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ARTICLE

Establishment of Leontocarididae fam. nov. for *Leontocaris* Stebbing, 1905 (Decapoda: Caridea)

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Abstract. A new caridean shrimp family, Leontocarididae **fam. nov.,** is established to accommodate the deep-water genus *Leontocaris* Stebbing, 1905, with nine species. The new family can be separated from all other caridean families by the extremely unequal and asymmetrical second pereiopods, with carpus subdivided into four subarticles, the first by far longest, and three much shorter, enlarged, distal subarticles; the chela of the major second pereiopod markedly enlarged, with twisted, lamina-like dactylus and tympanum on mesial face of the palm; the merus of the major second pereiopod with a flange on proximal mesial surface, forming together with the tympanum a chela locking mechanism; the antennal scaphocerite with lateral margin strongly dentate in distal half or third; the uropodal exopod with lateral margin strongly dentate in distal half; and the diagnostic late larval stages (*problemacaris* larva). *Leontocaris* is subdivided into three informal species groups based on the combination of several morphological characters.

Keywords. Caridean shrimps; Classification; New family; Species group; Phylogeny.

INTRODUCTION

Since the first attempts of phylogeny-based classification of the infraorder Caridea Dana, 1852, the family Hippolytidae Spence Bate, 1888 has been seen as problematic and likely non-monophyletic (Thompson, 1967; Christoffersen, 1987; Fransen, 2001; De Grave *et al.,* 2014). Christoffersen (1987, 1990) started dismembering Hippolytidae *sensu* Holthuis (1955), resurrecting older family names and proposing several new families and subfamilies. However, Christoffersen's (1987, 1990) classification was not taken into consideration by Chace (1992) and Holthuis (1993) and most of his families were placed in the synonymy of Hippolytidae by Chace (1997). Chace & Kensley (1992) removed *Yagerocaris* Kensley, 1988 from the Hippolytidae, transferring this genus to Alpheidae Rafinesque, 1815; this placement was subsequently confirmed by both morphological and molecular phylogenetic analyses (Anker *et al.,* 2006; Bracken *et al.,* 2009; Chow *et al.,* 2021).

Bracken *et al.* (2009) provided the first relatively comprehensive molecular phylogeny of Caridea based on a combined nuclear (18S rRNA) and a mitochondrial (16S rRNA) dataset and confirmed that "the family Hippolytidae represents a polyphyletic assemblage that qualifies for partitioning into several families as formerly suggested". Following a phylogenetic analysis based on two nuclear (enolase + Na-K ATPase α-subunit) and one mitochondrial (16S rRNA) genes, De Grave *et al.* (2014) redefined Hippolytidae, recognising five additional families: Lysmatidae Dana, 1852, Thoridae Kingsley, 1878, Bythocarididae Christoffersen, 1987, Barbouriidae Christoffersen, 1987, and Merguiidae Christoffersen, 1990, leaving open the question about the validity of Nauticarididae Christoffersen, 1987, Alopidae Christoffersen, 1987, and Merhippolytidae Christoffersen, 1990. However, several "morphologically aberrant" hippolytid genera (i.e., genera deviating from the basic morphology of *Hippolyte* Leach, 1814 and closely allied genera), such as *Leontocaris* Stebbing, 1905, *Caridion* Goës, 1864, *Alope* White, 1847, *Nauticaris* Spence Bate, 1888, *Merhippolyte* Spence Bate, 1888, *Eumanningia* Crosnier, 2000 and *Phycocaris* Kemp, 1916, were not included in the analysis of De Grave *et al.* (2014). Therefore, Hippolytidae, even after being restricted to 16 genera, remains a morphologically and ecologically heterogeneous assemblage.

The absence of molecular data greatly complicates the phylogenetic positioning of *Leontocaris* within Caridea. The attempts to extract DNA from specimens of *L. vanderlandi* Fransen, 2001 and *L. lar* Kemp, 1906 reported by Fransen (2001) and Chan *et al.* (2016), respectively, were unsuccessful.

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In Christoffersen's (1987) analysis, *Leontocaris* was recovered in a clade together with *Hippolyte* and *Phycocaris,* a rather unlikely relationship given the amount of morphological and ecological disparities between these three genera. Chace (1997) noted that "a 107-character non-cladistic analysis of the 40 genera originally assigned to the family seemed to support the concept of a reasonably homogeneous group, with the possible exception of *Leontocaris*". Fransen's (2001) brief discussion of the possible phylogenetic placement of *Leontocaris* and difficulties in defining Hippolytidae preceded the molecular analyses of Bracken *et al.* (2009) and De Grave *et al.* (2014). The author found several inconsistencies in Christoffersen's (1987) analysis and Chace's (1997) definition of Hippolytidae and suggested emending the diagnosis of the family to accommodate the aberrant characters of *Leontocaris.*

A thorough assessment of numerous morphological characters of the nine presently known species of *Leontocaris* (Stebbing, 1905; Kemp, 1906; Zarenkov, 1976; Bruce, 1990a; Taylor & Poore, 1998; Fransen, 2001; Poore, 2009; Ahyong, 2010; Komai & Chan, 2010; Cardoso & Fransen, 2012; Chan *et al.,* 2016) and a selection of genera currently assigned to Hippolytidae, including genera that morphologically strongly deviate from the more typical members of this family (e.g., *Caridion, Alope, Merhippolyte*), as well as some members of Bythocarididae, Thoridae, Lysmatidae and Barbouriidae (see comparative material below) strongly suggests that *Leontocaris* is not a hippolytid genus. The pronounced asymmetry of the second pereiopod (Figs. 1, 2) and the unique shape and articulation of the major second pereiopod are features that are completely incongruent not only with other hippolytids, but also with other members of the superfamily Alpheoidea Rafinesque, 1815. Other important autapomorphic characters of *Leontocaris* are the strong serration of the lateral margin of the scaphocerite and uropodal exopod (not found in all other genera currently assigned to Hippolytidae and presumably allied families), and the presence of a spiniform seta on the ischium of the third and fourth pereiopods in most species (absent in all other genera of Hippolytidae and allied families, except for *Calliasmata*). In addition, the late larval stages of *Leontocaris,* which were described under the generic name *Problemacaris* Stebbing, 1921 (see Gordon, 1964), are very different from larvae of Hippolytidae and related families, where they are known (e.g., Terossi *et al.,* 2010; Ghory *et al.,* 2016). Therefore, a new family, Leontocarididae, is herein proposed to accommodate *Leontocaris.* The phylogenetic position of several other "hippolytoid" genera, for which new molecular data are now available, including *Caridion,* will be discussed elsewhere (Anker *et al.,* in prep.).

