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Phylogenetic analysis of the family Cyamidae (Crustacea: Amphipoda): a review based on morphological characters

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The family Cyamidae, known as whale lice, is analysed herein by cladistic methods based on morphological characters. The analysis was performed using the program TNT and was based on a data matrix of 71 characters × 31 terminal taxa, including all seven known genera. Results showed Cyamidae to be a monophyletic clade. ***Balaenocyamus* gen. nov.** is erected to include *Cyamus balaenopterae*, which has eight synapomorphies. The other six genera were monophyletic. In addition, two new subfamilies are proposed: **Isocyaminae subfam. nov.**, to include *Isocyamus*, *Orcinocyamus*, *Platycyamus*, *Neocyamus*, *Scutocyamus* and *Syncyamus*, and **Cyaminae subfam. nov.**, to include ***Balaenocyamus* gen. nov.** and *Cyamus*. A key to all eight genera of Cyamidae, including diagnoses of the family, subfamilies and genera, is provided.

ADDITIONAL KEYWORDS: cladistic analysis – Crustacea – new classification – new genera.

INTRODUCTION

Cyamids are amphipods that exclusively parasitize marine cetaceans (Rohde & Lützen, 2005) and are generally called whale lice. Cyamids range in length from 3 to 30 mm and spend their entire lives feeding on the skin of whales and dolphins (Rowntree, 1996). More cyamids are usually found on great whales from the superfamily Mysticeti Flower, 1864 than on toothed whales, the Odontoceti Flower, 1867 (Berzin & Vlasova, 1982). The family Cyamidae Rafinesque, 1815 comprises 32 species in seven genera (Margolis, McDonald & Boulsfield, 2000; Haney, De Almeida & Reis, 2004; Iwasa-Arai, Carvalho & Serejo, 2017). However, Ahyong *et al.* (2011) did not consider *Orcinocyamus* Margolis, McDonald & Boulsfield, 2000 to be a valid genus. Fourteen cyamid species belong to the genus *Cyamus* Latreille, 1796, including all the mysticete ectoparasites and a few cyamids from large odontocetes.

Formerly, Cyamidae was included in the suborder Caprellidea Dana, 1852, together with seven other families: Caprellidae Leach, 1814, Caprellinoididae Laubitz, 1993, Caprogammaridae Kudrjaschov & Vassilenko, 1966, Paracercopidae Vassilenko, 1968, Pariambidae Laubitz, 1993, Phtisicidae Vassilenko, 1968 and Protellidae McCain, 1970. Members of this suborder have degenerate abdomens and pereopods 3 and 4 (Barnard & Karaman, 1991; Laubitz, 1993; Ito, Wada & Aoki, 2008). Some previous research on the relationships within Caprellidea overlooked the family Cyamidae, owing to its distinct dorsoventral body shape and parasitic habit (Takeuchi, 1993). Laubitz (1993) proposed a hypothetical evolutionary scenario based on mouthpart morphology, where Caprellidea is polyphyletic with two distinct lineages; the Paracercopidae lineage gave rise to Caprellinoididae and Cyamidae and was close to Phtisicidae. Later, Ito *et al.* (2011) proposed a Caprellidea phylogeny based on 18S rRNA ribosomal data and found a clade comprising Cyamidae, Caprellidae and Caprogammaridae. Currently, the suborder Caprellidea is not accepted. Myers & Lowry (2003) established the relationship between the caprellids and the corophioids and treated them in the

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suborder Corophioidea Leach, 1814, which includes the superfamily Caprelloidea Leach, 1814 with five families: Caprellidae (including subfamilies Caprellinae Leach, 1814, Paracercopinae Vassilenko, 1972 and Phtisicinae Vassilenko, 1968), Caprogammaridae, Cyamidae, Dulichiidae Dana, 1849 and Podoceridae Leach, 1814. More recently, Cyamidae was accepted as part of the recently erected suborder Senticaudata Lowry & Myers, 2013, infraorder Corophiida, superfamily Caprelloidea, which includes the same five families previously stated (Lowry & Myers, 2013; 2017).

Haney (1999) performed the first modern cladistic revision of Cyamidae and suggested the raising of *Cyamus orcini* Leung, 1970 to genus status, which was later named by Margolis *et al.* (2000) as *Orcinocyamus*. Additionally, Haney (1999) attested the monophyly of Cyamidae and positioned *Caprellinoides mayeri* Pfeffer, 1888 (Caprelloidea: Caprellidae: Phtisicinae) as its sister species. According to Haney (1999), there are two major lineages of Cyamidae: one encompassing the genera associated with toothed whales and dolphins (Odontoceti), including *Isocyamus* Gervais & Van Beneden, 1859, *Neocyamus* Margolis, 1955, *Orcinocyamus* Margolis, McDonald & Boulsfield, 2000, *Platycyamus* Lütken, 1870, *Scutocyamus* Lincoln & Hurley, 1974 and *Syncyamus* Bowman, 1955; and the other associated mainly with Mysticeti, composed of the genus *Cyamus* Latreille, 1796. Unfortunately, the data are from an unpublished Master's thesis, but as there is very little information in the literature about Cyamidae evolution, Haney's analysis will be considered for comparison (Fig. 1).

Margolis *et al.* (2000) reviewed the systematics of whale lice from the Northeastern Pacific using a unique method, named by Bousfield as 'semi-phyletic' analysis, which encompasses phylogenetics and 'phyletically' ordered characters. Margolis *et al.* (2000) inferred some relationships between the Cyamidae genera and subgenera based on 24 morphological characters. The authors considered characters from the head, mouthparts, gnathopods, gills and pereopods. According to Margolis *et al.* (2000), *Cyamus* is the most 'primitive' genus and *Scutocyamus* the most 'advanced', with the remaining genera intermediate. Apart from *Cyamus* in the base, the only generic relationship that agrees with Haney's (1999) systematics is the clade *Syncyamus* + *Scutocyamus*, observed in a mostly derived position (Fig. 1). Furthermore, Margolis *et al.* (2000) suggested the erection of four subgenera, a classification that has not been accepted in more recent studies (Ahyong *et al.*, 2011).

Haney (1999) and Margolis *et al.* (2000) also explored the relationships among Cyamidae and Cetacea, including Haney's analysis of a host cladogram based on a comparison between parasites and host trees (Messenger & McGuire, 1998), where he found a correlation between cyamids from the narwhal *Monodon monoceros* Linnaeus, 1758 and the

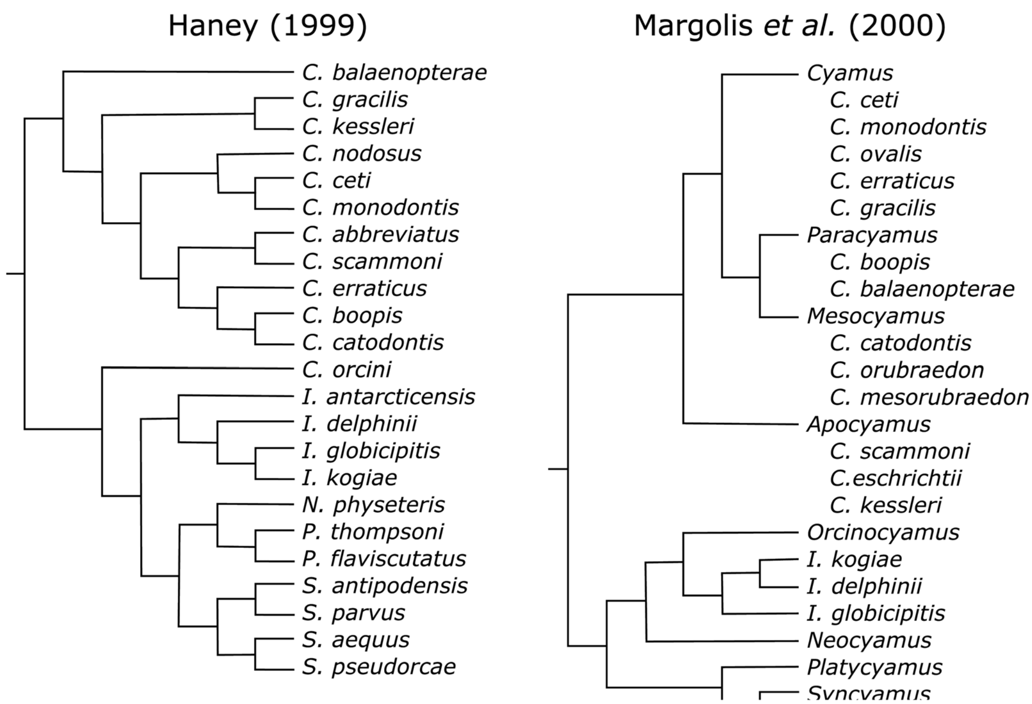


Figure 1. Phylogenetic relationships of Cyamidae inferred by Haney (1999) and Margolis *et al.* (2000). New, unpublished taxa were omitted. *Cyamus abbreviatus* corresponds to *Cyamus ovalis*.

beluga *Delphinapterus leucas* (Pallas, 1776), toothed whales from the family Monodontidae and the bowhead whale *Balaena mysticetus* Linnaeus, 1758. This finding suggests that cyamids may have dispersed to monodontids from a mysticete host, whereas the interrelationships among delphinid host and parasites were inconclusive. Additionally, Margolis *et al.* (2000) found that the phyletic classification of the Cyamidae closely corresponded to the Cetacea phylogeny, suggesting 'that members of "the most primitive" genus of their analysis (*Cyamus*), mainly occur on the "most primitive" groups of whales, (Mysticeti) and none on the most advanced group of Odontoceti (Delphinoidea)', whereas the apomorphic genera of cyamids are found only on apomorphic Odontoceti.

Acute ventral processes, called 'ventral spines' and used for attachment to cetacean hosts, have traditionally been used as a morphological character in Cyamidae taxonomy (Margolis, 1955; Leung, 1967; 1970a; Raga, 1988). They are cuticular projections present in most species on pereonite (Per)5–Per7, with one to three pairs on each pereonite. They are sexually dimorphic, where the number of processes may differ for the males (Fig. 10A) and females (Fig. 10B) of a species. Recent studies showed that there are intraspecific variations in the number of processes (Raga, 1988; Mariniello *et al.*, 1994; Martínez *et al.*, 2008; Iwasa-Arai *et al.*, 2017) for some cyamid species, and this variation might be correlated with the maturation stage of the individual or represent populations from distinct localities. Despite the intraspecific variations observed in the acute ventral processes in three species of Cyamidae [*Cyamus boopis* (Fig. 10A, B), *Syncyamus aequus* and *Isocyamus deltobranchium*], they were used in this study because of their importance for taxonomy and to gain a better understanding of their plasticity. Therefore, these processes corresponded to 15 characters in this analysis. Intraspecific variations were coded as polymorphic for the species *C. boopis*, *I. deltobranchium* and *S. aequus*. A schematic summary of the processes observed for each species is in Fig. 11 for males and Fig. 12 for females.

Other important characters used in this analysis include antenna 1 terminal article setal arrangement, shape and length of lateral and accessory gills, shape of the inferior margin of gnathopods' propodus and shape of oostegite plates.

As most specimens were collected during commercial whaling, studies on the taxonomy and ecology of the group are often old, with six works published in the last two decades (Martin & Heyning, 1999; Margolis *et al.*, 2000; Wardle, Haney & Worthy, 2003; Haney *et al.*, 2004; Kaliszewska *et al.*, 2005; Iwasa-Arai *et al.*, 2017). Attempts to recover the phylogenetic relationships among cyamids from molecular data (Callahan, 2008; Iwasa-Arai, Serejo & Rodríguez-Rey, 2017) are scarce and are hampered by the age of the samples. Collections from museums are a source of untouched material and, despite the difficulty of molecular studies, they are of great value for cladistic analysis. Thus, morphological characters from both museums and freshly collected samples were used to perform a phylogenetic analysis of Cyamidae.

MATERIAL AND METHODS

The institution acronyms are as follows: AM, Australian Museum; CMNC, Canadian Museum of Nature; IB, Instituto de Biologia; LCME, Laboratório Central de Microscopia Eletrônica; MNHN, Muséum National d'Histoire Naturelle; MNRJ, Museu Nacional, Rio de Janeiro; NMV, Museum Victoria; UFRJ, Universidade Federal do Rio de Janeiro; UFSC, Universidade Federal de Santa Catarina; and ZMUC, Zoological Museum of the University of Copenhagen.

Materials included in the phylogenetic analyses were obtained from the institutions listed in Table 1. Specimens were fixed with 4% formalin (ZMUC, CMNC) and preserved in 70% ethanol, or fixed and preserved in 70% ethanol. Appendages and mouthparts of dissected specimens were mounted on glass slides and sealed with euparal mounting media. Specimen preparation for scanning electron microscopy (SEM) was performed following a protocol adapted from Felgenhauer (1987), dried at critical point, and sputter-coated with gold. Micrographs were taken with SEM JEOL JSM-6390LV (JEOL Ltd, Tokyo, Japan) at *Laboratório Central de Microscopia Eletrônica* (LCME/UFSC), SC, Brazil, and with JEOL JS6510 (JEOL Ltd) at the *Laboratório de Imagens em Microscopia Óptica e de Varredura* (LABIM/UFRJ), RJ, Brazil. Photos of character states were taken at the *Laboratório de Carcinologia* (MNRJ), RJ, Brazil using a Zeiss Discovery V20 (Zeiss Ltd, Baden-Württemberg, Germany) stereomicroscope high-resolution digital camera system with ZEN software (Zeiss Ltd).

Character matrix and outgroup

A character matrix was developed with 31 terminal taxa and 71 morphological characters (Tables 2 and 3), including two characters from the body in general, 13 from the head (antennae, and mouthparts including maxillipeds), 55 from the pereon (including gnathopods, pereopods, oostegites and penes) and one from the pleon (Table 2). Characters were combined into multistate groupings to avoid overly dependent characters, resulting in 38 binary characters and 26 multistate characters, presented according to Sereno (2007). The characters were obtained from published and unpublished data (Haney, 1999; Margolis *et al.*, 2000) and by detailed observation of the material.

