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Copepod Parasites of the Fatheads (Pisces, Psychrolutidae) and Their Implication on the Phylogenetic Relationships of Psychrolutid Genera

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ABSTRACT—Nine species of psychrolutids kept in the Marine Zoology of Hokkaido University were found to carry eight species of copepod parasites. The parasites and their hosts are: *Bobkabata kabatabobbus* Hogans and Benz, 1990 on *Malacocottus zonurus* Bean; *Chondracanthus parvus* n. sp. on *Eurymen gyrinus* Gilbert and Burke; *Chondracanthus yabei* n. sp. on *Dasycottus setiger* Bean and *M. zonurus*; *Ch. yanezi* Atria, 1980 on *Psychrolutes phrictus* Stein and Bond; *Caligus similis* n. sp. on *Neophrynichthys latus* (Hutton); *Clavella adunca* (Strøm, 1762) on *M. zonurus*; *Neobrachiella amphipacifica* Ho, 1982 on *Ambophthalmos angustus* (Nelson), *Cottunculus* sp., *D. setiger*, *Ebinania brephocephala* (Jordan and Starks), *E. vermiculata* Sakamoto, and *P. phrictus*; and *Naobranchia occidentalis* Wilson, 1915 on *D. setiger* and *M. zonurus*. *Chondracanthus parvus* is closest to *Ch. deltoideus* Fraser, 1920, but differs from it in having only one pair of small knobs on the head and carrying a pair of lateral processes on the second pediger. *Chondracanthus yabei* resembles *Ch. yanezi* Atria, 1980, but can be distinguished from it by the presence of three, low protrusions on the mid-dorsal surface of the trunk; besides, maxillule also shows difference. As the name indicates, *C. similis* resembles several species of *Caligus* that bear a short abdomen and a formula of I; IV on the exopod of leg 4. However, it can be separated from them by the combination of the following characters: a genital complex distinctly smaller than the cephalothoracic shield, a pair of relatively short caudal rami, a smooth dentiform process on maxillule, and a pair of truncate tines on sternal furca.

Analysis of the occurrence of *Chondracanthus* on the psychrolutid fishes shows that the phylogeny of *Chondracanthus* is in congruence with that of the Psychrolutidae. It implies that parasitism of *Chondracanthus* occurred after the *Dasycottus* clade diverged off the main stock of the Psychrolutidae and the occurrence of *Ch. yabei* on *D. setiger* is resulted from a later colonization.

Key words: parasitic copepods, *Chondracanthus*, psychrolutid fishes, coevolution

INTRODUCTION

Psychrolutidae is a small family of marine fishes comprising 40 species classified in nine genera (Froese and Pauly, 2004). In the late 1980s, one of us (KN) examined intermittently for copepods parasitic on the psychrolutid fishes kept in the collection of the Marine Zoology of Hokkaido University. Altogether 400 fishes belonging to 13 species in eight genera were examined. The fishes were collected from the Bering Sea, Gulf of Alaska, Aleutian Islands, Kuril Islands, Kamchatka, Sea of Okhotsk, New Zealand, and Patagonia, in addition to Japan.

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Eight species of parasitic copepods were recovered from nine species of the fatheads (Psychrolutidae) kept in the collection of the Marine Zoology of Hokkaido University (Table 1). The four species that failed to yield copepod parasites are: *Cottunculus ganulosus* Karrer, *Malacocottus gibber* Sakamoto, *Psychrolutes paradoxus* Günther, and *P. inermis* (Vaillant). Five of the eight species of parasites are known and the remaining three species are new to science, with two species of *Chondracanthus* and one species of *Caligus*. This is the first time to record the occurrence of *Caligus* from the psychrolutids. The five know species are: *Bobkabata kabatabobbus* Hogans and Benz (Hogans and Benz, 1990), *Chondracanthus yanezi* Atria (Ho, 1982), *Clavella adunca* (Strøm) (Kabata, 1979), *Naobranchia occidentalis* Wilson (Ho and Kim, 1995), and *Neobrachiella*

Table 1. Psychrolutid fishes in the collection of the Marine Zoology of Hokkaido University examined and the copepod parasites found.