MATERIAL AND METHODS

The material used in this study is deposited in the following institutions: MNHN, Muséum National d'Histoire Naturelle, Paris, France; RMNH, Naturalis Biodiversity Center, Leiden, Netherlands; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; and FLMNH UF, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA.

Material examined: *Leontocaris lar* Kemp, 1906: 1 female, MNHN-IU-2014-11001, Celtic Sea, Petite Sole Canyon, 48°08.369′N, 08°48.289′W, BobEco cruise, R/V Pourquoi Pas?, ROV Victor6000, dive 471, depth 615 m, 25.09.2011. *Leontocaris vanderlandi* Fransen, 2001: 1 ovig. female, holotype, RMNH.D.42663, Seychelles, N of Platte Island atoll, 05°48′S, 55°22′E, NIOP-E, sta. SEY.795, depth 600 m, rectangular dredge, coral rubble with calcareous rocks and sand, 07.01.1993.

Comparative material: *Alope australis* Baker, 1904: 1 male, 1 female, MNHN-IU-2022-5592, Australia, New South Wales, Coogee near Sydney, rock pools, 1920. *Caridion gordoni* (Spence Bate, 1858): 1 ovig. female, USNM 1739419, Canada, Gulf of Maine, Central Jordan Basin, 43°20′17.9″N, 67°12′28.4″W, Cross Border Coral Habitat Exploration 2024, R/V Henry Bigelow, ROV ROPOS, HB2405 cruise, depth 223.1 m, suction sample, leg. M.S. Nizinski, 27.07.2024. *Cryptocheles pygmaea* Sars, 1870: 2 females, MNHN-IU-2024-7306, Norway, Trondheim fjord, A.M. Edwards, 1903. *Gelastreutes crosnieri* Bruce, 1990b: 1 male, MNHN-IU-2024-7307, Vanuatu, SANTO 2006 Expedition, sta. AT14, 15°23.7′-24.0′S, 167°12.9′-13.5′E, depth 102-120 m, leg. MNHN team, 19.09.2006. *Lebbeus rubrodentatus* Bruce, 2010: 2 specimens (not sexed, probably females), MNHN-IU-2024-7357, Indonesia, Tanimbar Island, KARUBAR 1991 Expedition sta. DW44, R/V Baruna Jaya 1, 07°52′S, 131°48′E, depth 291-295 m, 29.10.1991. *Merhippolyte kauaiensis* (Rathbun, 1906): 1 female, MNHN-IU-2022-5591, French Polynesia, Marquesas Islands, Tahuata, depth 300-700 m, cage trap, leg. J. Poupin, 30-31.01.1988. *Merhippolyte peroni* Ledoyer, 1990: 1 female, MNHN-IU-2018-5782, St. Paul and Amsterdam archipelago, W of Saint-Paul Island, Cap-Horn Campaign, depth 390-420 m, cage trap, 26.03.1979. *Mimocaris heterocarpoides* Nobili, 1903: 1 ovig. female, MNHN-IU-2024-7305, Indonesia, Selat Malaka, depth 14 m, dredge, leg. K.M. Madidihang, 22.01.1980. *Parhippolyte misticia* (Clark, 1989): 1 male, MNHN-2011-9038, French Polynesia, Marquesas Islands, Pakaihi I Te Moana, Marquises 2011-2012 Campaign, Nuku Hiva – Ekamako, sta. MQ1-GR, 08°56.21′N, 140°05.45′W, depth 10 m, leg. AAMP, 28.01.2012.

Taxonomic section

Leontocarididae fam. nov.

Leontocarididae Anker *et al.,* 2006: 2515 (no diagnosis provided, *nomen nudum*).

Diagnosis: Carapace with well-developed, long rostrum, latter sometimes longer than carapace, armed with both dorsal and ventral teeth, ventral margin not

forming deep ventral blade; antennal spine present, hepatic/branchiostegal spine absent; carapace ridges absent. Third pleonite with or without mid-dorsal hump. Telson with 2-5 pairs of dorsal spines. Eyes well pigmented; cornea globular. Antennal scaphocerite with lateral margin serrate in distal half or third. Mandible with palp composed of 1-2 articles. Third maxilliped without exopod. First pereiopods chelate, equal, symmetrical, carpo-propodal grooming apparatus absent; chela simple, with corneous fingertips. Second pereiopods chelate, markedly unequal in length and size, extremely asymmetrical in shape; carpus subdivided into 4 subarticles on both sides, 1st subarticle by far longest, three distal subarticles short, enlarged. Major second pereiopod reaching beyond double length of carapace in full extension; merus with distinct flange on proximal mesi-