Table 1. Species examined and included in the character matrix

Taxon	Host	Locality	Collection number/reference
Caprella penantis Leach, 1814	Free living (outgroup)	Rio de Janeiro, Brazil	MNRJ 23713
Phtisica marina Slabber, 1769	Free living (outgroup)	Arraial do Cabo, RJ, Brazil	MNRJ 6054
Caprogammarus gurjanovae Kudrjaschov & Vassilenko, 1966	Free living (outgroup)		Kudrjaschov & Vassilenko, 1966
Cyamus balaenopterae KH Barnard, 1931	*Balaenoptera acutorostrata*	Tonga	AM P90037
	Balaenoptera sp.	Antarctica	AM P41262
			AM P77561
Cyamus boopis Lütken, 1870*	*Megaptera novaeangliae*	Iceland	ZMUC CRU-12; ZMUC CRU-8190
Cyamus catodontis Margolis, 1954	*Physeter macrocephalus*	British Columbia, Canada	ZMUC CRU-592
Cyamus ceti (Linnaeus, 1758)	*Balaena mysticetus*	Alaska, USA	CMNC 2000-0019
Cyamus erraticus Roussel de Vauzème, 1834	*Eubalaena australis*	Santa Catarina, Brazil	MNRJ 67664–67667
	Eubalaena glacialis	British Columbia, Canada	ZMUC CRU-7570
Cyamus eschrichtii Margolis, McDonald & Bousfield, 2000	*Eschrichtius robustus*	California, USA	Margolis *et al.*, 2000
Cyamus gracilis Roussel de Vauzème, 1834	*Eubalaena australis*	Santa Catarina, Brazil	MNRJ 67673–67677
Cyamus kessleri A. Brandt, 1873	*Eschrichtius robustus*	California, USA	ZMUC CRU-8647
Cyamus mesorubraedon Margolis, McDonald & Bousfield, 2000	*Physeter macrocephalus*	British Columbia, Canada	Margolis *et al.*, 2000
Cyamus monodontis Lütken, 1870*	*Monodon monoceros*	Greenland	ZMUC CRU-467
Cyamus nodosus Lütken, 1861*	*Monodon monoceros*	Greenland	ZMUC CRU-494
Cyamus orubraedon Waller, 1989	*Berardius bairdii*	Northwest Pacific Ocean	CMNC 2000-0033
		Vancouver Island, Canada	CMNC 2000-0035
Cyamus ovalis Roussel de Vauzème, 1834	*Eubalaena australis*	Santa Catarina, Brazil	MNRJ 67668–67672
	Eubalaena glacialis	Iceland	ZMUC CRU-7679
Cyamus scammoni Dall, 1872	*Eschrichtius robustus*	California, USA	ZMUC CRU-7695
Isocyamus antarcticensis Vlasova, 1982	*Orcinus orca*	Antarctica	Berzin & Vlasova, 1982
Isocyamus delphinii (Guérin-Méneville, 1836)	*Globicephala macrorhynchus*	Ceará, Brazil	02C1921/527
Isocyamus deltobranchium Sedlak-Weinstein, 1992	*Orcinus orca*	Port Phillip Bay, VIC, Australia	NMV J60927
Isocyamus indopacetus Iwasa-Arai & Serejo, 2017	*Indopacetus pacificus*	New Caledonia	MNHN-IU-2014-12863
Isocyamus kogiae Sedlak-Weinstein, 1992	*Kogia brevieps*	Queensland, Australia	Sedlak-Weinstein, 1992a
Neocyamus physeteris Margolis, 1955	*Physeter macrocephalus*	locality unknown	AM P68272
Orcinocyamus orcini (Leung, 1970)	*Orcinus orca*	Senegal	Margolis *et al.*, 2000
Platycyamus flaviscutatus Waller, 1989	*Berardius bairdii*	Japan	Waller, 1989
Platycyamus thompsoni (Gosse, 1855)	*Hyperoodon ampullatus*	Faroe Islands	ZMUC-CRU 7696
Scutocyamus antipodensis Lincoln & Hurley, 1980	*Cephalorhynchus hectori*	New Zealand	Lincoln & Hurley, 1980
Scutocyamus parvus Lincoln & Hurley, 1974	*Lagenorhynchus albirostris*	North Sea	Lincoln & Hurley, 1974a
Syncyamus aequus Lincoln & Hurley, 1981	*Stenella coeruleoalba*	South Africa	Haney, 1999
Syncyamus ilheusensis Haney, De Almeida & Reis, 2004	*Globicephala macrorhynchus*	Ceará, Brazil	MNRJ 26767
Syncyamus pseudorcae Bowman, 1955	*Pseudorca crassidens*	Gulf of Mexico	Bowman, 1955

Locality and institution number are provided for each species. Reference is provided for species coded according to the original description or redescription.
*Species based on lectotypes.

Table 2. Characters and character states used in the analysis

1. Body, compression: lateral (0); dorsoventral (1).
2. Body, length relative width: less than two times (0); between two and three times (1); more than four times (2) (Fig. 3A–C).
3. Antenna 1, length relative to body length: 1/2 (0); 1/3 (1); ¼ (2); 1/5 (3); more than 1/6 (4) (Fig. 3D–G).
4. Antenna 1, terminal article, inner face: sparsely setiferous (0); continuous band of setae (1); multiple groupings (2); smooth (3) (Figs 4A–C and 5A, B).
5. Antenna 2, number of articles: six (0); four (1); three (2); two (3) (Fig. 4D–G).
6. Antenna 2, length relative to terminal article of antenna 1: longer than (0); subequal to (1); shorter than (2) terminal article of antenna 1.
7. Left mandible of male, incisor, teeth: seven (0); six (1); five (2); four (3) (Fig. 4H, I).
8. Left mandible, *lacinia mobilis*, teeth: seven (0); six (1); five (2); four (3) (Fig. 4H).
9. Right mandible, incisor, teeth: seven (0); six (1); five (2); four (3) (Fig. 4J, K).
10. Right mandible, *lacinia mobilis*, upper grinding surface: multituberculate with teeth (0); multituberculate without tooth (1); smooth (2); with five teeth (3) (Fig. 6A, B).
11. Lower lip, inner lobes, fusion: partially fused (0); fully fused (1) (Fig. 7A, B).
12. Maxilla 2, outer lobe: absent (0); present (1) (Fig. 7C–E).
13. Maxilla 2, inner lobes: separate (0); fused (1) (Fig. 7C–E).
14. Maxilliped, inner lobes, shape: subtriangular (0); round (1) (Fig. 7F, G).
15. Maxilliped, palp: present (0); absent (1) (Fig. 7H).
16. Pereonite 2, anterolateral margin, process: absent (0); present (1) (Fig. 8A, B).
17. Pereonite 2 of male, anterolateral margin angle: 180° (0); 120° (1); 240° (2) (Fig. 8C–E).
18. Pereonite 2 of female, anterolateral margin angle: 180° (0); 120° (1); 240° (2) (Fig. 8F–H).
19. Pereonite 2, posterolateral margin, knoblike process: absent (0); present (1) (Fig. 8A, B).
20. Pereonite 3 of male, posterolateral margin, knoblike process: absent (0); present (1) (Fig. 8I, J).
21. Pereonite 3 of female, posterolateral margin, knoblike process: absent (0); present (1) (Figs. 8K, L).
22. Pereonite 4 of male, posterolateral margin, knoblike process: absent (0); present (1) (Fig. 8I, L).
24. Pereonites 3 and 4 of male, width relative to width of pereonite 5: wider (0); subequal (1); narrower (2) (Fig. 9A–C).
25. Pereonites 3 and 4 of female, width relative to width of pereonite 5: wider (0); subequal (1); narrower (2) (Fig. 9D–F).
26. Oostegites 3, shape: rectangular (0); triangular (1); boot-shaped (2); rounded (3) (Fig. 9G–I).
27. Oostegites 4, shape: boot-shaped (0); rounded (1); rounded with crevices (2) (Fig. 9J–L).
28. Pereonite 5, genital valves, posterolateral margin, acute process: absent (0); present (1) (Fig. 9M, N).
29. Pereonite 5, genital valves, anterior margin, setae: absent (0); present (1).
30. Pereonite 5 of male, ventral face, pair of anterior processes: absent (0); present (1) (Figs 10A and 11).
31. Pereonite 5 of male, ventral face, pair of posterior processes: absent (0); present (1) (Fig. 11).
32. Pereonite 5 of female, ventral face, pair of anterior processes: absent (0); present (1) (Figs 10B and 12).
33. Pereonite 6 of male, ventral face, pair of anterior processes: absent (0); present (1) (Fig. 11).
34. Pereonite 6 of male, ventral face, pair of lateral processes: absent (0); present (1) (Fig. 11).
35. Pereonite 6 of male, ventral face, pair of posterior processes: absent (0); present (1) (Fig. 11).
36. Pereonite 6 of female, ventral face, pair of anterior processes: absent (0); present (1) (Fig. 12).
37. Pereonite 6 of female, ventral face, pair of lateral processes: absent (0); present (1) (Fig. 12).
38. Pereonite 6 of female, ventral face, pair of posterior processes: absent (0); present (1) (Fig. 12).
39. Pereonite 7 of male, ventral face, pair of anterior processes: absent (0); present (1) (Fig. 11).
40. Pereonite 7 of male, ventral face, pair of posterior processes: absent (0); present (1) (Fig. 11).
41. Pereonite 7 of male, ventral face, pair of posterior processes, position: central (0); lateral (1) (Fig. 11).
42. Pereonite 7 of female, ventral face, pair of anterior processes: absent (0); present (1) (Fig. 12).
43. Pereonite 7 of female, ventral face, pair of posterior processes: absent (0); present (1) (Fig. 12).
44. Pereonite 7 of female, ventral face, pair of posterior processes, position: central (0); with lateral (1) (Fig. 12).
45. Penes, shape: bulbous (0); stout (1); narrow (2).
46. Gnathopod 1, propodus, size ratio to propodus of gnathopod 2: smaller, <⅙ (0); smaller, ~¼ (1); smaller, ~½ (2), subequal (3).
47. Gnathopod 1, propodus, palm, process, shape: minute acute process (0); with broad proximal expansion (1); with broad lunate expansion (2); with elongate expansion (3); with bilobed expansion (4) (Fig. 13A–E).
48. Gnathopod 2 of male, propodus, palm, distal process: absent (0); present (1).
49. Gnathopod 2 of male, propodus, palm, distal process, shape: subacute (0); subquadrate (1); oval (2) (Fig. 14A, C).

Table 2. Continued

50. Gnathopod 2 of male, propodus, palm, distal process, size relative to proximal process: larger than (0); shorter than (1); subequal to (2) (Fig. 14B–D).
51. Gnathopod 2 of male, propodus, palm, proximal process, shape: subacute (0); oval (1) (Fig. 14B–D).
52. Gnathopod 2 of male, propodus, palm, proximal process, size: large (0); minute (1).
53. Gnathopod 2 of female, propodus, palm, proximal process: absent (0); present (1) (Fig. 14E).
54. Gnathopod 2 of female, propodus, palm, proximal process, size: large (0); minute (1) (Fig. 14F–H).
55. Gnathopod 2 of female, propodus, palm, distal process, shape: subacute (0); oval (1).
56. Gnathopod 2 of female, propodus, palm, distal process, size relative to proximal process: larger (0); shorter (1) (Fig. 14G, H).
57. Pereonites 3 and 4, lateral gill, rami: uniramous (0); biramous (1); multiramous (more than five rami) (2) (Fig. 15A–F).
58. Pereonite 3, lateral gill, length: not reaching head margin (0); reaching head margin (1); as long as wide (2) (Fig. 15E, F).
59. Pereonites 3 and 4, accessory gill of male: absent (0); present (1) (Fig. 15C, D).
60. Pereonites 3 and 4, accessory gill of male, shape: symmetrically bilobed (0); unsymmetrically bilobed (1); spinelike (2); subtriangular (3); cylindrical (4) (Fig. 16A–F).
61. Pereonites 3 and 4, accessory gill of male, length relative to length of lateral gills: much shorter (0); shorter (1); subequal in length (2).
62. Pereonites 3 and 4, accessory gill of female: absent (0); present (1) (Fig. 17A, B).
63. Pereonites 3 and 4, accessory gill of female, outer margin, shape: straight (0); serrate (1) (Fig. 17C, D).
64. Pereonites 3 and 4, lateral gills, spine-like process: absent (0); present (1).
65. Pereonites 5–7, anterolateral margin, shape: straight (0); invaginated (1) (Fig. 17E, F).
66. Pereopods 5–7, basis, anterodistal margin, process: absent (0); present (1) (Fig. 18A–C).
67. Pereopods 5–7, basis, anterodistal margin, process, direction: distal (0); ventral (1) (Fig. 18B, C).
68. Pereopods 5–7, carpus, anterodistal margin, expansion: absent (0); present (1) (Fig. 18D, E).
69. Pereopods 5–7, carpus, posterior margin, spine-like process: absent (0); present (1) (Fig. 18F).
70. Pereopods 5–7, dactylus, angle of recurve: <50° (0); >70° (1) (Fig. 19A, B).
71. Pleopods of male, terminal portion, shape: round (0); digitiform (1).

Polarization of the characters was conducted through outgroup comparison. The relationship between ingroup and outgroup was not constrained, and the monophyly of the ingroup was assumed, based on previous research, especially for the relationships among the species and genera of Cyamidae. Thus, *Caprella penantis* Leach, 1814 and *Phtisica marina* Slabber, 1769 (family Caprellidae) and *Caprogammarus gurjanovae* Kudrjaschov & Vassilenko, 1966 (family Caprogammaridae) were chosen as outgroups, because they were considered to be sister groups to Cyamidae in the evolution of Caprelloidea (Myers & Lowry, 2003; Ito *et al.*, 2011).

Phylogenetic analysis

The data matrix was constructed using MESQUITE 2.74 (Maddison & Maddison, 2010) and analysed using the heuristic search of parsimony criterion available in TNT 1.1 (Goloboff, Farris & Nixon, 2008), with implicit weighting (1.566, 1.839, 2.163, 2.556, 3.041, 3.655, 4.458, 5.554, 7.136, 9.622, 14.097) calculated based on Mirande (2009). The tree topology that shared the highest number of nodes with the other trees was considered the most stable, as measured by subtree prune and regraft (SPR) distances (Goloboff *et al.*, 2008). The analysis was conducted following the traditional search, with 8000 replications and 500 trees held per replicate. Polymorphic characters were considered unordered. The branch-swapping algorithm used was 'tree bisection and reconnection' (TBR). Assessment of support for each branch was calculated using a bootstrap of 1000 replicates (Felsenstein, 1985); Bremer support (Bremer, 1994) was evaluated with TNT, with values given as relative numbers. Character polarization was conducted *a posteriori* according to Nixon & Carpenter (1993), and character otimization was made with WINCLADA (Nixon, 2002).

The abbreviations used are as follows: AG, accessory gill; Ant, antenna; CI, consistency index; Gn, gnathopod; l, left; L, length; LG, lateral gill; LL, lower lip; Md, mandible; P, pereopod; Per, pereonite; Pl, pleopod; Pn, penes; r, right; RI, retention index; and S, state.

RESULTS

Phylogenetic analysis

Heuristic searches under the implicit weights of 1.839, 2.163, 2.556, 3.041, 3.655 and 4.458 resulted in a single, most parsimonious tree with fits of 33.526, 31.394, 29.179, 26.912, 24.476 and 21.926, respectively (L = 293 steps; CI = 38 and RI = 68; Fig. 2). This tree topology was used for the following data interpretation: Clade 3 encompasses the family Cyamidae and two major clades: Isocyaminae subfam. nov. grouping of the genera *Orcinocyamus*, *Isocyamus*, *Platycyamus*, *Neocyamus*, *Scutocyamus* and *Syncyamus* (clade 4) and Cyaminae subfam. nov. (clade 5) grouping *Cyamus* and the proposed new genus, *Balenocyamus* gen. nov. Clade numbers are represented above branches and were used to polarize and describe characters.

The term 'homoplastic synapomorphy' refers to synapomorphic characters that were rejected as a secondary homology (De Pinna, 1991), and thus, less inclusive character states which were shared by more than one clade (e.g. Wheeler, Schuh & Bang, 1993; Polotow, Carmichael & Griswold, 2015; Gomes-da-Silva & Souza-Chies, 2017; Gueratto, Mendes & Pinto-da-Rocha, 2017).

