data.

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
<i>Procaris ascensionis</i>	-	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0
<i>Hippolyte varians</i>	-	0	0	3	1	1	1	1	1	0	0	0	1	0	0	0	0	0
<i>L. amplexipes</i>	1	1	1	2	1	1	1	1	2	0	0	1	0	0	0	0	0	1
<i>L. lar</i>	1	1	2	2	1	1	1	1	2	-	-	0	0	0	1	1	0	1
<i>L. pacificus</i>	0	1	2	2	1	1	1	1	2	-	-	0	0	1	1	1	1	2
<i>L. paulsoni</i>	0	1	2	2	1	1	1	1	2	1	-	0	0	1	1	1	1	2
<i>L. vanderlandi</i>	1	1	1	1	1	1	1	1	2	1	1	0	1	0	0	1	0	0

Character 10. These spines were not described by Kemp for *Leontocaris lar* nor by Bruce for *Leontocaris amplexipes*. As no large series of specimens of these species are available the variation of this character cannot be measured. The character might turn out to be less informative when more material becomes available.

Character 11. These structures are difficult to observe. Since the original descriptions did not mention a character state for *Leontocaris lar*, *L. pacificus* and *L. paulsoni*, this character was here coded as missing data for these species. *Hippolyte varians*, and many other members of the Hippolytidae (sensu Chace, 1997) also show this feature, indicating that an entire cutting edge might be the apomorphic state for the genus *Leontocaris*. If so, the entire cutting edge in *L. vanderlandi* should be regarded a reversal.

Character 12. Autapomorphy for *Leontocaris amplexipes*.

Character 13. As both states occur in several caridean groups including the Hippolytidae (sensu Chace, 1997) this character is here regarded only informative on a low taxonomic level.

Character 14. With regards to both *Procaris ascensionis* and *Hippolyte varians*, the presence of a postero-dorsal tooth on the third abdominal segment in species of *Leontocaris* is apomorphic. However, this character state occurs in several groups of Caridea. The character is here regarded only informative on a low taxonomic level.

Character 15. With regards to both *Procaris ascensionis* and *Hippolyte varians*, the presence of a tooth on the pleura of the fifth abdominal segment in species of *Leontocaris* is apomorphic. However, this character state occurs in several groups of Caridea. Therefore, the character is here regarded only informative on a low taxonomic level.

Character 16. Within the Hippolytidae (sensu Chace, 1997) the presence of a serrate lateral margin on the scaphocerite is an apomorphy. This character state occurs in several genera outside the Hippolytidae, such as *Periclimenaeus* (Palaemonoidea), *Pontophilus* (Crangonoidea) and *Psalidopus* (Psalidopidae), which seem phylogenetically remote from *Leontocaris* and hence are more likely non homologous structures having originated through parallel evolution.

Character 17 and 18. A transformation series can be made from 1) a primitive state in which only two pairs of dorsal marginal spines occur on the telson and a

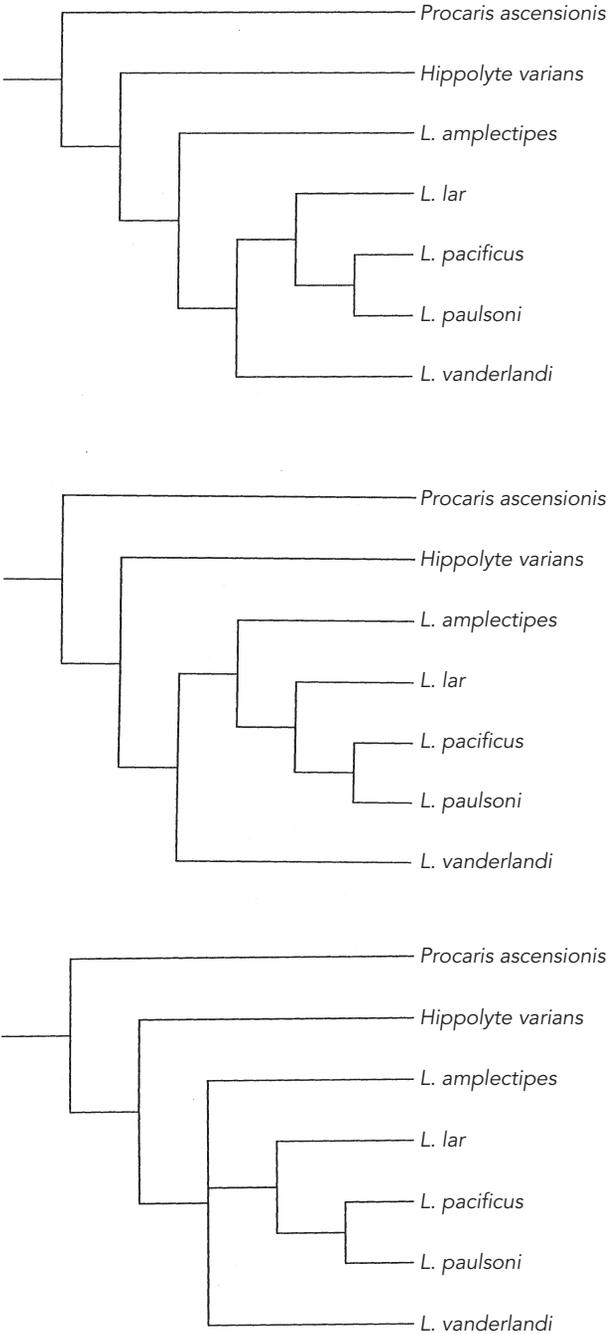


Fig. 27. Phylogenetic trees of *Leontocaris* based on the characters listed in Table 1 and the matrix in Table 2; a, most parsimonious tree, length = 26; b, only tree with length = 27; c, consensus tree (both strict and 50 % majority rule).

series of spines on the distal margin, through 2) a state in which part of the terminal spines (2-3) move to the lateral margin during development, to 3) a state in which all spines are situated marginal and the terminal margin is reduced to a small bifid apex.

Conclusions.—There is good support for the hypothesis that *Leontocaris* represents a monophyletic group. Direction within *Leontocaris* is mainly caused by character 18, defining *Leontocaris pacificus* together with *Leontocaris paulsoni* as a monophyletic group. The position of the other species is less clear as homoplasy levels are higher in this part of the tree. Homoplasy is mainly caused by the characters 4 and 18. More weight to character 4 would favour the tree in fig. 27b, whereas fig. 27a represents the hypothetical tree in which character 18 gets more weight. A better understanding of the phylogenetic relations within the Hippolytidae (sensu Chace, 1997) could reveal a more suitable outgroup to give direction to the lower part of the *Leontocaris* clade.

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