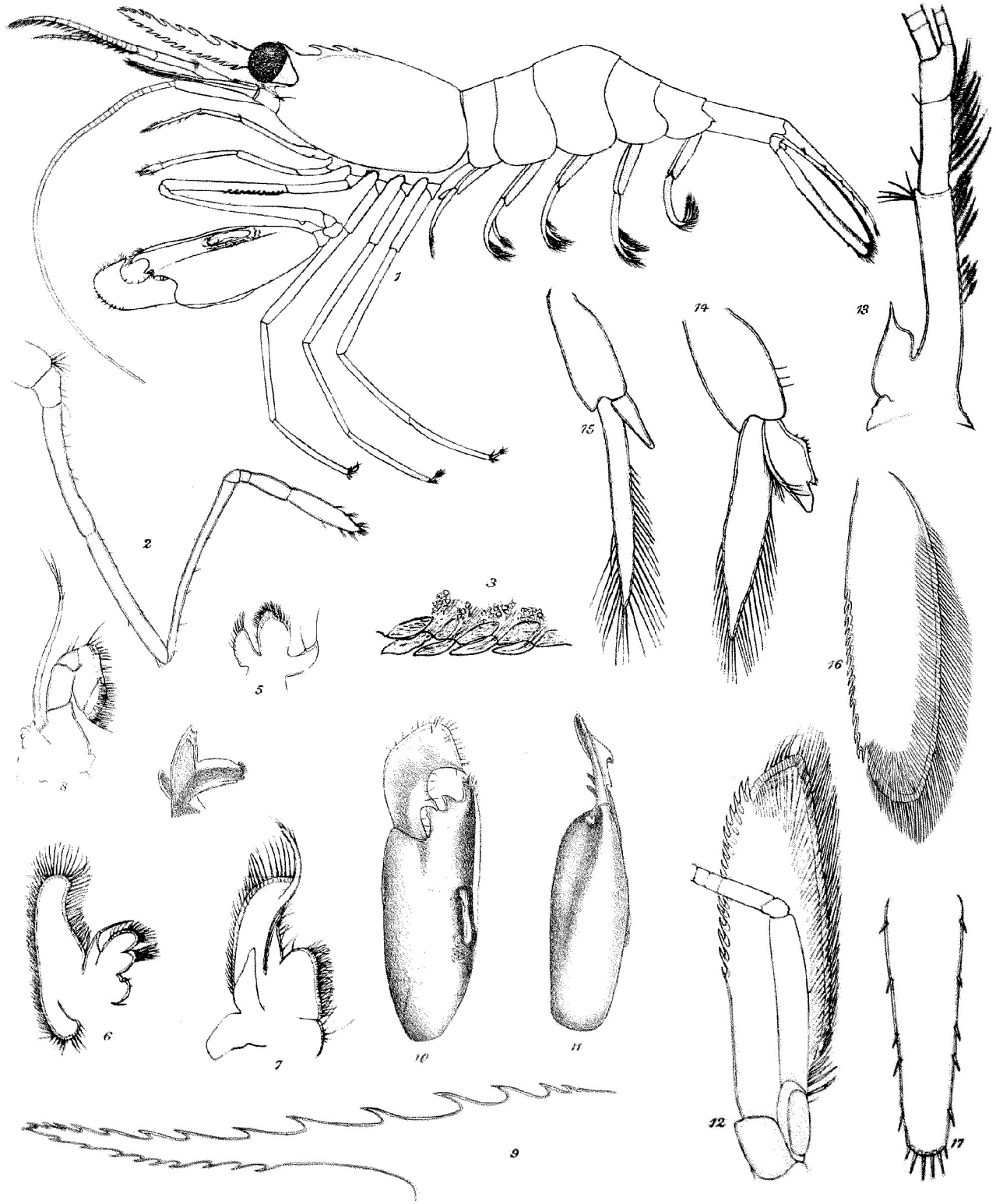

Figure 1. Original illustrations of *Leontocaris lar* Kemp, 1906, the second species described in the genus *Leontocaris* Stebbing, 1905 (Leontocarididae), based on a male specimen dredged off Ireland (from Kemp, 1910; not to scale; see legend for pl. 17 in Kemp 1910 for details).

al surface, latter with denticulate setae or papillae, sometimes with tubercles; 2nd to 4th subarticles of carpus short, subquadrate or cup-shaped, sometimes with processes, 3rd and 4th forming main bending point; chela conspicuously enlarged; palm swollen, subcylindrical, mesial central surface with tympanum; dactylus twisted, strongly compressed, lamina-like. Minor second pereiopod slender; distal 3 subarticles aligned or with bending point, usually between 2nd and 3rd or between 3rd and 4th subarticles; chela small, simple. Third to fifth pereiopods slender; ischium of 3rd and 4th pereiopods with single spiniform seta or unarmed; merus of 3rd to 5th pereiopods with

Figure 2. Three species of the genus *Leontocaris* Stebbing, 1905 (Leontocarididae) from seamounts off southern Australia: *Leontocaris alexander* Poore, 2009 [A-D]; *Leontocaris amplectipes* Bruce, 1990 [E-I] and *Leontocaris yarramundi* Taylor & Poore, 1998 [J] (see Poore, 2009 for details), showing general habitus with major second pereiopod unfolded (A, E, F, J, rostrum broken distally in A and J), intact rostrum (D), anterior half of carapace and frontal appendages (G), major second pereiopod folded (B), chela of major second pereiopod from different angles (C, H, I, tympanum visible in C). Background minimally cleaned in all photographs. Photographic credits: CSIRO/Karen Gowlett-Holmes.

or without row of spiniform setae; propodus undivided; dactylus with ventral margin bearing row of slender serrulate setae. Male first pleopod with appendix interna. Male second pleopod with appendix masculina. Uropod with lateral margin of exopod serrate. Gill-exopod formula: 6 pleurobranchs (Mxp 3 + P1-5); 0-1 arthrobranch (Mxp3); 2 lobe-like epipods (Mxp1-2); 0 strap-like epipods; 1 podobranch (Mxp2); 2 exopods (Mxp1-2) [based on tables in Zarenkov (1976) and Fransen (2001)]. Late larval stages: *problemacaris* larvae, characterised by carapace armed with two or three long spines on dorsal hump; pleon armed with long spines or clusters of spines; antennae with long spines; most pleopods present in later stages; and asymmetrical second pereiopods, with one chela distinctly larger, and traces of carpal subdivision (Stebbing, 1921; Gordon, 1964).

Type genus: *Leontocaris* Stebbing, 1905, with 9 species: *L. paulsoni* Stebbing, 1905 (larval stages described as *Problemacaris spinetum* Stebbing, 1921), type species; *L. lar* Kemp, 1906 (larval stages described as *Problemacaris boschmai* Gordon, 1964); *L. pacifica* Zarenkov, 1976 (originally described as *L. pacificus*); *L. amplectipes* Bruce, 1990a; *L. bulga* Taylor & Poore, 1998; *L. yarramundi* Taylor & Poore, 1998; *L. vanderlandi* Fransen, 2001; *L. alexander* Poore, 2009; *L. smarensis* Cardoso & Fransen, 2012.

Other genera included: None.

Distribution: Indo-West Pacific (6 species, including 3 in southern Australia, see Fig. 2), East Pacific (1 species), North-East and Central Atlantic (2 species) (Cardoso & Fransen, 2012); larval forms known from various North Atlantic localities, South Atlantic (Tristan da Cunha, South Africa off Cape Town) and South Pacific off New Zealand (Gordon, 1964).