DISCUSSION

The unusual body form and lifestyle of whale lice has already provided insight into the monophyly of Cyamidae. This was corroborated by 12 synapomorphies, including the body dorsoventrally compressed [S1(1)], reduced number of articles on Ant2 [S5(1)], the presence of acute ventral processes on Per5–Per7 [S30(1)–S44(1)], oostegites 3 other than rounded [S26(0)], shape of penes [S45(1)], shape of Gn2 [S48(1)] and length of lateral gills [S58(0)] (Fig. 20). Haney (1999), based on cladistic methods, also found that Cyamidae was a monophyletic group, using diagnostic character states such as marked dorsoventral depression of the body, antenna 1 and 2 of four or fewer articles, uniarticulate maxillulary palp and absence of maxilliped endites. Furthermore, our analysis defined two major clades, treated as Isocyaminae subfam. nov. (clade 4), encompassing *Isocyamus*, *Neocyamus*, *Orcinocyamus*, *Platycyamus*, *Scutocyamus* and *Syncyamus* (Figs 2 and 20), and Cyaminae subfam. nov. (clade 5), including *Cyamus* and *Balaenocyamus* gen. nov. (Figs 2 and 20). Clade 4 was supported by seven synapomophies. Three were non-homoplastic:

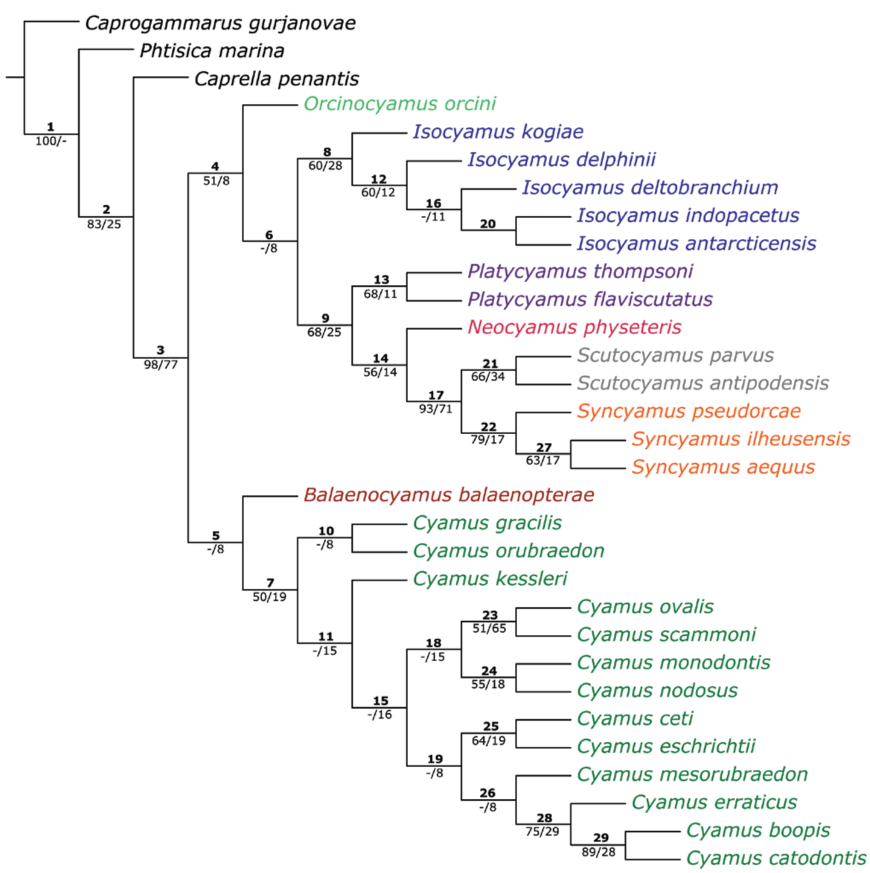


Figure 2. Phylogenetic tree proposal for Cyamidae. Clade numbers are represented above branches in bold. Bootstraps >50% and Bremer support are represented below branches.

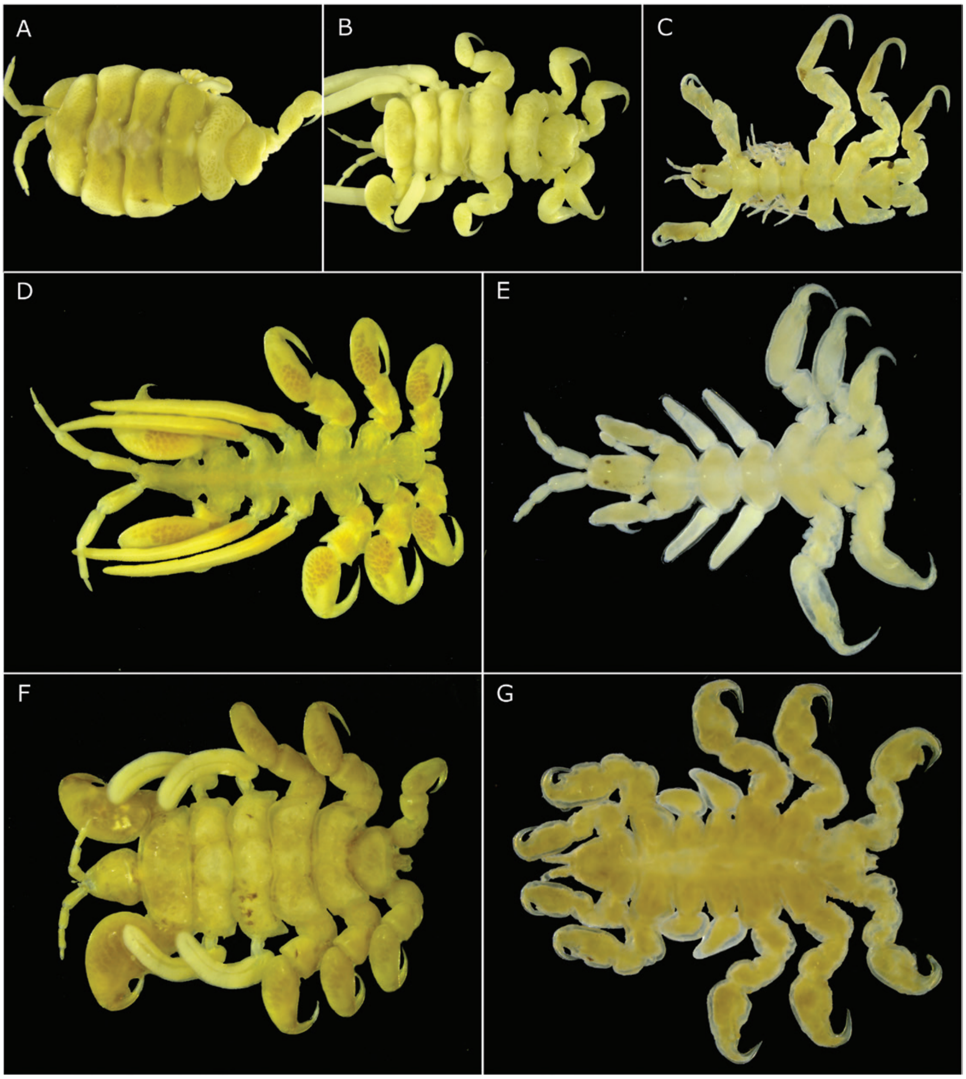


Figure 3. A–C, character 2. A, body length less than two times width (*Cyamus scammoni*). B, less than two times longer than broad (*Cyamus kessleri*). C, body more than four times longer than broad (*Neocyamus physeteris*). D–G, character 3. D, antenna 1 length one-quarter of body size (*Cyamus boopis*). E, antenna 1 length one-third of body size (***B. balaenopterae* comb. nov.**). F, antenna 1 length one-quarter of body size. G, antenna 1 length less than one-sixth of body size (*Platycyamus thompsoni*).

S10(1) (right *lacinia* multituberculate without teeth), S13(1) (inner lobes of maxilla 2 fused) and S45(2) (penes narrow and elongated). *Orcinocyamus orcini*, previously described as *Cyamus orcini*, was separately positioned from the *Cyamus* clade, corroborating Haney's (1999) suggestion to estabilish a new genus for this species. Later on, Margolis *et al.*, (2000) created the genus *Orcinocyamus*. Haney (1999) and Margolis *et al.*, (2000) also observed two major clades within Cyamidae: one comprised *Orcinocyamus*, *Isocyamus*, *Neocyamus*, *Platycyamus*, *Scutocyamus* and *Syncyamus*, and another comprised *Cyamus s.l.* (Fig. 1). In Haney's analysis, *Orcinocyamus* is presented as the basalmost genus of the clade composed of all non-*Cyamus s.l.* genera, whereas Margolis *et al.*, (2000) observed two clades; one comprised (*Orcinocyamus*, *Isocyamus*) *Neocyamus*, and another comprised *Platycyamus* (*Scutocyamus*, *Syncyamus*). In this analysis, *Orcinocyamus* is the sister group of clade 6, which was defined by six synapomophies: three non-homoplastic [S12(0), S60(3) and S64(1)] and three homoplastic [S5(2), S24(2) and S50(0)]. *Isocyamus* (clade 8) constitutes a monophyletic group supported by seven synapomorphies, including four non-homoplastic: S4(1) continuous band of setae on terminal article of Ant1, S6(2) Ant2 shorter than terminal

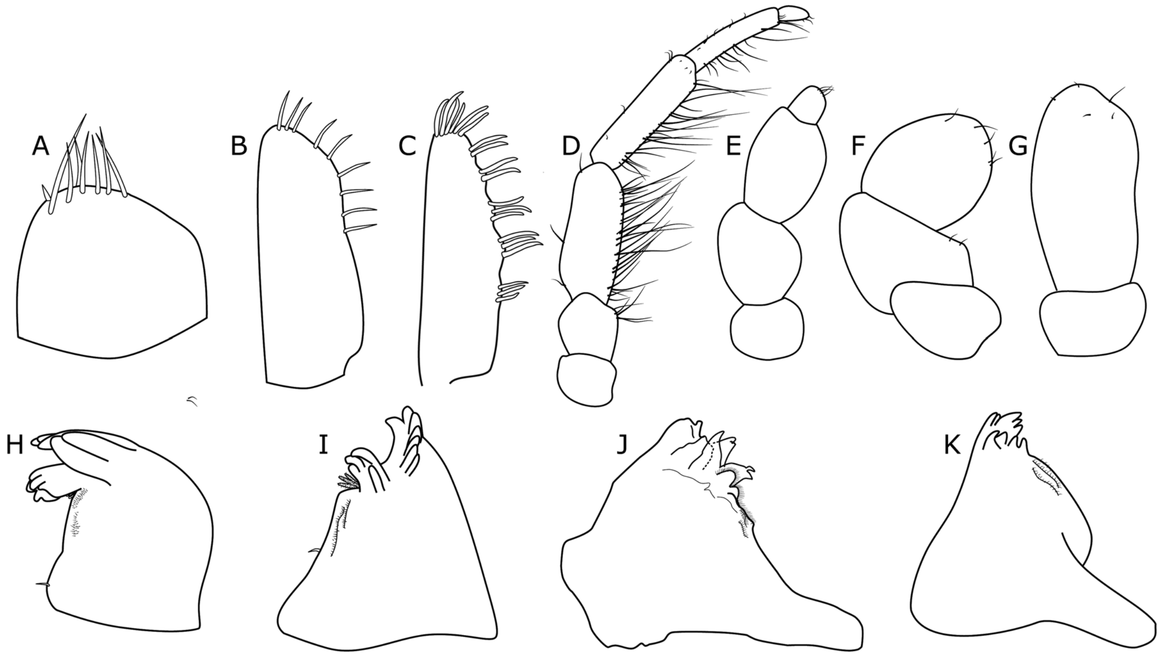


Figure 4. A–C, character 4. A, terminal article of antenna 1 without setal arrangement (*Platycyamus thompsoni*). B, terminal article of antenna 1 with a continuous band of seta (*Isocyamus deltobranchium*). C, terminal article of antenna 1 with multiple groupings of seta (*Cyamus boopis*). D–G, character 5. D, antenna 2 with six articles (*Caprella penantis*). E, antenna 2 with four articles (*Cyamus monodontis*). F, antenna 2 with three articles (*Platycyamus thompsoni*). G, antenna 2 with two articles (*Neocyamus physeteris*). H, I, characters 7 and 8. H, left mandible with five-toothed incisor and five-toothed *lacinia mobilis* (*C. monodontis*). I, left mandible with seven-toothed incisor (*Cyamus nodosus*). J, K, character 9. J, right mandible with six-toothed incisor (*Syncyamus ilheusensis*). K, right mandible with five-toothed incisor (*C. monodontis*).

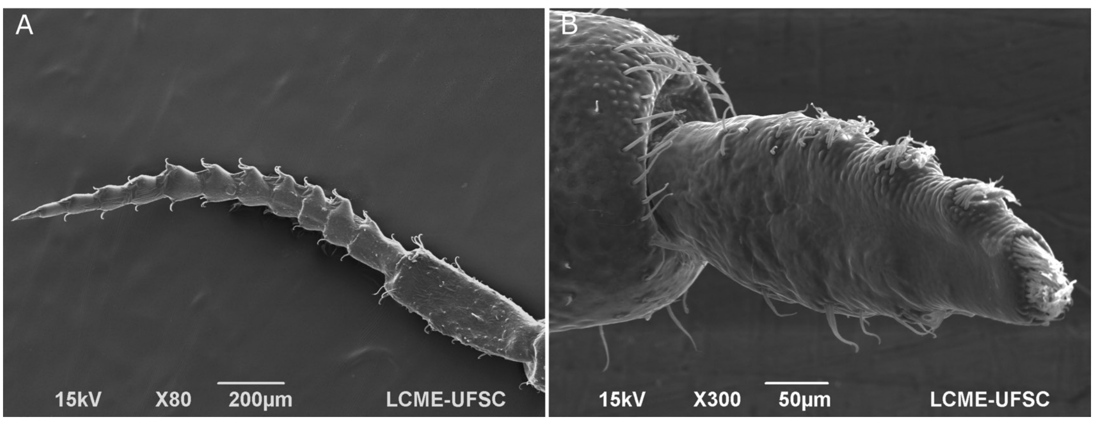


Figure 5. A, flagellum of antenna 1 of *Caprella penantis*. B, terminal article of antenna 1 of *Cyamus erraticus*.

article of Ant1, S14(1) inner lobes of rounded maxillipeds and S61(1) AG shorter or subequal in length to LG; and three homoplastic: S10(0) *lacinia mobilis* of rMd multituberculate with teeth, S16(1) presence of process at the anterior margin of Per2 and S59(1) presence of AG on male. *Isocyamus* is the sister group to clade 9, which includes *Platycyamus*, *Neocyamus*, *Scutocyamus* and *Syncyamus*. *Isocyamus delphinii*, the type species of the genus, is the most cosmopolitan whale louse species, found in all oceans and on a great range of hosts. Both *I. kogiae* and *I. antarctisensis* are only known to parasitize one host species, *Kogia breviceps* and *Orcinus orca*, respectively (Berzin & Vlasova, 1982; Sedlak-Weinstein, 1992a). *Isocyamus*

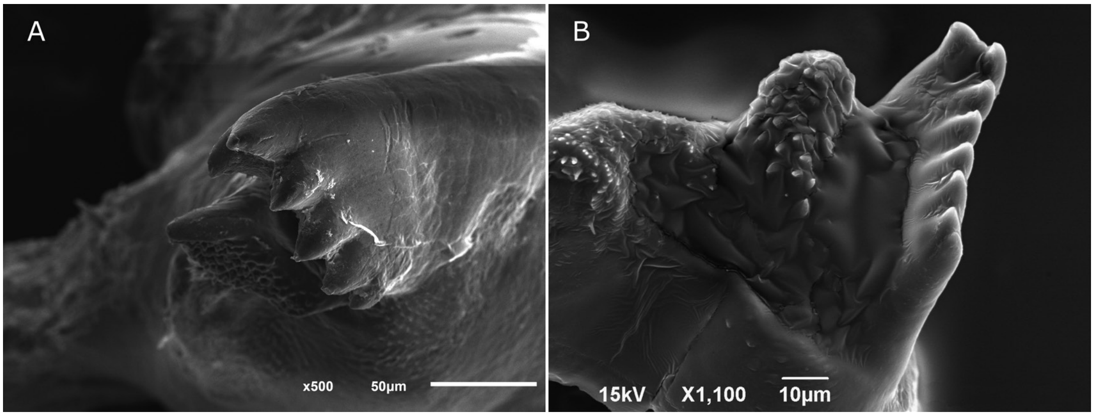


Figure 6. A, B, character 10. A, *lacinia mobilis* of right mandible multituberculate with one tooth (*Cyamus ovalis*). B, *lacinia mobilis* of right mandible multituberculate without tooth (*Neocyamus physeteris*).