Remarks: All members of Leontocarididae can be easily diagnosed by the exaggeratedly asymmetrical, unequal, uniquely shaped second pereiopods, the distolaterally serrate antennal scaphocerite and the laterally serrate uropodal exopod (Figs. 1, 2). The heterogeneous subdivision of the carpus of the major second pereiopod into a very long first subarticle and three short, enlarged, somewhat rigidly articulating three distal subarticles, with a strong bend between the second and third subarticle (Figs. 1, 2), cannot be more different from the more uniform subdivision of the second pereiopod seen in other Hippolytidae (*s. lat.*) and putatively related families. The major second pereiopod of *Leontocaris* also bears what has been described as a locking mechanism between the palm and the merus (Bruce, 1966, 1990a: fig. 6; Poore, 2009: fig. 3), representing a further important autapomorphic feature of the new family. This locking mechanism consists of (1) a tympanum on the central mesial surface of the palm, represented by a deep elongate fissure (= slit) or a somewhat broader, more lens- or drum-shaped area with soft membrane, sometimes with a central micropore, and typically surrounded by digitiform papillae or villi (except in one species, *L. amplectipes*), and (2) an elongate flange or groove on the proximal mesial surface of the merus, furnished with structures described as denticulate setae or papillae (e.g., Bruce, 1990a; Fransen, 2001; Poore, 2009). Bruce (1966) compared the locking mechanism of *Bathypalaemonella humilis* Bruce, 1966 (Bathypalaemonellidae) with that of *Leontocaris lar* and concluded that they are structurally very different. The same author also noted the fact that both *Bathypalaemonella* and *Leontocaris* lack statocysts and suggested that they "may normally inhabit narrow tubes or burrows on the sea bottom". The exact function of the major second pereiopod of leontocaridid shrimps has been speculated upon but remains a mystery (Bruce, 1990a; Poore, 2009), which is also true for bathypalaemonellids. Even though the general biology of both Leontocarididae and Bathypalaemonellidae remains largely unknown, recent *in situ* observations from ROVs show that they associate with deep-water scleractinians, antipatharians and alcyonaceans (e.g., Cardoso, 2010; Ahyong, 2010; Chan *et al.,* 2016; Komai *et al.,* 2022), confirming Kemp's (1910) observations on the possible association of *L. lar* with deep-water antipatharians or scleractinians (*Lophelia*).

Leontocaris can be seen as a morphologically relatively homogeneous genus, although some species-specific variation does occur, for instance, in the shape, length and dentition of the rostrum, the shape of the third and fifth pleonites, the dorsal and posterior armature of the telson, and the armature of the third to fifth pereiopods. The intrageneric variation in rostral features (Fig. 2D, G) is normal and is found in many other caridean shrimp genera. In some species of *Leontocaris,* the third pleonite presents a prominent mid-dorsal hump, which can be blunt or acutely produced, overhanging the proximal margin of the fourth pleonite (Fig. 2A). The posteroventral margin of the fifth pleuron can be rounded or produced into a sharp tooth (with intraspecific variation observed in at least one species, Cardoso & Fransen, 2012), whereas its posterior margin sometimes has additional small teeth. The telson is armed with two to five pairs of dorsal spines; its posterior margin is either rounded and armed with four to six pairs of stout spiniform setae or sharply bifid, without spiniform setae. The merus of the third to fifth pereiopods often bears four to seven spiniform setae but is unarmed in three species. Similarly, the ischium of the third and fourth pereiopods is typically armed with one spiniform seta, which is sometimes inserted on its ventromesial surface (Fransen, 2001: fig. 21; Poore, 2009: fig. 4e, f), but is unarmed at least in *L. amplectipes* according to Bruce (1990a: fig. 4L). Some of this variation was used in the delimitation of species groups below and may reflect phylogenetic affinities.

Fransen (2001) and Poore (2009) performed morphology-based cladistic analyses of most or all species known at that time. For instance, Poore (2009) in his analysis used 17 "informative characters" (out of 25, six ordered) of *Leontocaris,* recovering two or three clades, depending on methods used. Independently from these analyses, three morphologically more or less well-defined groups can be recognised in *Leontocaris,* as follows:

Group 1, defined by (1) carapace with 2 epigastric teeth; (2) posterior margin of 3rd pleonite with strong dorsal hook; (3) posterior margin of telson narrow, with 2 projecting teeth; (4) dorsolateral margins of telson with 6-7 pairs of spiniform setae; (5) minor 2nd pereiopod with all 4 carpal subarticles aligned or with distal subarticles moderately bent. This group, which can be called the *L. paulsoni* group, contains the following species:

Leontocaris paulsoni: rostrum horizontal, about as long as carapace; carapace with 2 epigastric teeth; posterior margin of 3rd pleonite with strong dorsal hook; dorsolateral margins of telson with 7 pairs of spiniform setae; posterior margin of telson narrow, with 2 projecting teeth; minor 2nd pereiopod with carpal subarticles moderately bent between 1st and 2nd; tympanum unknown; merus of 3rd to 5th pereiopods unarmed (needs confirmation) [off South Africa] (Stebbing, 1905; Poore, 2009).

Leontocaris pacifica: rostrum strongly curving upwards, distinctly longer than carapace; carapace with 2 epigastric teeth; posterior margin of 3rd pleonite with strong dorsal hook; dorsolateral margins of telson with 7 pairs of spiniform setae; posterior margin of telson narrow, with 2 projecting teeth; minor 2nd pereiopod with carpal subarticles moderately bent between 1st and 2nd and between 3rd and 4th; tympanum unknown; merus of 3rd to 5th pereiopods armed with spiniform setae [off Chile] (Zarenkov, 1976).

Leontocaris alexander: rostrum strongly curving upwards, distinctly longer than carapace; carapace with 2 epigastric teeth; posterior margin of 3rd pleonite with strong dorsal hook; dorsolateral margins of telson with 6 pairs of spiniform setae; posterior margin of telson narrow, with 2 projecting teeth; minor 2nd pereiopod with carpal subarticles aligned; tympanum: drum-like area with papillae; merus of 3rd to 5th pereiopods armed with spiniform setae [off SE Australia] (Poore, 2009).

Group 2, defined by (1) carapace with epigastric teeth, sometimes postorbital without epigastric teeth but with some teeth in postorbital position; (2) posterior margin of 3rd pleonite unarmed; (3) posterior margin of telson broadly rounded, with spiniform setae; (4) dorsolateral margins of telson with 4-5 pairs of spiniform setae; (5) minor 2nd pereiopod with all 4 carpal subarticles aligned or with distal subarticles strongly bent (most species). This group, which can be called the *L. lar* group, contains the following species:

Leontocaris lar: rostrum directed slightly upwards, about as long as carapace; carapace with 3-4 epigastric teeth; posterior margin of 3rd pleonite unarmed; dorsolateral margins of telson with 5 pairs of spiniform setae; posterior margin of telson broadly rounded, with spiniform setae; minor 2nd pereiopods with strong bend between 2nd and 3rd carpal subarticles; tympanum: fissure with papillae; merus of 3rd to 5th pereiopods unarmed (according to Kemp, 1910) or armed with spiniform setae (reexamination of MNHN-2014-11001) [off Ireland and NW France] (Kemp, 1910; Chan *et al.,* 2016; see discussion below).

Leontocaris smarensis: rostrum variable from almost horizontal to strongly curving upwards, distinctly longer to about as long as carapace; carapace with 3-6 epigastric teeth; posterior margin of 3rd pleonite unarmed; dorsolateral margins of telson with 5 pairs of spiniform setae; posterior margin of telson broadly rounded, with spiniform setae; minor 2nd pereiopod with carpal subarticles aligned; tympanum: drum-like area with papillae; merus of 3rd to 5th pereiopods armed with spiniform setae [Mid-Atlantic Ridge] (Cardoso & Fransen, 2012; see discussion below).

Leontocaris yarramundi: rostrum curving upwards, about as long as carapace; carapace with 4 epigastric teeth; posterior margin of 3rd pleonite unarmed; dorsolateral margins of telson with 4 pairs of spiniform setae; posterior margin of telson broadly rounded, with spiniform setae; minor 2nd pereiopod with carpal subarticles aligned; tympanum: fissure surrounded by papillae; merus of 3rd to 5th pereiopods armed with spiniform setae [off S Australia] (Taylor & Poore, 1998; Poore, 2009).

Leontocaris amplectipes: rostrum horizontal, shorter than carapace; carapace without epigastric teeth but with 3 mid-dorsal teeth in postorbital position; posterior margin of 3rd pleonite unarmed; dorsolateral margins of telson with 4 pairs of spiniform setae; posterior margin of telson broadly rounded, with spiniform setae; minor 2nd pereiopod with strong bend between 3rd and 4th carpal subarticles; tympanum: fissure not surrounded by papillae; merus of 3rd to 5th pereiopods unarmed [off S Australia] (Bruce, 1990a; Poore, 2009).

Group 3, defined by (1) carapace with 1 epigastric tooth or without epigastric teeth but with some teeth in postorbital position; (2) posterior margin of 3rd pleonite unarmed; (3) posterior margin of telson broadly rounded, with spiniform setae; (4) dorsolateral margins of telson with 2 pairs of spiniform setae; (5) minor 2nd pereiopod with distal carpal subarticles moderately to strongly bent. This group, which can be called the *L. vanderlandi* group, contains the following species:

Leontocaris vanderlandi: rostrum horizontal, as long as or shorter than carapace; carapace without epigastric teeth but with 2 mid-dorsal teeth in postorbital position; posterior margin of 3rd pleonite unarmed; dorsolateral margins of telson with 2 pairs of spiniform setae; posterior margin of telson broadly rounded, with spiniform setae; minor 2nd pereiopod with strong bend between 3rd and 4th carpal subarticles; tympanum: small drum-like area with papillae; merus of 3rd to 5th pereiopods armed with spiniform setae [Seychelles] (Fransen, 2001).

Leontocaris bulga: rostrum curving upwards, about as long as carapace; carapace with 1 epigastric tooth

and 2 mid-dorsal teeth in postorbital position; posterior margin of 3rd pleonite unarmed; dorsolateral margins of telson with 2 pairs of spiniform setae; posterior margin of telson broad, slightly rounded, with spiniform setae; minor 2nd pereiopod with strong to moderate bend between 3rd and 4th carpal subarticles; tympanum: drum-like area with papillae; merus of 3rd to 5th pereiopods armed with spiniform setae [off S Australia and Mozambique Channel] (Taylor & Poore, 1998; Komai & Chan, 2010).

The *L. paulsoni* group was recovered by Fransen (2001, with *L. paulsoni* and *L. pacifica*) and Poore (2009, all three species). The *L. lar* group was partly recovered by Poore (2009: fig. 1a, with *L. lar, L. yarramundi* and *L. amplectipes*), but not by Fransen (2001). Indeed, the inclusion of *L. amplectipes* in the *L. paulsoni* group is tentative as this species differs in several aspects from the other species placed in this group (see above). Finally, the *L. vanderlandi* group appears to be morphologically well defined and was also recovered by Poore (2009). Thus, the above diagnoses/definitions of the three informal species groups may have a phylogenetic implication and can also be used for taxonomic purposes, especially if further species are discovered.

Chan *et al.* (2016) suggested that *L. smarensis* may be a synonym of *L. lar;* however, we prefer to keep the former species valid, at least for the time being. Chan *et al.* (2016: fig. 1D) showed that the mandibular palp of their specimen identified as *L. lar* had no distal setae, whilst three long distal setae were illustrated by Cardoso & Fransen (2012: fig. 2C) for the holotype of *L. smarensis.* In addition, comparing the minor second pereiopods illustrated by Kemp (1910: pl. 17, fig. 2) and Cardoso & Fransen (2012: fig. 4A), one can observe a strong bend in the distal carpal subarticles in the former species *vs.* aligned carpal subarticles in the latter species. The specimens of *L. lar* illustrated by Kemp (1910: pl. 17, fig. 17) and Chan *et al.* (2016: fig. 1G) also have a somewhat narrower telson (cf. Cardoso & Fransen, 2012: fig. 4C). The most conspicuous difference between *L. smarensis* and *L. lar* as illustrated by Kemp (1910: pl. 17, fig. 1), which remained unnoticed by Cardoso & Fransen (2012) and Chan *et al.* (2016), is the presence of row of spiniform setae on the meri of the third to fifth pereiopods in the former species and their absence in the latter species (cf. Fig. 1-1; Cardoso & Fransen, 2012: fig. 4B). However, a reexamination of the female identified as *L. lar* by Chan *et al.* (2016) (MNHN-IU-2014-11001) showed that these spiniform setae are present in that specimen on both sides, for instance, in the number of five, six and three on the third, fourth and fifth pereiopod, respectively, on the right side (S. De Grave, pers. comm.). Therefore, Kemp's (1910) general habitus drawing of *L. lar* (reproduced in Fig. 1-1) may not be accurate, i.e., Kemp may have simply overlooked the spiniform setae on the meri of the walking legs, perhaps because they are sometimes not directly visible in lateral view, not illustrating them in the general habitus figure and also not mentioning them in the otherwise very detailed descriptive text. On the other hand, if Kemp's (1910) illustration is correct, it would imply a misidentification of the specimen reported as *L. lar* by Chan *et al.* (2016) and the presence of two species of *Leontocaris* in the north-eastern Atlantic, viz. *L. lar* of Kemp (1906, 1910) and a species closely related to or identical with *L. smarensis.* Whatever the case may be, it seems more reasonable to keep both species valid until more evidence (new material and molecular comparisons) becomes available.