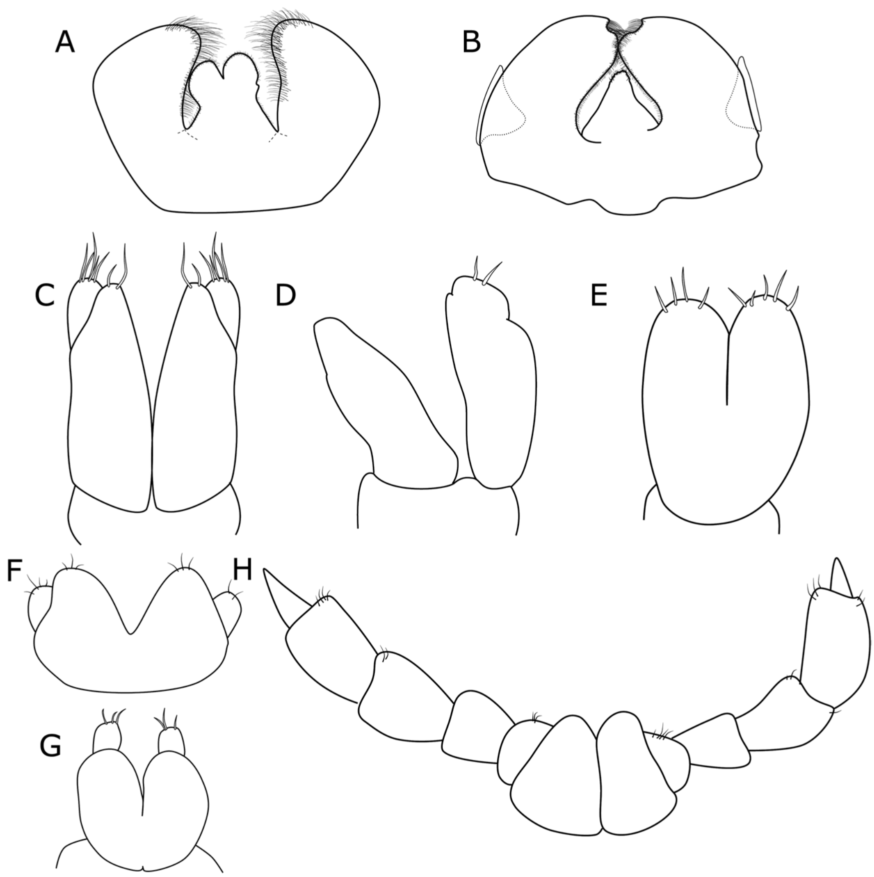


Figure 7. A, B, character 11. A, inner lobes of lower lip partially fused (*Cyamus nodosus*). B, inner lobes of lower lip fully fused (*Isocyamus indopacetus*). C–E, characters 12 and 13. C, outer lobes of maxilla 2 present, inner lobes separate (*C. nodosus*). D, outer lobes of maxilla 2 absent, inner lobes separate (*I. indopacetus*). E, outer lobes of maxilla 2 absent, inner lobes partly fused (*Isocyamus deltobranchium*). F–H, characters 14 and 15. F, maxillipeds subtriangular, without palp (*C. nodosus*). G, maxillipeds rounded, without palp (*I. indopacetus*). H, maxillipeds subtriangular, with palps (*Cyamus monodontis*).

indopacetus is the latest species of Cyamidae described from Longman's beaked whale, *Indopacetus pacificus* (Iwasa-Arai, Carvalho & Serejo, 2017). According to Margolis *et al.* (2000), it is very likely that further new species of whale lice will be described from stranded ziphiid whales. All *Isocyamus* species were found in

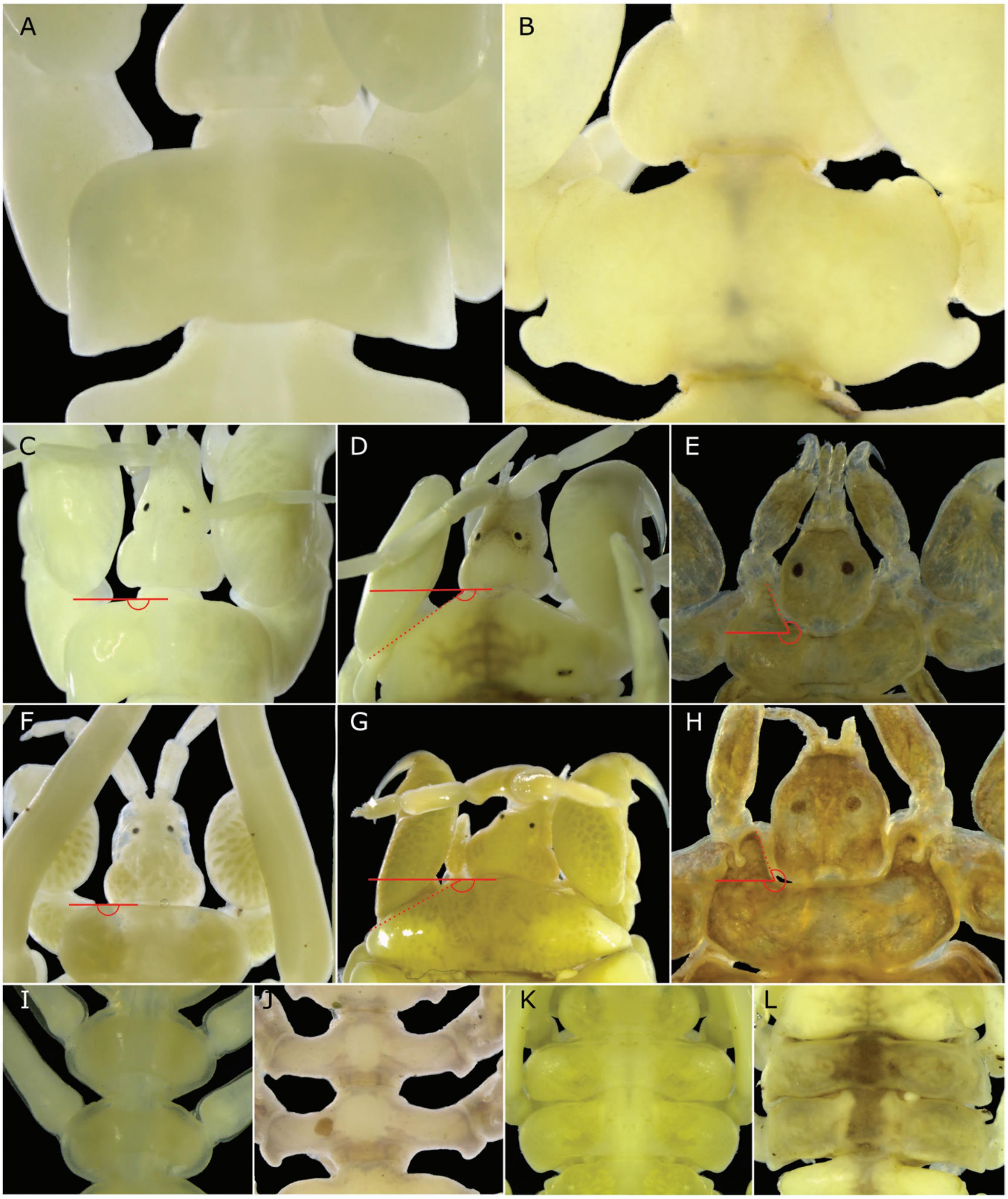
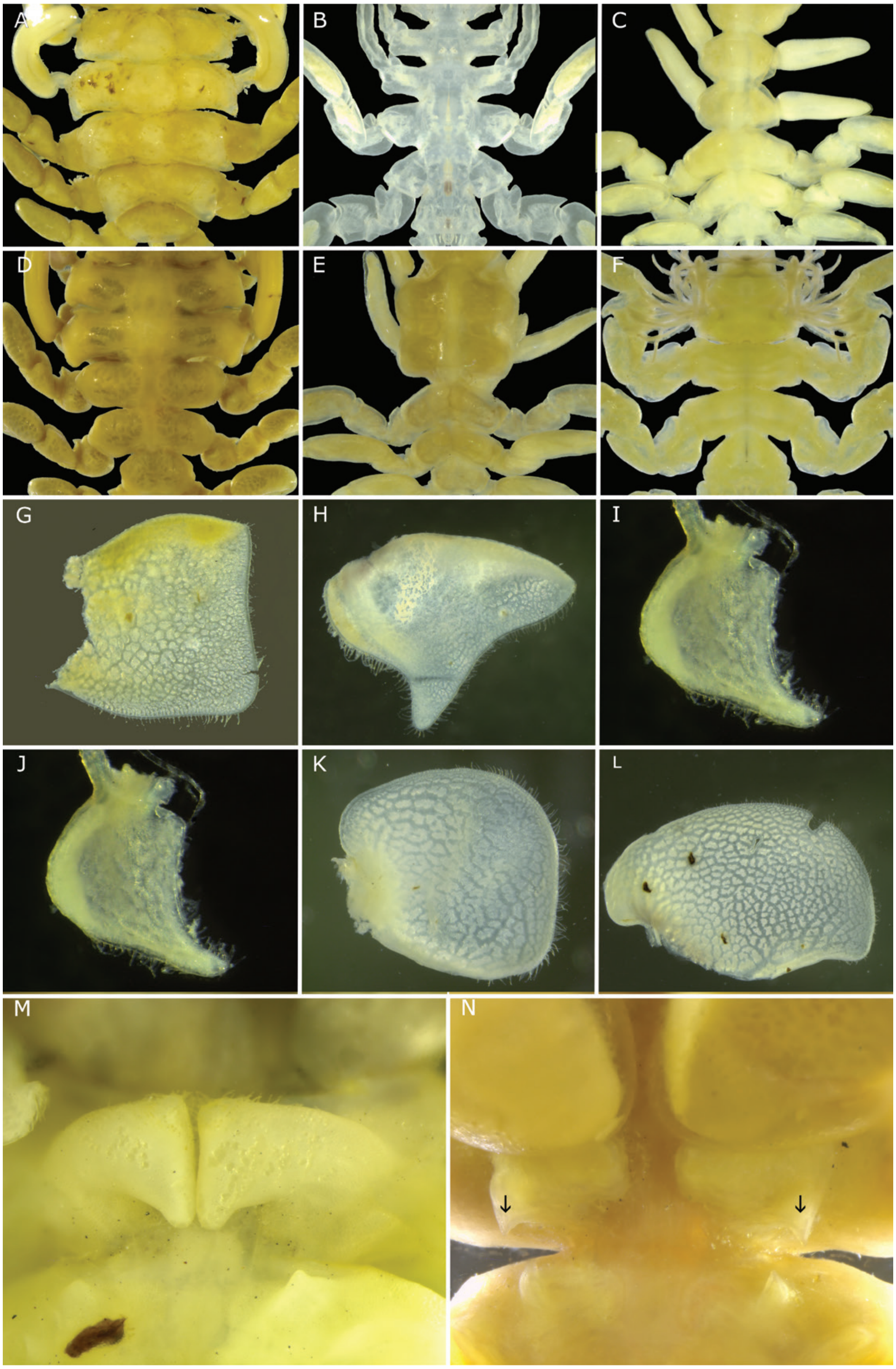


Figure 8. A, B, characters 16 and 19. A, pereonite 2, anterolateral and posterolateral margins without process (*Cyamus gracilis*). B, pereonite 2, anterolateral and posterolateral margins with processes (*Cyamus erraticus*). C–E, character 17. C, male, anterolateral margin of pereonite 2 angle of recurve 180° to pereonite 1 (*C. gracilis*). D, male, anterolateral margin of pereonite 2 angle of recurve of 120° (*Cyamus ovalis*). E, male, anterolateral margin of pereonite 2 angle of recurve of 240°, towards pereonite 1 (*Syncyamus ilheusensis*). F–H, character 18. F, female, anterolateral margin of pereonite 2 angle of recurve 180°, parallel to pereonite 1 (*Cyamus kessleri*). G, female, anterolateral margin of pereonite 2 angle of recurve 120° (*Cyamus scammoni*). H, female, anterolateral margin of pereonite 2 angle of recurve of 240°, towards pereonite 1 (*S. ilheusensis*). I–J, characters 20 and 22. I, male, pereonites 3 and 4 without posterolateral process (***Balaenocyamus balaenopterae* comb. nov.**). J, male, pereonites 3 and 4 with posterolateral processes (*Cyamus boopis*). K, L, characters 21 and 23. K, female, pereonites 3 and 4 without posterolateral process (*Cyamus monodontis*). L, pereonites 3 and 4 with posterolateral processes (*C. ovalis*).



odontocetes, from the bottlenose dolphin (*Tursiops truncatus*) to orcas (*Orcinus orca*) and beaked whales (Table 4).

Platycyamus includes two species: *Platycyamus thompsoni* and *Platycyamus flaviscutatus* Waller, 1989. *Platycyamus* is the only genus with subequal length of Gn1 and Gn2 [S46(3)], and the other homoplastic synapomorphies that define the genus are S19(1) presence of a knoblike process on posterolateral margin of Per2, and S66(1) process on basis of P5–P7. *Platycyamus* is

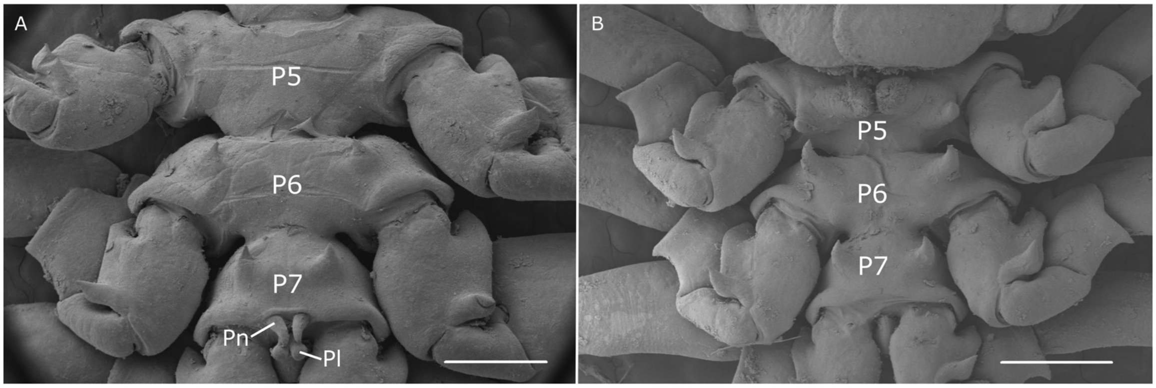


Figure 10. Pereonites 5–7 and acute ventral processes. A, male of *Cyamus boopis* (scale bar = 1 mm). B, female of *C. boopis* (scale bar = 1 mm). Pl, pleopod; Pn, penes.

the sister taxon of clade 14, which includes *Neocyamus*, *Scutocyamus* and *Syncyamus*. According to Haney (1999), *Platycyamus* was positioned as the sister clade of *Neocyamus*, whereas for Margolis *et al.*, (2000), it was closely related to *Scutocyamus* and *Syncyamus*. *Platycyamus* is recorded on beaked whales of the family Ziphiidae (Table 4).

Neocyamus, a monotypic genus, includes *Neocyamus physeteris*, which is found on sperm whales (*Physeter macrocephalus*). Its morphology greatly differs from other cyamids, from body shape to gills. It is also the only species where females bear pleopods. A central bilobed expansion in the propodus of Gn1 [S47(4)] and lateral gills multiramous [S57(2)] are unique character states among cyamids. Eight other homoplastic synapomorphies were observed for *N. physeteris*: S2(2) body length more than four times width, S4(3) two articles on Ant2, S6(1) Ant2 subequal in length to terminal article of Ant1, S7(0) incisor of lMd of male with seven teeth, S9(0) incisor of rMd with seven teeth, S32(1) pair of anterior processes on Per5 of female, S45(1) penes stout, S56(0) distal process of propodus of Gn2 of female larger than proximal process, and S65(1) anterolateral margin of Per5–Per7 invaginated. *Neocyamus* is the sister group of clade 17 (*Scutocyamus* + *Syncyamus*).

The *Scutocyamus* + *Syncyamus* grouping (clade 17) was supported by the highest support values (bootstrap = 93; Bremer = 71), a relationship already suggested by Lincoln & Hurley (1974a), who observed the similarities between these genera. The group was defined by three non-homoplastic synapomorphies: S5(4) Ant2 with one article, S26(2) and S27(0) (boot-shaped oostegite plates), and 10 homoplastic synapomorphies (Fig. 20). *Scutocyamus* includes *Scutocyamus parvus* and *Scutocyamus antipodensis* Lincoln & Hurley, 1980 and was treated in this study based on the original descriptions (Lincoln & Hurley, 1974a; 1980). *Scutocyamus parvus* was described from the white-beaked dolphin (*Lagenorhynchus albirostris* Gray, 1846) from the North Sea and *S. antipodensis* was described from Hector's dolphin, *Cephalorhynchus hectori* (P. J. Van Beneden, 1881), endemic to New Zealand (Table 4). *Syncyamus* is composed of *S. pseudorcae* Bowman, 1955, *S. aequus* Lincoln & Hurley, 1981 and *S. ilheusensis* Haney, De Almeida & Reis, 2004. *Syncyamus chelipes* (Costa, 1866) appears to be a *Syncyamus* species, though the type series is lost, its host is unknown, and the name *S. chelipes* is a *nomen dubium* (Haney, 1999). *Syncyamus pseudorcae*, the type species of the genus, was recorded from the false killer whale (*Pseudorca crassidens*) and the Clymene dolphin, *Stenella clymene* (Carvalho *et al.*, 2010). *Syncyamus aequus* was recorded from the common dolphin *Delphinus delphis*, *Stenella coerolualba*, *Stenella longirostris* and *T. truncatus* (Table 4). *Syncyamus ilheusensis* was described from *Globicephala macrorhynchus*

Figure 9. A–C, Character 24. A, male, pereonites 3 and 4 wider than pereonite 5 (*Cyamus nodosus*). B, male, pereonites 3 and 4 subequal in width to pereonite 5 (*Cyamus catodontis*). C, male, pereonites 3 and 4 narrower than pereonite 5 (***Balaenocyamus balaenopterae* comb. nov.**). D–F, character 25. D, female, pereonites 3 and 4 wider than pereonite 5 (*Cyamus ceti*). E, female, pereonites 3 and 4 subequal in width to pereonite 5 (***B. balaenopterae* comb. nov.**). F, female, pereonites 3 and 4 narrower than pereonite 5 (*Neocyamus physeteris*). G–I, character 26. G, oostegite 3 rectangular (*Cyamus monodontis*). H, oostegite 3 triangular with terminal process (*Cyamus boopis*). I, oostegite boot shaped (*Syncyamus ilheusensis*). J–L, character 27. J, oostegite 4 boot shaped (*S. ilheusensis*). K. oostegite 4 oval (*Cyamus gracilis*). L, oostegite 4 oval with crevice (*Cyamus ovalis*). M, N, character 28. M, posterolateral margin of genital valves without process (*C. ovalis*). N, posterolateral margin of genital valves with processes (*C. ceti*).

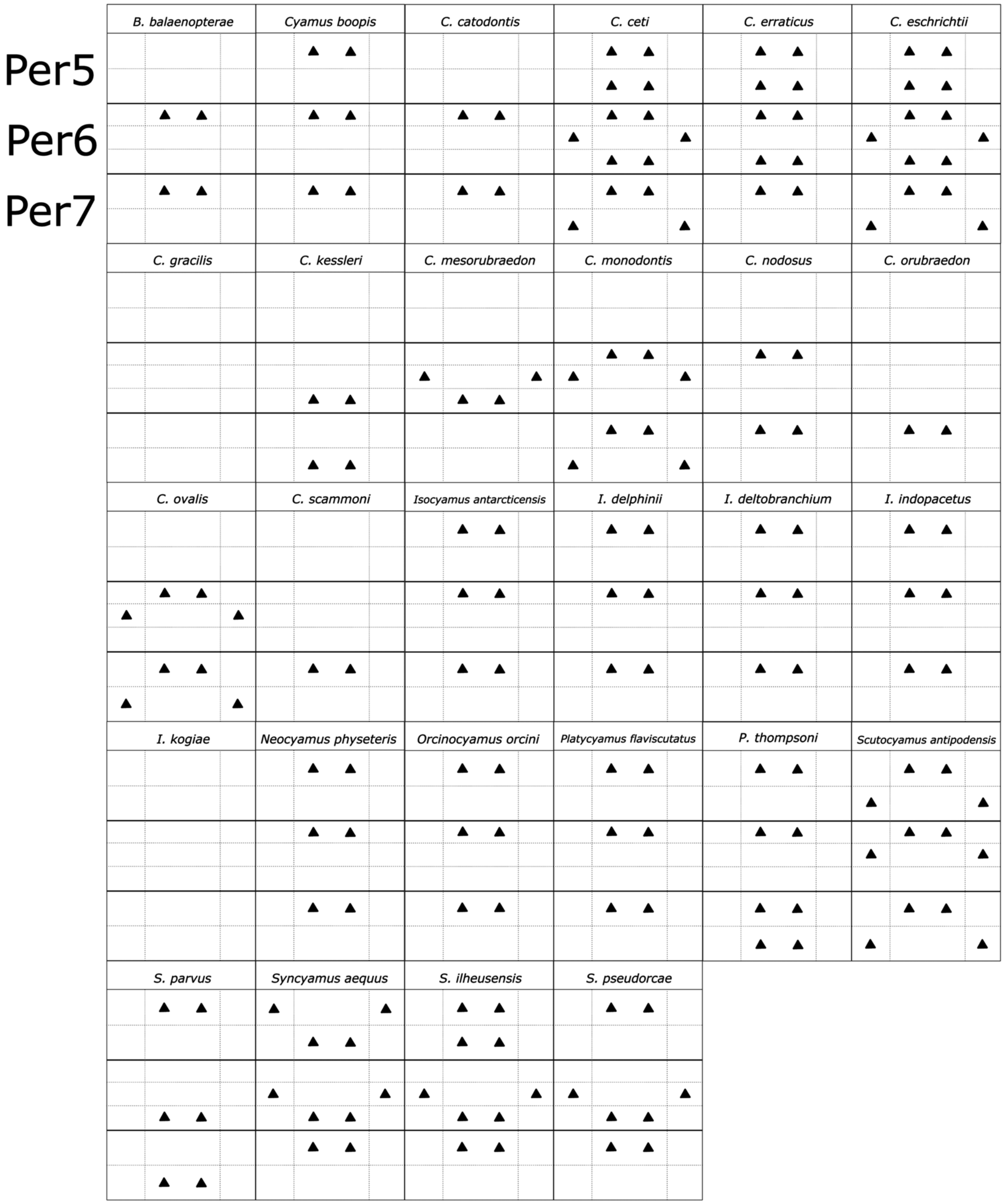


Figure 11. Schematic diagram of acute ventral processes of males observed in each species in this study. Per, pereonite.

from Atlantic waters and was recently recorded from *Peponocephala electra* and *S. clymene* (Iwasa-Arai, Carvalho & Serejo, 2017).

Clade 5 is treated as the subfamily Cyaminae subfam. nov. Synapomorphies of the subfamily are: S4(2) multiple groupings of setae on terminal article of Ant1, S29(1) presence of setae on the anterior margin of the genital valve, and S45(1) penes stout and S59(1) presence of AG in males. *Cyamus* is the largest genus of Cyamidae, nowadays composed of 14 recognized species of baleen whales and large odontocetes (Ahyong *et al.*, 2011). In this analysis,

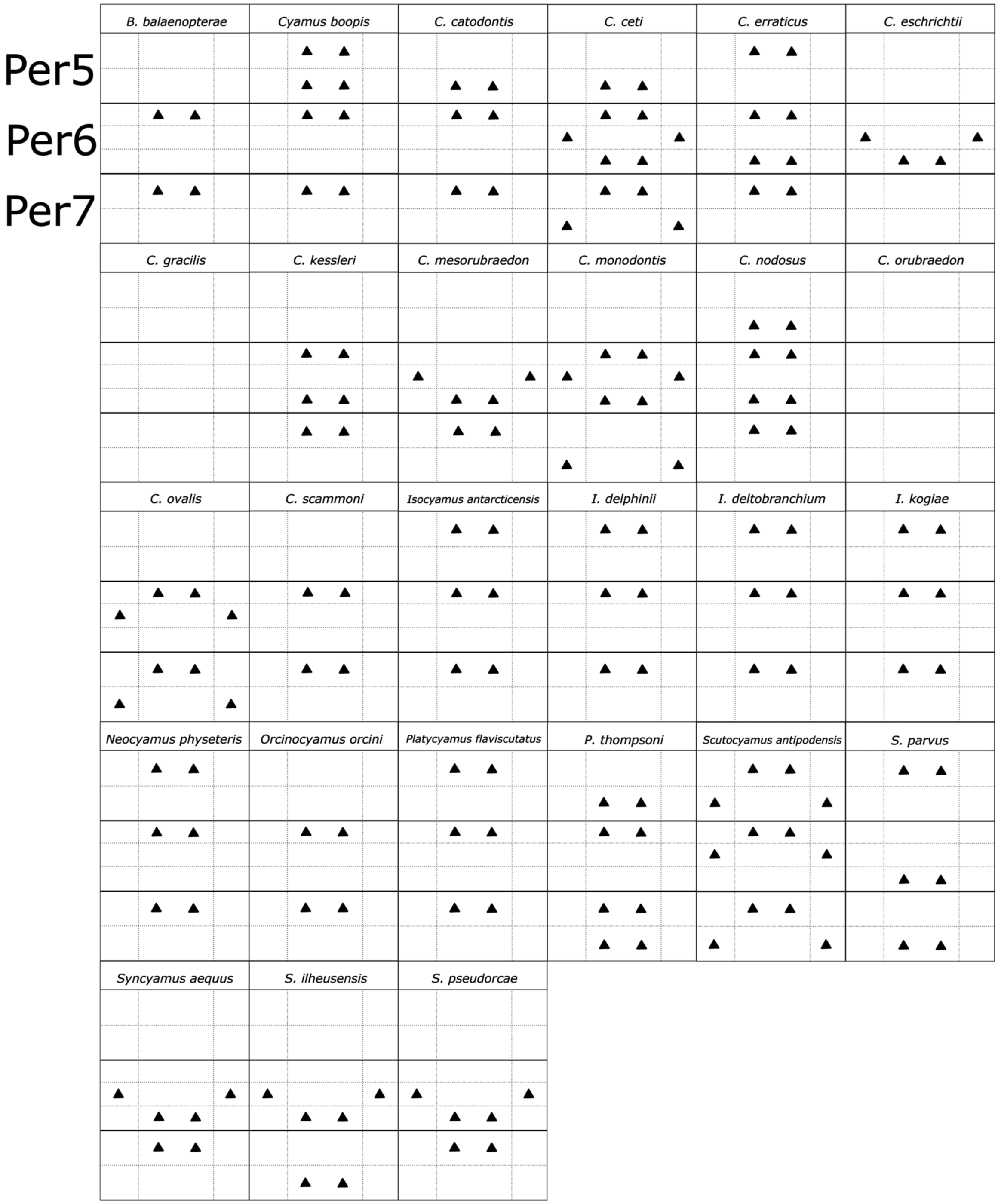


Figure 12. Schematic diagram of acute ventral processes of females observed in each species in this study. Per, pereonite.

C. balaenopterae is tranferred to *Balaenocyamus* gen. nov. based on eight synapomorphies. Haney (1999) also observed *C. balaenopterae* as basal and substantially different to other *Cyamus* species. *Cyamus balaenopterae* also did not fit in a previous *Cyamus* diagnosis (Margolis *et al.*, 2000). *Balaenocyamus balaenopterae* comb. nov. is an ectoparasite of rorqual whales, such as *Balaenoptera musculus*, *Balaenoptera acutorostrata* and *Balaenoptera physallus*, in contrast to the *Cyamus* species, which are mostly host specific. *Balaenocyamus balaenopterae* comb. nov. showed several character states not shared by the other *Cyamus*

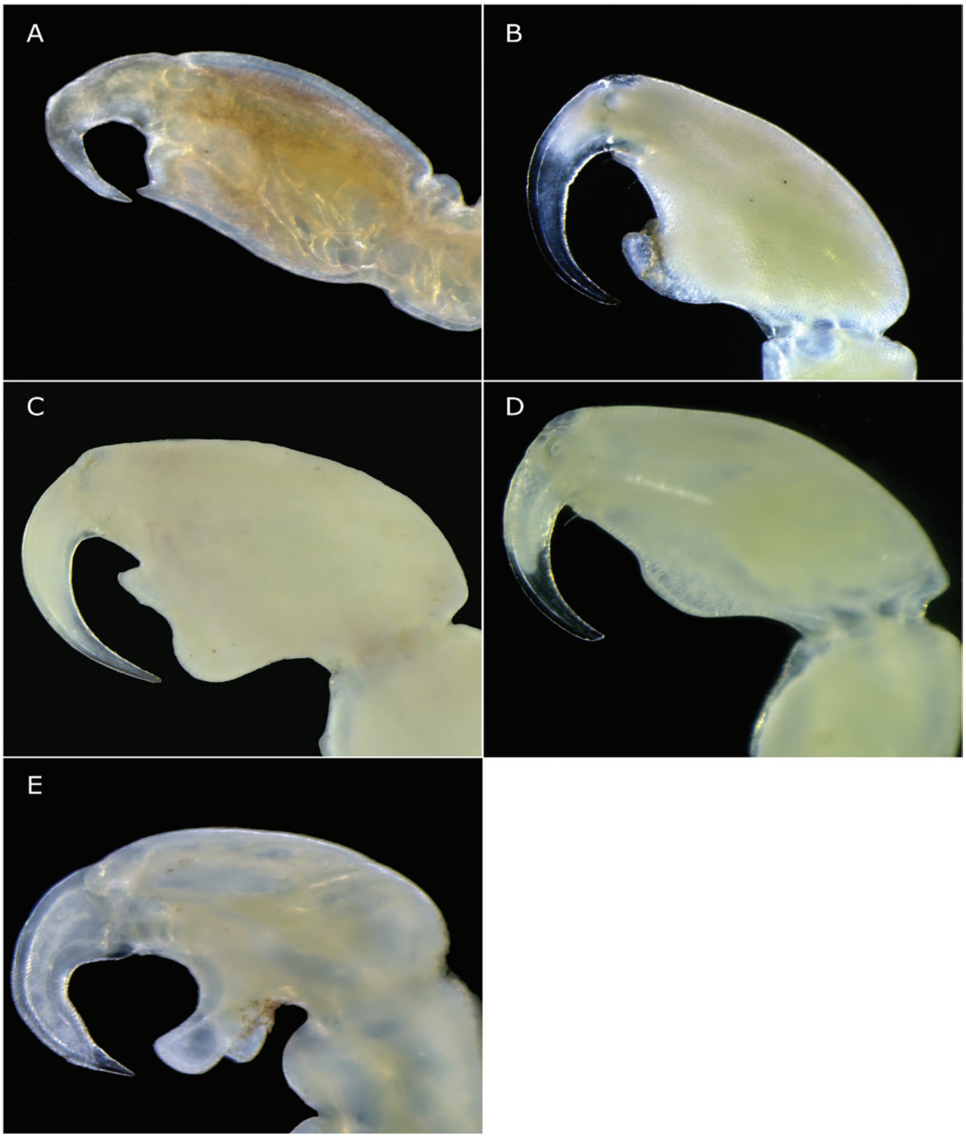


Figure 13. A–E, Character 47. A, palm of gnathopod 1 with minute acute process (*Syncyamus ilheusensis*). B, palm of gnathopod 1 with a broad proximal expansion (*Cyamus gracilis*). C, palm of gnathopod 1 with a lunate expansion (*Cyamus boopis*). D, palm of gnathopod 1 with an elongate expansion (*Cyamus ovalis*). E, palm of gnathopod 1 with a central bilobed expansion (*Neocyamus physeteris*).

species (clade 7): characters from its mouthparts [S7(1), S9(0)] and pereon [S21(1), S24(2), S33(1), S60(2), S66(1) and S67(1)].

Clade 7, the *Cyamus s.s.* group, is supported by four non-homoplastic synapomorphies: Ant1 relative to body length [S3(3)], posterolateral margins of Per3 and Per4 of male bearing knoblike processes [S20(1) and S21(1)] and lateral gills mostly 10 times longer than broad [S58(1)], and two homoplastic synapomorphies [S11(0) and S25(0)]. *Cyamus s.s.* is the only Cyamidae genus that has a plesiomorphic state of partly fused inner lobes of LL [S11(0)]. *Cyamus gracilis* and *Cyamus orubraedon* (clade 10) are the sister group of all other *Cyamus*, sharing seven homoplastic synapomorphies [S15(1), S23(1), S36(0), S42(0), S50(0), S52(1) and S53(0)].

The proximity of *Cyamus kessleri* and *C. gracilis* was also observed by Haney (1999), who did not include *C. orubraedon*. Margolis *et al.* (2000) placed *C. kessleri*, *C. orubraedon* and *C. gracilis* in three different subgenera, *Cyamus*, *Mesocyamus* and *Apocyamus* (Fig. 1). *Cyamus kessleri* is the sister group of clade 15, and shares four synapomorphies, one non-homoplastic [S62(1), presence of AG in females] and three homoplastic [S35(1), S38(1) and S40(1)].