The subdivision of the second pereiopod carpus has been seen as one of the most important characters in deep phylogeny of Caridea (Thompson, 1967; Christoffersen, 1987, 1990), leading to the revival of the Polycarpidea Spence Bate, 1888 concept (see review in Christoffersen, 2020). Following the Polycarpidea hypothesis, the second pereiopod carpus became subdivided into multiple units (subdivisions, subarticles) in the ancestor of a large and important clade containing Pandaloidea Haworth, 1825, Crangonoidea Haworth, 1825 and Alpheoidea Rafinesque, 1815, becoming secondarily undivided in *Thalassocaris* Stimpson, 1860 (now in Pandalidae Haworth, 1825, see Liao *et al.,* 2019) and all Crangonidae Haworth, 1825. However, Polycarpidea was not recovered in the analysis of Bracken *et al.* (2009), supporting Thompson's (1967) idea that the subdivision of the second pereiopod carpus may have occurred independently in multiple caridean lineages. These results do not necessarily mean that the reversals from the ancestrally subdivided carpus back to undivided carpus cannot occur. Based on the position of two genera formerly placed in the family Thalassocarididae Spence Bate, 1888 in Liao *et al.* (2019), this reversal occurred within Pandalidae, with the subdivision of the second pereiopod carpus reduced to two subarticles in *Chlorotocoides* Kemp, 1925 and completely lost in *Thalassocaris.* More generally, the striking differences between the second pereiopods of *Chlorotocoides* and *Thalassocaris* and the remaining pandalid genera point to the great evolutionary plasticity of this appendage.

De Grave *et al.* (2014) did not discuss the evolution of the multiarticulate condition of the second pereiopod carpus in the Hippolytidae (*s. lat.*), but their results show that it may have either evolved several times or evolved once and was secondarily lost in some lineages. The current incomplete and therefore unsatisfactory knowledge of the caridean phylogeny combined with the absence of molecular data for *Leontocaris* do not allow to propose a more substantiated hypothesis on the phylogenetic affinities of this peculiar shrimp lineage. However, the above-listed significant differences in the subdivision pattern of the second pereiopod carpus between Leontocarididae and Hippolytidae + allied families point to the possibility of a convergent evolution. Within Hippolytidae, another example of a rather unusual and uniquely shaped second pereiopod is seen in *Caridion,* with only two subarticles in the carpus and elongate, slender chela fingers (Coutière, 1899: fig. 296bis; Lebour, 1930: pl. 4). As a matter of fact, the first pereiopod chela of *Caridion,* with its curved and distally pointed fingers (Coutière, 1899: fig. 296bis) also differs from the

more typical hippolytid chela, with stout fingers ending in blunt, corneous, dark fingertips. These and several other morphological discrepancies with other hippolytids combined with preliminary molecular data (COI) indicate that *Caridion* is not an hippolytid genus (Anker *et al.*, in prep.).

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REFERENCES

Ahyong, S.T. 2010. New species and new records of Caridea (Hippolytidae: Pasiphaeidae) from New Zealand. *Zootaxa,* 2372: 341-357. https://doi.org/10.11646/zootaxa.2372.1.26.

Anker, A.; Ahyong, S.T.; Palmer, A.R. & Noël, P.Y. 2006. Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. *Evolution,* 60(12): 2507-2528. https://doi.org/10.1111/j.0014-3820.2006.tb01886.x.

Baker, W.H. 1904. Notes on South Australian decapod Crustacea. Part I. *Transactions and Proceedings and Report of the Royal Society of South Australia,* 28: 146-161.

Bracken, H.D.; De Grave, S. & Felder, D.L. 2009. Phylogeny of the infraorder Caridea based on mitochondrial and nuclear genes (Crustacea: Decapoda). *In:* Martin, J.W.; Crandall, K.A. &. Felder, D.L. (Eds.). *Decapod crustacean phylogenetics.* Boca Raton, CRC Press. p. 274-300. (Crustacean Issues, 18) https://doi.org/10.1201/9781420092592-c14.

Bruce, A.J. 1966. *Bathypalaemonella humilis* sp. nov., a new species of shrimp from the South China Sea (Decapoda, Campylonotidae). *Crustaceana,* 11(3): 277-287. https://doi.org/10.1163/156854066X00595.

Bruce, A.J. 1990a. *Leontocaris amplectipes* sp. nov. (Hippolytidae), a new deep-water shrimp from southern Australia. *Memoirs of Museum Victoria,* 51: 121-130. https://doi.org/10.24199/j.mmv.1990.51.09.

Bruce, A.J. 1990b. Crustacea Decapoda: *Gelastreules crosnieri* gen. nov., sp. nov. (Hippolytidae) from New Caledonia. *Mémoires du Muséum National d'Histoire Naturelle,* (A), 145: 137-147. (Crosnier, A. (Ed.). Résultats des Campagnes MUSORSTOM, Vol. 6)

Bruce, A.J. 2010. *Lebbeus rubrodentatus* sp. nov. (Crustacea: Caridea: Hippolytidae) from the Australian North West Shelf. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory,* 26: 75-78. https://doi.org/10.5962/p.287462.

Cardoso, I.A. 2010. First record of family Bathypalaemonellidae (Caridea: Decapoda) on Brazilian deep-sea coral reefs. *Marine Biodiversity Records,* 3: e108. https://doi.org/10.1017/S1755267210000941.

Cardoso, I. & Fransen, C.H.J.M. 2012. A new species of the deepwater shrimp genus *Leontocaris* (Hippolytidae: Caridea) from the South Mid-Atlantic Ridge. *Journal of the Marine Biological Association of the United Kingdom,* 92(5): 1083-1088. https://doi.org/10.1017/S0025315412000458.

Chace, F.A. Jr. 1992. On the classification of the Caridea (Decapoda). *Crustaceana,* 63: 70-80. https://doi.org/10.1163/156854092X00299.

Chace, F.A. Jr. 1997. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907-1910, part 7: families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae. *Smithsonian Contributions to Zoology,* 587: 1-106. https://doi.org/10.5479/si.19436696.391.1.

Chace, F.A. Jr. & Kensley, B. 1992. The cardiac notch in decapods. *Journal of Crustacean Biology,* 12(3): 442-447. https://doi.org/10.2307/1549038.

Chan, T.-Y.; van den Beld, I.M.J. & De Grave, S. 2016. A further record of the rare hippolytid shrimp *Leontocaris lar* Kemp, 1906 (Decapoda, Caridae) from the Celtic Sea, off north-western France. *Crustaceana,* 89(2): 251-257. https://doi.org/10.1163/15685403-00003515.

Chow, L.H.; De Grave, S.; Anker, A.; Poon, K.K.Y.; Ma, K.Y, Chu K.H.; Chan, T.Y. & Tsang, L.M. 2021. Distinct suites of pre- and post-adaptations indicate independent evolutionary pathways of snapping claws in the shrimp family Alpheidae (Decapoda: Caridea). *Evolution,* 75(11): 2898-2910. https://doi.org/10.1111/evo.14351.

Christoffersen, M.L. 1987. Phylogenetic relationships of hippolytid genera, with an assignment of new families for the Crangonoidea and Alpheoidea (Crustacea, Decapoda, Caridea). *Cladistics,* 3(4): 348-362. https://doi.org/10.1111/j.1096-0031.1987.tb00898.x.

Christoffersen, M.L. 1990. A new superfamily classification of the Caridea (Crustacea, Pleocyemata) based on phylogenetic pattern. *Journal of Zoological Systematics and Evolutionary Research,* 28: 94-106. https://doi.org/10.1111/j.1439-0469.1990.tb00369.x.

Christoffersen, M.L. 2020. Polycarpidea C.S. Bate 1888 [M.L. Christoffersen], converted clade name. *In:* de Quieroz, K.; Cantino, P. & Gauthier, J. (Eds.). *Phylonyms. A companion to the PhyloCode,* Boca Raton, CRC Press. p. 605-608.

Clark, J. 1989. *Koror misticius,* new genus, new species (Decapoda: Hippolytidae), a cave shrimp from Palau. *Journal of Crustacean Biology,* 9(3): 445-452. https://doi.org/10.1163/193724089X00421.

Coutière, H. 1899. Les "Alpheidae", morphologie externe et interne, formes larvaires, bionomie. Paris, Masson. 559p., pls. 1-6. (Thèses Série A. n. 321). [*Annales des Sciences Naturelles, Zoologie,* Série 8, 9, 1, 1-559.] https://doi.org/10.5962/bhl.title.13143.

Crosnier, A. 2000. A new genus and species of hippolytid shrimp (Decapoda, Caridea) from Wallis Island, south-west Pacific. *Journal of Crustacean Biology,* 20(5): 109-115. https://doi.org/10.1163/1937240X-90000013.

Dana, J.D. 1852-1855. Crustacea, Part 1. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N., 13: 1-685 [1852]. Atlas, 1-27, pls. 1-96 [1855]. C. Sherman, Philadelphia.

De Grave, S.; Li, C.P.; Tsang, L.M.; Chu, K.H.; Chan, T.-Y. 2014. Unweaving hippolytoid systematics (Crustacea, Decapoda, Hippolytidae): resurrection of several families. *Zoologica Scripta,* 43(5): 496-507. https://doi.org/10.1111/zsc.12067.

Fransen, C.H.J.M. 2001. *Leontocaris vanderlandi,* a new species of hippolytid shrimp (Crustacea: Decapoda: Caridea) from the Seychelles, with an analysis of phylogenetic relations within the genus. *Zoologische Verhandelingen, Leiden,* 334: 57-76.

Ghory, F.S.; Kazmi, Q.B. & Siddiqui, F.A. 2016. Complete larval development of *Saron marmoratus* (Olivier, 1811) reared under laboratory conditions (Crustacea: Decapoda: Hippolytidae). *International Journal of Research Studies in Zoology,* 2: 47-65. https://doi.org/10.20431/2454-941X.0203005.

Goës, A. 1864. Crustacea Decapoda Podophthalma marina Sueciæ, interpositis speciebus norvegicus aliisque vicinis, enumerat. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar,* 20: 161-180.

Gordon, I. 1964. On the larval genus *Problemacaris* Stebbing, and its probable identity (Crustacea, Decapoda). *Zoologische Mededelingen, Leiden,* 39(35): 331-347. Available: https://repository.naturalis.nl/pub/318683/ZM1964039035.pdf.

Haworth, A.H. 1825. A new binary arrangement of the macrurous Crustacea. *Philosophical Magazine and Journal,* 65(323): 183-184. https://doi.org/10.1080/14786442508628417.

Holthuis, L.B. 1955. The recent genera of the caridean and stenopodidean shrimps (Class Crustacea, Order Decapoda, Supersection Natantia) with keys for their determination. *Zoologische Verhandelingen, Leiden,* 26: 1-157. Available: https://repository.naturalis.nl/pub/317800/ZV1955026001.pdf.

Holthuis, L.B. 1993. *The recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda) with an appendix on the order Amphionidacea.* Nationaal Natuurhistorisch Museum, Leiden. https://doi.org/10.5962/bhl.title.152891.

Kemp, S.W. 1906. Preliminary descriptions of two new species of Carida from the West Coast of Ireland. *Annals and Magazine of Natural History, London, Ser. 7,* 17: 297-300. https://doi.org/10.1080/00222930608562525.

Kemp, S.W. 1910. The Decapoda Natantia of the coasts of Ireland. *Reports of the Department of Agriculture and Technical Instruction for Ireland, Scientific Investigations of the Fisheries Branch,* 1908: 1-190. https://doi.org/10.5962/bhl.title.53732.