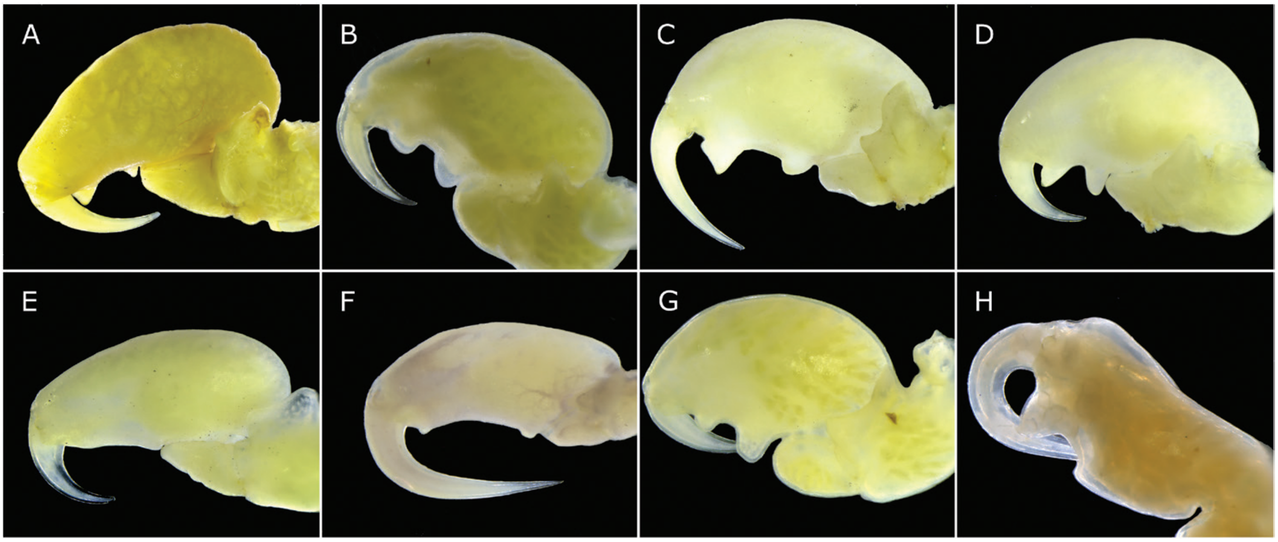


Figure 14. A–D, characters 48–52. A, male, distal palmar process of gnathopod 2 subacute, larger than proximal process (*Cyamus scammoni*). B, male, distal palmar process ovate, shorter than proximal process (*Cyamus kessleri*). C, male, distal palmar process subquadrate, larger than proximal process (*Cyamus erraticus*). D, male, distal palmar process subacute, subequal in length to proximal process (*Cyamus ovalis*). E–H, characters 53–56. E, female, distal and proximal processes lacking (*Cyamus gracilis*). F, female, distal and proximal processes minute, subequal in length (*Cyamus boopis*). G, female, distal process large, but smaller than proximal process (*C. kessleri*). H, female, distal process large and subacute, proximal process lacking (*Syncyamus ilheusensis*).

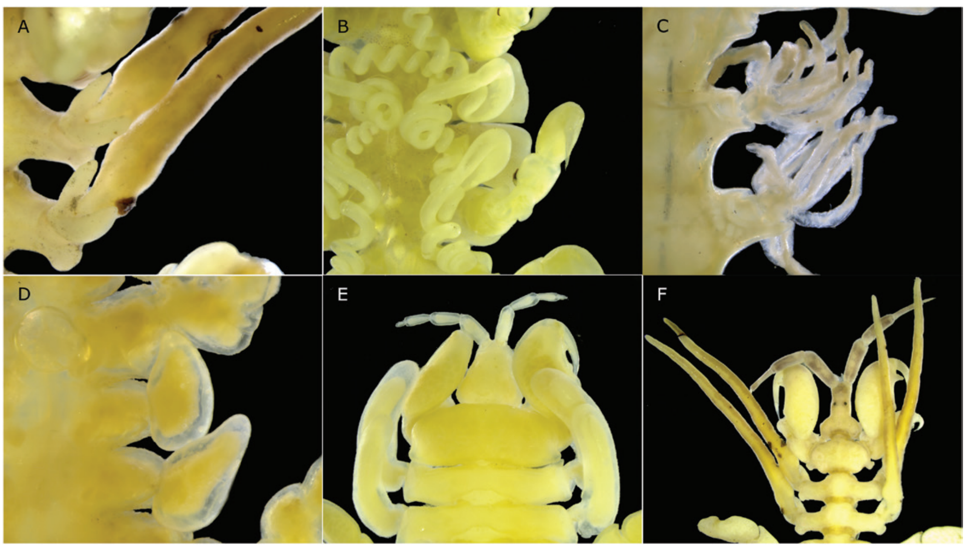


Figure 15. A–C, character 57. A, lateral gills uniramous (*Cyamus boopis*). B, lateral gills biramous (*Cyamus scammoni*). C, lateral gills multiramous (*Neocyamus physeteris*). D, lateral gill short and uniramous, without accessory gill (*Platycyamus thompsoni*), E, F, character 58. E, lateral gills not reaching head margin (*Cyamus monodontis*). F, lateral gills elongate, surpassing head margin (*C. boopis*).

Clade 15 is well supported by seven synapomorphies, including two non-homoplastic: seven with anterolateral acute ventral processes [S41(1) and S44(1)]] and five homoplastic [S3(0), S24(0), S33(1), S37(1) and S47(3)]. The clade includes the species *Cyamus ovalis*, *Cyamus scammoni*, *Cyamus monodontis*, *Cyamus nodosus*, *Cyamus ceti*, *Cyamus eschrichtii*, *Cyamus mesorubraedon*, *Cyamus erraticus*, *C. boopis* and *Cyamus catodontis*.

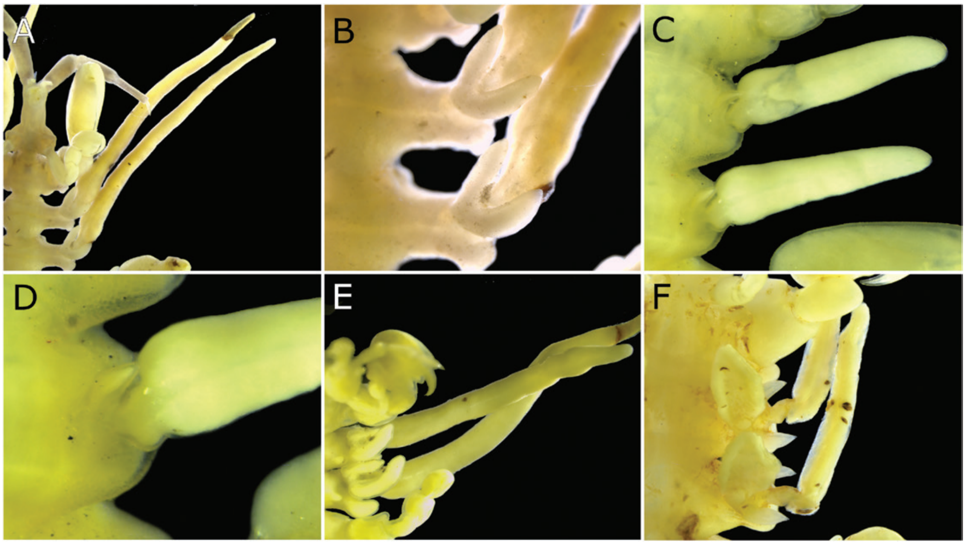


Figure 16. A–F, characters 59–61, accessory gills of males. A, accessory gills symmetrically bilobed, much shorter than lateral gills (*Cyamus boopis*). B, zoom of accessory gill (*C. boopis*). C, accessory gills spinelike, much shorter than lateral gills (***Balaenocyamus balaenopterae* comb. nov.**). D, zoom of accessory gill (***B. balaenopterae* comb. nov.**). E, accessory gills much shorter than lateral gills, asymmetrically bilobed (*Cyamus kessleri*). F, accessory gills subtriangular, shorter than lateral gills (*Isocyamus indopacetus*).

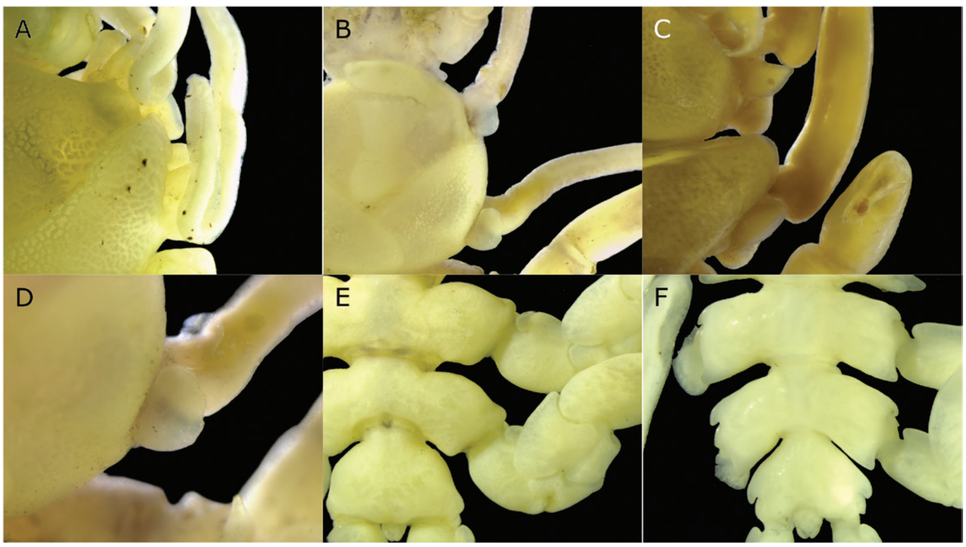


Figure 17. A–D, characters 62 and 63, accessory gills of females. A, accessory gills absent, showing lateral gills only (*Cyamus ovalis*). B, accessory gills of *Cyamus boopis*. C, accessory gills of *Cyamus ceti*, straight. D, accessory gills of *C. boopis* (zoom), with serrated margin. E, F, character 65. E, anterolateral margin of pereonites 5–7 straight, without invagination (*Cyamus erraticus*). F, anterolateral margin of pereonites 5–7 with invagination (*Cyamus gracilis*).

Clade 18 clusters *C. ovalis* + *C. scammoni* and *C. nodosus* + *C. monodontis*, and is supported by three synapomorphies, [S17(1)] Per2 angle recurve of 120°, [S23(1)] knoblike process on the posterolateral margin of Per4 of female and [S35(0)] absence of posterior processes on Per6 of male. *Cyamus ovalis* + *C. scammoni* is also well supported by eight synapomorphies. These are the largest Cyamidae species, and their morphology is quite different from other cyamids. Non-homoplastic synapomorphies include anterolateral margins of Per2 of female 120° [S18(1)] and remarkable oostegite 4 with crevices [S27(2)]. Homoplastic synapomorphies include a robust body [S2(0)], absence of posterior ventral processes on Per6 of female [S38(0)], biramous LG

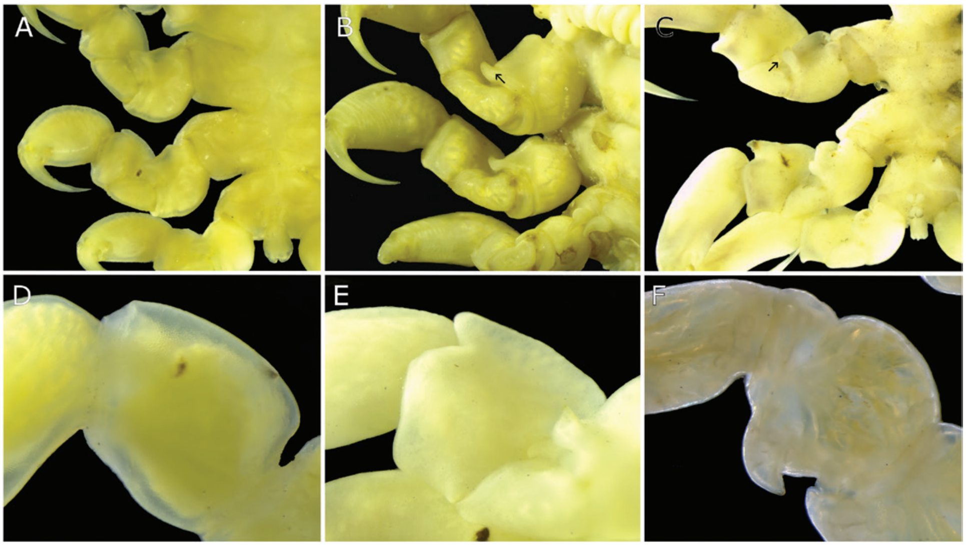


Figure 18. A–C, characters 66 and 67. A, basis of pereopods 5–7 without process on anterodistal margin (*Cyamus monodontis*). B, basis of pereopods 5–7 with process distally directed on anterodistal margin (*Cyamus scammoni*). C, basis of pereopods 5–7 with process centrally directed on anterodistal margin (*Cyamus boopis*). D–F, characters 68 and 69. D, carpus of pereopods 5–7 flat, without any ornamentation (*Cyamus kessleri*). E, carpus of pereopods 5–7 with an anterodistal expansion (*Cyamus erraticus*). F, carpus of pereopods 5–7 with a spinelike process on distal margin (*Syncyamus ilheusensis*).

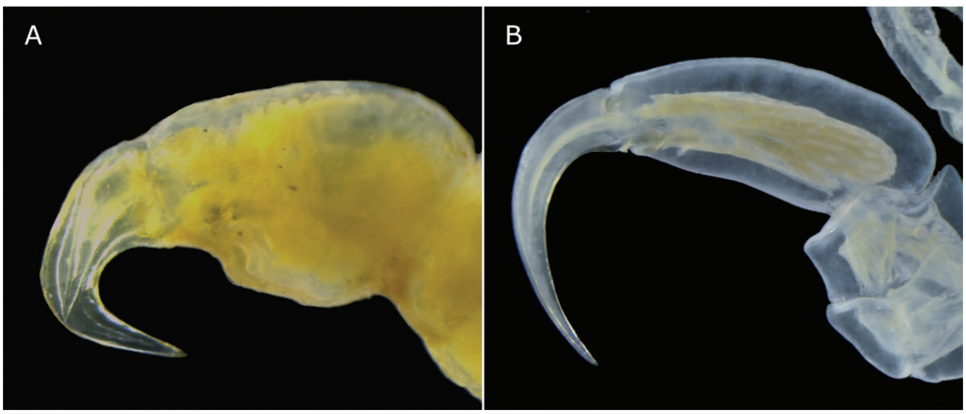


Figure 19. Character 70. Dactylus recurve of pereopods 5–7. A, <50° (*Platycyamus thompsoni*). B, >70° (*Cyamus catodontis*).

[S57(1)], AG of Per3 and Per4 cylindrical [S60(4)], AG of male subequal in length to LG [S61(2)] and absence of AG in females [S62(0)].

Clade 24, composed of *C. nodosus* and *C. monodontis*, is supported by five synapomorphies, including Ant1 length of ¼ of body length [S3(2)], right incisor with six teeth [S9(2)], absence of knoblike process on posterolateral margin of Per3 [S20(0)], acute processes on genital valves [S28(1)] and LG three to six times longer than wide [S58(0)]. *Cyamus nodosus* and *C. monodontis* are exclusive parasites of the large-toothed whales, beluga *D. leucas* and narwhal *M. monoceros*, and they can occur in both host species (Margolis, 1954; Leung, 1967).