Kemp, S.W. 1916. XXI. Notes on Crustacea Decapoda in the Indian Museum. VII. Further notes on Hippolytidae. *Records of the Indian Museum,* 12(8): 385-405. https://doi.org/10.26515/rzsi/v12/i8/1961/163039.

Kemp, S.W. 1925. XVII. Notes on Crustacea Decapoda in the Indian Museum. XVII. On various Caridea. *Records of the Indian Museum,* 27(4): 249-342. https://doi.org/10.26515/rzsi/v27/i4/1925/163447.

Kensley, B. 1988. New species and records of cave shrimps from the Yucatan Peninsula (Decapoda: Agostocarididae and Hippolytidae. *Journal of Crustacean Biology,* 8(4): 688-699. https://doi.org/10.1163/193724088X00521.

Kingsley, J.S. 1878. List of the North American Crustacea belonging to the suborder Caridea. *Bulletin of the Essex Institute,* 10: 53-71 [1879].

Komai, T. & Chan, T.Y. 2010. Two new pandalid shrimps and the discovery of the second specimen of the rare hippolytid shrimp *Leontocaris bulga* Taylor & Poore, 1998 (Crustacea, Decapoda) from the Mozambique MAINBAZA cruise. *Zoosystema,* 32(4): 625-641. https://doi.org/10.5252/z2010n4a6.

Komai, T.; Tsuchida, S. & Fujiwara, Y. 2022. New record of a rarely collected caridean shrimp *Bathypalaemonella pandaloides* (Rathbun, 1906) (Decapoda: Bathypalaemonellidae) from the West Mariana Ridge, northwestern Pacific. *Zootaxa,* 5129: 272-284. https://doi.org/10.11646/zootaxa.5129.2.7.

Leach, W.E. 1814. Crustaceology. *In:* Brewster, D. (Ed.). *The Edinburgh Encyclopaedia,* Edinburgh, Balfour. v. 7, p. 385-437; 765-766.

Lebour, M.V. 1930. The larval stages of *Caridion,* with a description of a new species, *C. steveni*. *Proceedings of the Zoological Society of London,* 100(1): 181-194. https://doi.org/10.1111/j.1096-3642.1930.tb00972.x.

Ledoyer, M. 1990. Mysidacés et Caridés benthiques (Crustacea) de la Campagne MD 50/Jasus aux iles Saint-Paul et Amsterdam (Océan Indien). *Mésogée,* 50: 45-51.

Liao, Y.; De Grave, S.; Kamai, T. & Chan, T.-Y. 2019. Systematic analysis of the caridean shrimp superfamily Pandaloidea (Crustacea: Decapoda) based on molecular and morphological evidence. *Molecular Phylogenetics and Evolution,* 134: 200-210. https://doi.org/10.1016/j.ympev.2019.02.006.

Nobili, G. 1903. Contributo all fauna carcinologia di Borneo. *Bollettino dei Musei di Zoologia ed Anatomia comparata della Regia, Università di Torino,* 18: 1-32.

Poore, G.C.B. 2009. *Leontocaris alexander,* a new deepwater hippolytid shrimp from Tasmanian seamounts with a phylogeny of the genus (Crustacea: Caridea). *Crustaceana,* 82(7): 951-967. https://doi.org/10.1163/156854009X427478.

Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés.* Palermo. 224p. https://doi.org/10.5962/bhl.title.106607.

Rathbun, M.J. 1906. The Brachyura and Macrura of the Hawaiian Islands. *Bulletin of the United States Fish Commission, Washington,* 23: 827-930, pls. 1-24. Available: https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/fish-bull/fb23%283%29.4.pdf.

Sars, G.O. 1870. Nye Dybvandscrustaceer fra Lofoten. *Forhandlinger i Videnskabs-Selskabet i Christiana,* 1869: 147-174.

Spence Bate, C.S. 1858. A new British *Hippolyte. The Natural History Review,* 5: 51-53.

Spence Bate, C.S. 1888. Report on the Crustacea Macrura dredged by H.M.S. "Challenger" during the years 1873-1876. *In: Report on the Scientific Results of the Voyage of H.M.S. "Challenger" during the years 1873-76, Zoology,* London. v. 24, i-xc, 1-942, pls. 1-157.

Stebbing, T.R.R. 1905. South African Crustacea. part III. *Marine Investigations of South Africa,* 4: 21-123, pls. 17-26. https://doi.org/10.5962/p.366546.

Stebbing, T.R.R. 1921. III. Some Crustacea of Natal. *Annals of the Durban Museum,* 3: 12-26, pls. 1-5. https://journals.co.za/doi/pdf/10.10520/AJA0012723X_1610.

Stimpson, W. 1860. Prodromus Descriptionis Animalium Evertabratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, C. Ringgold et J. Rogers Ducibus, observavit descripsit. *Proceedings of the Philadelphia Academy of Sciences,* 1860: 22-47. https://doi.org/10.5962/bhl.title.51447.

Taylor, J. & Poore, G.C.B. 1998. A review of the genus *Leontocaris* (Crustacea: Caridea: Hippolytidae) with descriptions of three species from southeastern Australian seamounts and slope. *Memoirs of the Museum of Victoria,* 57: 57-69. https://doi.org/10.24199/j.mmv.1998.57.03.

Terossi, M.; Cuesta, J.A.; Wehrtmann, I.S. & Mantelatto, F.L. 2010. Revision of the larval morphology (Zoea I) of the family Hippolytidae (Decapoda, Caridea), with a description of the first stage of the shrimp *Hippolyte obliquimanus* Dana, 1852. *Zootaxa,* 2624: 49-66. https://doi.org/10.11646/zootaxa.2624.1.2.

Thompson, J.R. 1967. Comments on phylogeny of section Caridea (Decapoda Natantia) and the phylogenetic importance of the Oplophoroidea. *In: Proceedings of the Symposium on Crustacea held at Ernakulam from January 12 to 15, 1965. Part 1. Symposium Series 2.* Mandapam Camp, Marine Biological Association of India. p. 314-326.

White, A. 1847. Descriptions of new or little-known Crustacea in the collection of the British Museum. *Proceedings of the Zoological Society of London,* 15: 118-126. Available: https://biostor.org/reference/235836.

Zarenkov, N.A. 1976. On the fauna of decapods of the waters adjacent to South America *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii,* 5: 8-18 [in Russian].

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