Clade 19 comprises *C. ceti*, *C. scammoni*, *C. mesorubraedon*, *C. erraticus*, *C. boopis* and *C. catodontis*. They share knoblike processes on the posterolateral margins of Per2 and Per3 [S19(1) and S21(1)] and a process on the base of Per5–Per7 [S66(1)]. *Cyamus ceti*, type species of *Cyamus*, was described from the bowhead whale *B. mysticetus* and also recorded from grey whales *Eschrichtius robustus*. *Cyamus eschrichtii* was described by Margolis *et al.* (2000) based on material from 20 grey whales, and is the closest species to *C. ceti*. *Cyamus eschrichtii* was coded based on the original description. The clade 25 (*C. ceti* + *C. eschrichtii*) was supported by homoplastic synapomorphies of

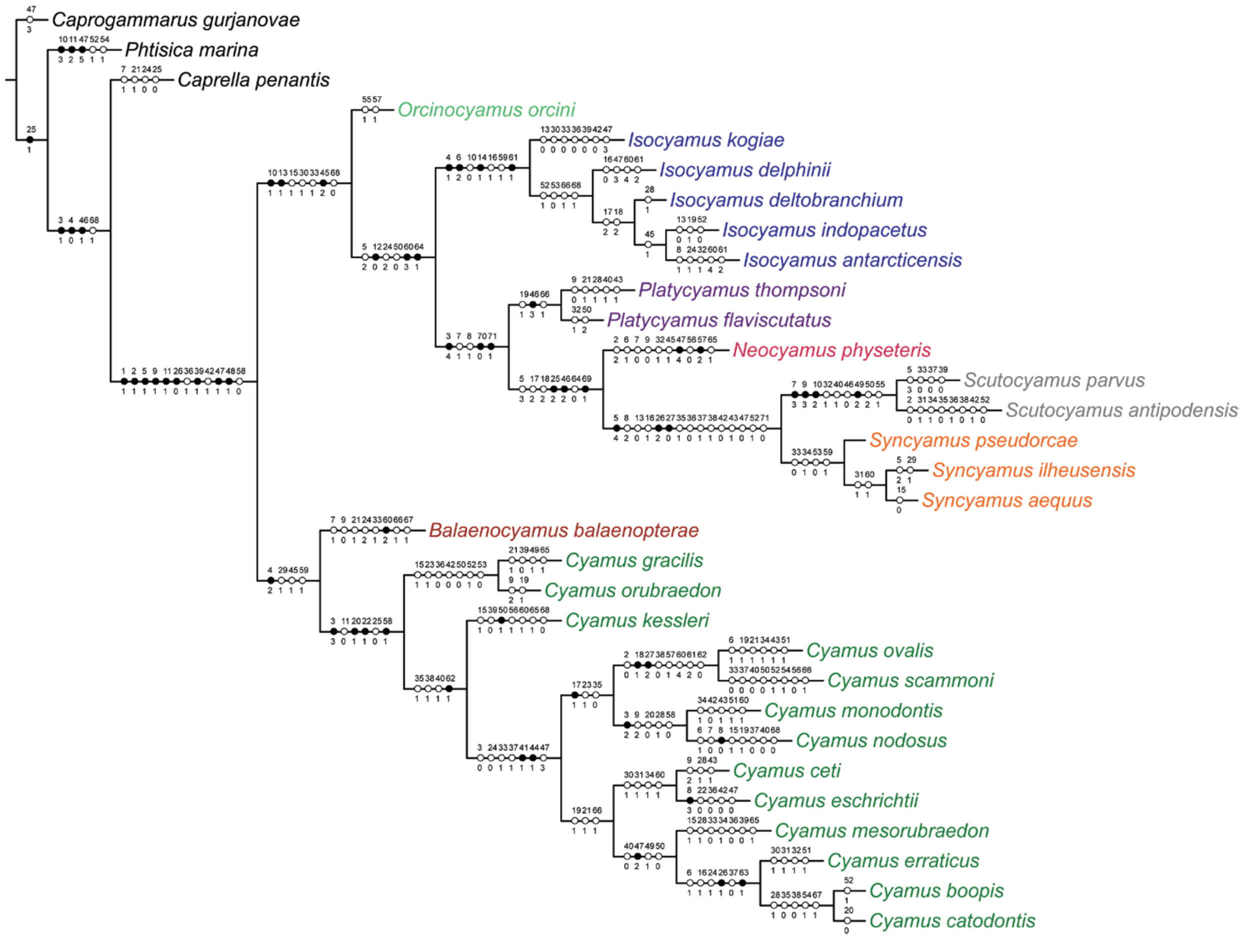


Figure 20. Details of the cladogram obtained using implied weighting. Black circles represent non-homoplastic synapomorphies; white circles represent homoplastic synapomorphies. Numbers above branches represent the characters, and states are represented below.

acute ventral processes [S30(1), S33(1) and S34(1)] and the shape of the AG in males [S60(1)].

Clade 26 is supported by four synapomorphies, one non-homoplastic, [S47(2)] palm of Gn1 with a broad lunate expansion, and three homoplastic: [S40(0)] absence of anterior ventral processes on Per7 of males, [S49(1)] distal process of Gn2 subquadrate and [S50(0)] distal process of Gn2 larger than proximal process. *Cyamus mesorubraedon* was described by Margolis *et al.*, (2000) based on three specimens co-occurring with *C. eschrichtii* (host *E. robustus*). However, the authors stated that the examined material came from *P. macrocephalus*. Examination of that material was not possible, and *C. mesorubraedon* was coded based on the original description.

Clade 28, represented by *C. erraticus*, *C. boopis* and *C. catodontis*, was already discussed because of the morphological similarities described by Margolis (1955); Haney (1999) also recovered the same clade in his analysis. Margolis *et al.* (2000) proposed that each of these species should be placed in different subgenera. Clade 28 is supported by six synapomophies, two non-homoplastic: S26(1), the shape of oostegites 3 and S63(1), shape of accessory gills of female, and four homoplastic: S6(1), S16(1), S24(1) and S37(0). Clade 29 (*C. boopis* + *C. catodontis*) was supported by five homoplastic synapomorphies: S28(1) presence of acute process on the posterolateral margin of the genital valve, S35(0) absence of posterior ventral processes on Per6 of male, S38(0) absence of posterior ventral processes on Per6 of female, S54(1) minute proximal process of propodus of Gn2 of female and S67(1) process ventrally directed on the anterodistal margin of basis of P5–P7. Previous authors commented on the similarities between *C. catodontis* and *C. bahamondei* Buzeta, 1963, both ectoparasites of sperm whales (Stock, 1973; Fransen & Smeenk, 1991; Haney, 1999), stating that they are possibly the same species. Haney (1999) examined the type material of both species and concluded that *C. bahamondei* is a junior synonym of

Table 3. Character matrix with 31 terminal taxa and 71 morphological characters used in the analysisNumerals within the matrix represent the character states listed and discussed in the results, (A) polymorphic states 0 and 1, (?) missing data, and (–) no applicable character.

		1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Phtisica marina	0203002223	2100000000	0001131000	0000000000	-00-0050--	01110?000-	-0-000-001	0
Caprogammarus gurjanovae	020300222?	0102000000	00010??0?0	0000000000	-00-0030--	00100?000-	-0-010-001	?
Caprella penantis	0210001220	0100000000	1000031000	0000000000	-00-0100--	00100?000-	-0-000-101	?
Cyamus balaenopterae	1112101200	1100000000	1002101010	0010010010	-10-111102	0010020012	00-0011101	0
Cyamus boopis	1102112210	0100A10011	1101011111	0110010010	-10-112110	0111020110	0110011101	0
Cyamus catodontis	1102112210	0100010010	1101011110	0010010010	-10-112110	0011020110	0110011101	0
Cyamus ceti	1102102220	0100000011	1100001111	1011111111	1111113102	00?00?0111	0100010101	0
Cyamus erraticus	1102112210	0100A10011	1101011011	1110110110	-10-112110	1010020110	0110010101	0
Cyamus eschrichtii	11021?2310	0100000?11	?0?0001011	1011101111	100-110102	00????0111	0100010101	0
Cyamus gracilis	1132102210	0100100001	1111001010	0000000000	-00-111110	010-?-0110	00-010-101	0
Cyamus kessleri	1132102210	0100100001	0101001010	0000110101	010-111101	0010010111	010010-001	0
Cyamus mesorubraedon	11021?2210	0100100?11	?1?00?11?0	0001101100	-10-112110	00????0110	0100110101	0
Cyamus monodontis	1122102220	0100001000	0110001110	0011011111	1011113102	1010020011	010000-101	0
Cyamus nodosus	1122110020	0100101010	0110001110	0010010110	-10-113102	0010020010	010000-001	0
Cyamus orubraedon	1132102220	0100100?11	?1?1?????0	0000000010	-00-111100	01????0110	0??000-101	0
Cyamus ovalis	1002112210	0100001111	1110002010	0011011011	1111113102	1010021114	20-000-101	0
Cyamus scammoni	1002102210	0100001101	0110002010	0000010010	-10-113100	0111001114	20-0010101	0
Isocyamus antacticensis	1111222210	1011112200	0001001001	0110010010	-10-111100	0111000014	10-1010101	0
Isocyamus delphinii	1111222210	1011100000	0002101001	0010010010	-10-213100	010-?-0014	20-1010101	0
Isocyamus deltobranchium	1111222210	1011112200	0002101101	0010010010	-10-211100	010-?-0013	10-1010101	0
Isocyamus indopacetus	1111222210	1001112?10	?0?2?????1	0?100???10	-???111100	00????0013	1??1010101	0
Isocyamus kogiae	1111222210	1001110011	0????01001	0000000000	-00-111100	0010000013	00-100-001	0
Neocyamus physeteris	1240310101	1010102200	0002201001	0110010010	-10-124100	001000200-	-0-010-010	2
Orcinocyamus orcini	1110102211	1110100?00	00?1101001	0010010010	-10-211102	001012100-	-0-000-001	0
Platycyamus flaviscutatus	10404011?1	1010100011	1????010010	110010010	-10-233100	001002000-	-0-100-000	2
Platycyamus thompsoni	1140401101	1010100010	1002101101	0010010011	0110231100	001002000-	-0-1010000	2
Scutocyamus antipodensis	1140403232	1000112200	0????20001	1110110111	1111203122	011112000-	-0-000-010	1
Scutocyamus parvus	1140403232	1000112200	0002220001	0100100101	0010200122	011112000-	-0-000-010	1
Syncyamus aequus	1140401221	1000112200	0????20001	1001101110	-010220100	010-0-0011	00-000-010	0
Syncyamus ilheusensis	1140201211	1000112200	0002220011	1001101110	-010220100	010-0-0011	00-000-010	1
Syncyamus pseudorcae	1140401221	1000112200	0????20001	0001101110	-010220100	010-0-0013	00-000-010	0

C. catodontis, accepted herein. Similarities between *C. boopis* and *C. catodontis* were also commented on by Margolis (1955), Haney (1999) and Iwasa-Arai *et al.* (2017) and could have led to previous misidentifications of these species in their specific hosts.

The subgenera relationships within *Cyamus* suggested by Margolis *et al.* (2000) were not recovered in our analysis. One of the most substantial differences was that *B. balaenopterae* comb. nov. and *C. boopis* were grouped together in the same subgenera,

Table 4. List of recorded cetacean hosts for Cyamidae

Cyamid	Host	Reference
Cyamus balaenopterae	*Balaenoptera physalus*	Barnard, 1931; Leung, 1965
	Balaenoptera musculus	Barnard, 1931
	Balaenoptera acutorostrata	Berzin & Vlasova, 1982
Cyamus boopis	*Megaptera novaeangliae*	Lütken, 1870; Sars, 1895; Hurley, 1952; Margolis, 1955; Leung, 1965; Rowntree, 1996; Carvalho *et al.*, 2010; Iwasa-Arai *et al.*, 2017
	Eubalaena australis	Iwasa-Arai *et al.*, 2017
Cyamus catodontis	*Physeter macrocephalus*	Margolis, 1955; Leung, 1965; Berzin & Vlasova, 1982
Cyamus ceti	*Eschrichtius robustus*	Dall, 1872; Leung, 1965, 1976
	Balaenoptera mysticetus	Leung, 1965; Margolis *et al.*, 2000; Callahan, 2008
Cyamus erraticus	*Eubalaena australis*	Roussel de Vauzème, 1834; Sawaya, 1938; Leung, 1965; Kaliszewska *et al.*, 2005; Iwasa-Arai *et al.*, 2017c
Cyamus eschrichtii	*Eubalaena glacialis*	Margolis, 1955; Leung, 1965; Rowntree, 1996; Kaliszewska *et al.*, 2005
Cyamus gracilis	*Eubalaena australis*	Roussel de Vauzème, 1834; Kaliszewska *et al.*, 2005; Iwasa-Arai *et al.*, 2017
	Eubalaena glacialis	Leung, 1965; Rowntree, 1996; Kaliszewska *et al.*, 2005
Cyamus kessleri	*Eschrichtius robustus*	Leung, 1965, 1967, 1976; Berzin & Vlasova, 1982; Callahan, 2008
Cyamus mesorubraedon	*Physeter macrocephalus* or *Eschrichtius robustus*	Margolis *et al.*, 2000
Cyamus monodontis	*Delphinapterus leucas*	Lütken, 1893
	Monodon monoceros	Lütken, 1870; Leung, 1965; Berzin & Vlasova, 1982
Cyamus nodosus	*Delphinapterus leucas*	Margolis, 1954; Berzin & Vlasova, 1982
	Monodon monoceros	Margolis, 1955; Leung, 1965
Cyamus orubraedon	*Berardius bairdii*	Waller, 1989; Margolis *et al.*, 2000
Cyamus ovalis	*Eubalaena australis*	Roussel de Vauzème, 1834; Sawaya, 1938; Margolis, 1955; Kaliszewska *et al.*, 2005; Iwasa-Arai *et al.*, 2017
	Eubalaena glacialis	Margolis, 1955; Leung, 1965; Rowntree, 1996; Kaliszewska *et al.*, 2005
	Physeter macrocephalus	Leung, 1965
Cyamus scammoni	*Eschrichtius robustus*	Margolis, 1955; Leung, 1965, 1967, 1976; Berzin & Vlasova, 1982; Callahan, 2008
Isocyamus antarcticensis	*Orcinus orca*	Berzin & Vlasova, 1982
Isocyamus delphinii	*Delphinus delphis*	Berzin & Vlasova, 1982; Sedlak-Weinstein, 1992a
	Pseudorca crassidens	Bowman, 1955; Sedlak-Weinstein, 1991
	Graumpus griseus	Chevreux, 1913
	Globicephala macrorhynchus	Sedlak-Weinstein, 1992a
	Globicephala melas	Lincoln & Hurley, 1974b; Berzin & Vlasova, 1982
	Steno bredanensis	Lincoln & Hurley, 1974b
	Mesoplodon europaeus	Balbuena & Raga, 1991; Sedlak-Weinstein, 1992a
	Lagenorhynchus albirostris	Fransen & Smeenk, 1991; Sedlak-Weinstein, 1992a
	Peponocephala electra	Wardle *et al.*, 2003
	Phocoena phocoena	Berzin & Vlasova, 1982; Fransen & Smeenk, 1991; Sedlak-Weinstein, 1992a
	Orcinus orca	Sedlak-Weinstein, 1992a
	Tursiops truncatus	Balbuena & Raga, 1991; Sedlak-Weinstein, 1992a
Isocyamus deltobranchium	*Globicephala macrorhynchus*	Sedlak-Weinstein, 1992b
	Globicephala melas	Sedlak-Weinstein, 1992b
Isocyamus indopacetus	*Indopacetus pacificus*	Iwasa-Arai, Carvalho & Serejo, 2017
Isocyamus kogiae	*Kogia breviceps*	Sedlak-Weinstein, 1992a; Martin & Heyning, 1999

Table 4. Continued

Cyamid	Host	Reference
Neocyamus physeteris	*Physeter macrocephalus*	Leung, 1965; Lincoln & Hurley, 1974b; Berzin & Vlasova, 1982
	Phocoenoides truei	Leung, 1965
Orcinocyamus orcini	Orcinus orca	Leung, 1970b; Margolis *et al.*, 2000
Platycyamus flaviscutatus	*Berardius bairdii*	Waller, 1989; Margolis *et al.*, 2000
Platycyamus thompsoni	*Hyperoodon ampullatus*	Lütken, 1870; Leung, 1965
	Hyperoodon planifrons	Haney, 1999
	Mesoplodon grayi	Sedlak-Weinstein, 1991
Scutocyamus antipodensis	*Cephalorhynchus hectori*	Lincoln & Hurley, 1980
	Lagenorhynchus obscurus	Haney, 1999
Scutocyamus parvus	*Lagenorhynchus albirostris*	Lincoln & Hurley, 1974a; Fransen & Smeenk, 1991
Syncyamus aequus	*Delphinus delphis*	Lincoln & Hurley, 1981
	Stenella coeruleoalba	Lincoln & Hurley, 1981; Mariniello *et al.*, 1994
	Stenella longirostris	Sedlak-Weinstein, 1991
	Tursiops truncatus	Lincoln & Hurley, 1981; Raga 1988
Syncyamus ilheusensis	*Globicephala macrorhynchus*	Haney *et al.*, 2004; Iwasa-Arai, Carvalho & Serejo, 2017
	Peponocephala electra	Iwasa-Arai, Carvalho & Serejo, 2017
Syncyamus pseudorcae	*Pseudorca crassidens*	Bowman, 1955; Sedlak-Weinstein, 1991
	Stenella clymene	Carvalho *et al.*, 2010

whereas *B. balaenopterae* comb. nov. was observed as basal to *Cyamus s.s.*, with *C. boopis* closely related to *C. catodontis* and *C. erraticus*. Therefore, the subgenera classification proposed by Margolis *et al.* (2000) was rejected.

For an overall comparison of hosts and cyamid relationships, we based our observations on the phylogenetic study of Cetacea by Gatesy *et al.* (2013), which included fossil records and molecular data. Accoring to Gatesy *et al.* (2013), the family Balaenidae is the most plesiomorphic clade of Mysticeti, and Monodontidae is the most apomorphic clade within Odontoceti, contrary to Messenger & McGuire (1998), who suggested that *B. mysticetus* is closely allied with monodontids, facilitating the dispersal of cyamids from the bowhead whale to narwhal and/or belugas. Apparently, the transmission of cyamids between different host species is frequent, and single records of hosts might be overlooked (Iwasa-Arai *et al.*, 2017). Thus, it is difficult to analyse coevolutionary processes, yet more analysis is needed to compare host and cyamid relationships.

This study used novel characters, such as comparative ratios of gnathopods, gills and antennae, oostegites and acute ventral processes, for a phylogenetic assessment. Overall, the topology of our analysis corroborates previous analyses, whereas the relationships within *Cyamus s.s.* revealed deviate from previous studies. Molecular assessments of Cyamidae phylogeny may help to solve these problems. However, most of the available material is quite old and unsuitable for DNA extraction. For now, partnerships between systematists and cetacean monitoring organizations are the best option for collecting fresh samples. Finally, this study compiled previous, unpublished work on Cyamidae to be the first widely disseminated phylogenetic analysis of the family to use cladistic methods.

SYSTEMATICS

Infraorder Corophiida Leach, 1814 (*sensu* Lowry & Myers, 2013)

Superfamily Caprelloidea Leach, 1814

Family Cyamidae Rafinesque, 1815

Diagnosis: Body dorsoventrally depressed, usually smooth dorsally and often with adhesion acute processes ventrally. Antenna 1 and 2 number of articles reduced. Mouthparts reduced, adapted for parasitism; mandibles lacking palp, molar rudimentary. Gnathopods 1 and 2 strongly subchelate, unequal in size, dimorphic. Pereopods 3 and 4 absent; pereonites 3 and 4 with lateral coxal gills, usually with accessory gills on their base. Females with oostegite plates on Per3 and 4. Pereonites 5–7 robust with large dactyli for adhesion. Pleon very reduced, with small pleopods in males.

Type genus: Cyamus Latreille, 1796.

Habitat: Ectoparasites exclusive of Cetacea.

Subfamilies: Isocyaminae subfam. nov. and Cyaminae subfam. nov.

Subfamily **Isocyaminae subfam. nov.**

Diagnosis: Antenna 1 without setal arrangement or with a continuous band of setae on terminal article. Antenna 2 reduced, usually with fewer than four articles. *Lacinia mobilis* of right mandible multituberculate without tooth (except *Isocyamus*). Distal process of gnathopod 2 palm of female usually subequal in length to proximal process. Accessory gills of females absent.

Type genus: *Isocyamus* Gervais & Van Beneden, 1859.

Remarks: Species of this subfamily are generally smaller and parasitize small delphinids and ziphiids. *Physeter macrocephalus* is the only species to host whale lice from both subfamilies herein proposed.

Included genera: *Isocyamus* Gervais & Van Beneden, 1859, *Orcinocyamus* Margolis, McDonald & Boulsfield, 2000, *Neocyamus* Margolis, 1955, *Platycyamus* Lütken, 1870, *Scutocyamus* Lincoln & Hurley, 1974 and *Syncyamus* Bowman, 1955.

Isocyamus Gervais & Van Beneden, 1859

Diagnosis: Antenna 1 with a continuous band of setae on terminal article; antenna 2 longer than terminal article of antenna 1. *Lacinia mobilis* of right mandible with teeth; maxilliped inner lobes rounded. Accessory gills present, usually sausage shaped or subtriangular, large; spinelike process present on the base of lateral gills.

Type species: *Isocyamus delphinii* (Guérin-Méneville, 1836).

Remarks: *Isocyamus* is found in multiple host taxa. *Isocyamus delphinii* is the most widespread species, found in various delphinids, including the orca *O. orca* and bottlenose dolphin *T. truncatus* (Wardle *et al.*, 2003). *Isocyamus indopacetus* Iwasa-Arai & Serejo, 2017 is found on the Longman's beaked whale *I. pacificus*, one of the least studied cetaceans (Iwasa-Arai *et al.*, 2017).

Species: *Isocyamus delphinii* (Guérin-Méneville, 1836), *I. antarcticensis* Vlasova, 1982, *I. deltobrachium* Sedlak-Weinstein, 1992, *I. kogiae* Sedlak-Weinstein, 1992, *I. indopacetus* Iwasa-Arai & Serejo, 2017.

Orcinocyamus Margolis, 1955

Diagnosis: Antenna 1 four-articulated; antenna 2 small, four-articulated. Maxilliped lacking palps. Lateral gills bilobed; accessory gills absent. Pereonites 3 and 4 of male subequal in length to Per5; Per5–Per7 each bearing a pair of acute ventral processes; Per5–Per7 process on basis absent.

Type species: *Orcinocyamus orcini* (Leung, 1970).

Remarks: *Orcinocyamus orcini* was described by Leung (1970b) from *O. orca* and transferred to *Orcinocyamus* based on differing morphology and the semi-phyletic analysis performed by Margolis *et al.*, (2000), corroborated by Haney (1999) and the present study.

Species: *Orcinocyamus orcini* (Leung, 1970).

Neocyamus Margolis, 1955

Diagnosis: Body slender. Antenna 1 short, four-articulated, without setal arrangement; antenna 2 very small, two-articulated. Left *lacinia mobilis* seven dentate; right *lacinia mobilis* multituberculate without tooth. Maxilliped without palps. Palm of gnathopod 1 with a unique central bilobed expansion. Pereonites 3 and 4 very narrow, with multiramous lateral gills; accessory gills absent. Females with pleopods on pleon.

Type species: *Neocyamus physeteris* Margolis, 1955.

Remarks: *Neocyamus physeteris* is found in sperm whales *P. macroephalus*, the largest odontocete. *Neocyamus physeteris* is also the largest species of Odontocyaminae subfam. nov.

Species: *Neocyamus physeteris* Margolis, 1955.

Platycyamus Lütken, 1870

Diagnosis: Antenna 1, short, four-articulated, without setal arrangement on terminal article. Antenna 2 small, three-articulated. Maxilliped without palps. Gnathopod 1 palm very short, vertical, dactyli very recurved; gnathopod 2 palm short, subequal in length to gnathopod 1. Lateral gills short, subtriangular; accessory gills absent. Dactyli of Per5–Per7 very curved.

Type species: *Platycyamus thompsoni* (Gosse, 1855).

Remarks: *Platycyamus* is recognized as a genus ectoparasitic of beaked whales; it was previously believed that only beaked whales host this genus. However, in more recent studies ziphiid whales have been shown to host *Platycyamus*, *Isocyamus* and *Cyamus*.

Species: Platycyamus thompsoni (Gosse, 1855), *P. flaviscutatus* Waller, 1989.

SCUTOCYAMUS LINCOLN & HURLEY, 1974

Diagnosis: Body small, stout. Antenna 1 very reduced, two-articulated; antenna 2 minute, one-articulated. Gnathopod 1 simple, palm straight; gnathopod 2 without palm, with a particular crevisse bearing a spine. Pereonites 3 and 4 very short; lateral gills uniramous; accessory gills lacking. Oostegite plates boot shaped.

Type species: Scutocyamus parvus Lincoln & Hurley, 1974.

Remarks: Scutocyamus is a genus of small, temperate water dolphins, and its distribution is largely unknown. *Scutocyamus parvus* was reported from the white-beaked dolphin *Lagenorhynchus albirostris* from the North Sea, and later on, *S. antipodensis* was described from Hector's dolphins *Cephalorhynchus hectori* from New Zealand.

Species: Scutocyamus parvus Lincoln & Hurley, 1974; *S. antipodensis* Lincoln & Hurley, 1980.

SYNCYAMUS BOWMAN, 1955

Diagnosis: Antenna 1 short, four-articulated. Maxillipeds triangular, fused basally, palps lacking. Gnathopod 1 palm short, dactyli very recurved; gnathopod 2 propodus robust, palm short. Pereonites 3 and 4 short, with uniramous lateral gills. Accessory gills present. Oostegites plates 3–4 boot -shaped.

Type species: Syncyamus pseudorcae Bowman, 1955.

Remarks: Syncyamus is a widespread genus, apparently related to warm water dolphins.

Species: Syncyamus pseudorcae Bowman, 1955, *S. aequus* Lincoln & Hurley, 1981 and *S. ilheusensis* Haney, De Almeida & Reis, 2004.

CYAMINAE SUBFAM. NOV.

Diagnosis: Body usually large. Antenna 1 with multiple grouping of setae on terminal article; antenna 2 with four articles. *Lacinia mobilis* multituberculate with variation in the number of teeth. Lower lip with inner lobes partly fused (except *B. balaenopterae*). Lateral gills elongate. Accessory gills of male always present. Accessory gills of female usually present. Genital valve anterior margin setose. Carpus of pereopods usually with a process on posterior margin. Dactyli of pereopods slightly curved.

Type genus: Cyamus Latreille, 1796.

Remarks: This subfamily was erected based on the synapomorphies of *Balaenocyamus* gen. nov. and *Cyamus*, which were previously considered to be a single genus. Species of this subfamily are generally larger, host specific, and parasitize baleen whales and large odontocetes of the families Monodontidae, Ziphiidae and Physeteridae.

Genera: Cyamus Latreille, 1796, *Balaenocyamus* gen. nov.

***BALAENOCYAMUS* GEN. NOV.**

Diagnosis: Incisor of left mandible with six teeth, right incisor with seven teeth; lower lips inner lobes fully fused. Palm of gnathopod 1 with a broad proximal expansion. Pereonites 3 and 4 narrower than pereonite 5 in males and subequal in width in females. Pereonite 4 of male without posterolateral knoblike process. Accessory gills spinelike in males and absent in females.

Type species: Cyamus balaenopterae (KH Barnard, 1931).

Etymology: The specific epithet refers to the hosts associated with this genus, the family Balaenopteridae Gray, 1864.

Remarks: In contrast to *Cyamus* species, which are usually host specific, *Balaenocyamus* gen. nov. is more widespread and is found on large baleen whales of the family Balaenopteridae, such as *Balaenoptera musculus*, *B. physallus* and *B. acutorostrata*. *Balaenocyamus* gen. nov. differs from *Cyamus*, by: (1) incisor with six teeth (vs. five teeth); (2) lower lip inner lobes fully fused (vs. partly fused); (3) pereonites 3 and 4 narrower than pereonite 5 in males and subequal in width in females (vs. pereonites 3 and 4 wider or subequal in width to pereonite 5 in males and wider in females); (4) accessory gills spinelike in males and absent in females (vs. accessory gills usually bilobed in males and usually present in females); and (5) pereonite 4 of male straight, without posterolateral knoblike process (vs. pereonite 4 of male with a posterolateral knoblike process). Haney (1999) also found *B. balaenopterae* comb. nov. to be a basal group of *Cyamus* and commented on its plesiomorphic character states, suggesting *B. balaenopterae* comb. nov. to be an intermediate between Cyamidae and Caprellidae, according to its general morphology.

Although the position of *B. balaenopterae* within Mysticyaminae subfam. nov. has low statistical support (clade 3), the subfamily was recovered in all analyses, and most of the representatives of Mysticyaminae subfam. nov. are found parasitizing mysticetes.

Species: Cyamus balaenopterae (KH Barnard, 1931).

CYAMUS LATREILLE, 1796

Diagnosis: Antenna 1 usually long, with four articles. Incisor of left mandible usually with five teeth; lower lip partly fused. Pereonites 3 and 4 wider or subequal in width to pereonite 5 in males and wider in females. Pereonite 4 of male with a posterolateral knoblike process. Accessory gills of female usually present, oval.

Type species: Cyamus ceti (Linnaeus, 1758).

Remarks: Most species of *Cyamus* are host specific, and some whales can host more than one *Cyamus* species. It is the largest genus and is the most studied, owing to commercial whaling of and large amounts of parasites on slow-moving cetaceans.

Species: Cyamus ceti (Linnaeus, 1758), *C. boopis* Lütken, 1870, *C. catodontis* Margolis, 1954, *C. erraticus* Roussel de Vauzème, 1834, *C. eschrichtii* Margolis, McDonald & Boulsfield, 2000, *C. gracilis* Roussel de Vauzème, 1834, *C. kessleri* A Brandt, 1873, *C. mesorubraedon* Margolis, McDonald & Boulsfield, 2000, *C. monodontis* Lütken, 1870, *C. nodosus* Lütken, 1860, *C. ovalis* Roussel de Vauzème, 1834 and *C. scammoni* Dall, 1872.

KEY TO CYAMIDAE GENERA

1. Antenna 1 with multiple groupings of setae on terminal article, maxilliped palps usually present, anterior margin of genital valves setose, penes stout (Fig. 4C) .... Cyaminae subfam. nov. 2
– Antenna 1 without multiple groupings of setae on terminal article, maxilliped palps always absent, anterior margin of genital valves smooth, penes usually narrow (Fig. 4A, B) ...... Isocyaminae subfam. nov. 3
2. Pereonite 4 of male with a posterolateral knoblike process, pereonites 3 and 4 of female wider than pereonite 5, lower lip inner lobes partly fused, accessory gills of male usually bilobed, ectoparasite of large odontocetes and mysticetes (Figs 7A, J and 9D) .... *Cyamus* Latreille, 1796
– Pereonite 4 of male without a posterolateral knoblike process, pereonites 3 and 4 of female subequal in width to pereonite 5, lower lip inner lobes fully fused, accessory gills of male spinelike; lateral gills uniramous, ectoparasites of rorqual whales (Figs 7B, I, 9E and 16C, D) .... *Balaenocyamus* gen. nov.
3. Accessory gills of male present 4
– Accessory gills of male absent 5
4. Pereonites 3 and 4 of female subequal in width to pereonite 5, spinelike process on lateral gills base, ectoparasites of several odontocetes .... *Isocyamus* Gervais & Van Beneden, 1859
– Pereonites 3 and 4 of female narrower than pereonite 5, spinelike process on lateral gills base absent, ectoparasites of warm water dolphins .... *Syncyamus* Bowman, 1955
5. Lateral gills uniramous 6
– Lateral gills multiramous (more than one rami) 7
6. Body slender, lateral gills short, subtriangular, ectoparasites of beaked whales (Fig. 15D) .... *Platycyamus* Lütken, 1870
– Body stout, lateral gills short, cylindrical, ectoparasites of small temperate water dolphins .... *Scutocyamus* Lincoln & Hurley, 1974
7. Lateral gills multiramous (more than five rami), pleopods of female present, ectoparasites of large odontocetes (Figs 9F and 15C) .... *Neocyamus* Margolis, 1955
– Lateral gills birramous, pleopods of female absent, ectoparasites of large delphinids .... *Orcinocyamus* Margolis, McDonald & Boulsfield, 2000

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