Hosts (number examined)	Locality	Copepod Parasites
Ambophthalmos angustus (Nelson) (11)	western N Pacific	*Neobrachiella amphipacifica* Ho, 1982
Cottunculus granulosus Karrer (3)	Patagonia	(not found)
Cottunculus sp. (5)	New Zealand	*Neobrachiella amphipacifica* Ho, 1982
Dasycottus setiger Bean (115)	eastern Bering Sea	*Chondracanthus yabei* n. sp.
	eastern Bering Sea; off Usujiri, Hokkaido	*Neobrachiella amphipacifica* Ho, 1982
	eastern Bering Sea	*Naobranchia occidentalis* Wilson, 1915
Ebinania vermiculalata Sakamoto (16)	off Kushiro and Cape Erimo, Hokkaido; off Iwate, Ibaraki and Fukushima, Honshu	*Neobrachiella amphipacifica* Ho, 1982
Ebinania brephocephala (Jordan and Starks) (6)	off Kochi, Shikoku	*Neobrachiella amphipacifica* Ho, 1982
Eurymen gyrinus Gilbert and Burke (26)	off Funka Bay, Hokkaido	*Chondracanthus parvus* n. sp.
Malacocottus gibber Sakamoto (42)	off Ishikawa and Niigata of Honshu; southern Hokkaido	(not found)
Malacocottus zonurus Bean (137)	off Cape Erimo, Hokkaido and off Iwate, Honshu	*Bobkabata kabatabobbus* Hogans and Benz, 1990*
	Gulf of Alaska, Bering Sea, eastern N Pacific; eastern Bering Sea, Aleutian Islands, off Kamchatka, western N Pacific, Sea of Okhotsk	*Chondracanthus yabei* n. sp.
	eastern Bering Sea, Kurile Islands	*Clavella adunca* (Strøm)
	off Kamchatka	*Naobranchia occidentalis* Wilson, 1915
Neophrynichthys latus (Hutton) (8)	New Zealand	*Caligus similis* n. sp.
Psychrolutes inermis (Vaillant) (9)	western N. Pcific; off Mie, Honshu	(not found)
Psychrolutes paradoxus Gunther (9)	off Ishikawa, Honshu	(not found)
Psychrolutes phrictus Stein and Bond (20)	off Aomori, Honshu and off Iwate, Honshu	*Chondracanthus yanezi* Atria, 1980
	eastern Bering Sea; off Cape Erimo Hokkaido; off Aomori, Honshu; off Iwate, Honshu	*Neobrachiella amphipacifica* Ho, 1982

* The seven specimens of this species of parasite have been reported by Benz *et al.* (2002).

amphipacifica Ho (Ho, 1982)

Including the two new species to be reported in this paper, five species of *Chondracanthus* are now known to parasitize the psychrolutids. Thus, in this paper, in addition to describe the three species of parasitic copepods new to science, a cladistic analysis of the genus *Chondracanthus* was conducted to examine if there are historical (coevolutionary) relationships between the species of *Chondracanthus* and their psychrolutid hosts.

MATERIALS AND METHODS

The fatheads kept in the Marine Zoology of Hokkaido University were thoroughly examined for their external surface including gill and oral cavities. The copepod parasites were carefully removed and kept in 70% ethanol. In studying the parasites, the specimens were soaked in 85% lactic acid for a day or two before making dissection. The removed appendages and parts of the body were examined under the compound microscope by employing the hanging-drop method devised by Humes and Gooding (1964). Measurements of the body parts were taken after the specimens were soaked in lactic acid for a day. All drawings were made with the aid of a camera lucida. The type specimens of the three new species have been deposited in the National Museum of Natural History, Smithsonian Institution in Washington, D.C.

A cladistic analysis of the genus *Chondracanthus* was conducted by Ho (1991) to check into the phylogenetic relationships of the 37 species known then. With the addition of two new species, it becomes necessary to reanalyze the phylogeny. We conducted anew the cladistic analysis by using the same set of 37 morphological characters utilized by Ho (1991). No new characters were utilized in this analysis because many species are still unknown of their fine structures. The data matrix of the 37 characters and their states in 39 species of *Chondracanthus* as used in the new cladistic analysis is given in Appendix 1. The wanted analysis was performed with the computer program HENNIG86 Version 1.5 (Farris, 1988). The commands "mhennig*" and "bb*" were employed to produce multiple, shortest trees through performance of extended branch swapping.

RESULTS

Description of new species

Family Chondracanthidae Milne Edwards, 1840

Chondracanthus parvus n. sp.

(Figs. 1–2)

Material examined: 1 ♀ (carrying a ♂) on inner side of operculum of smooth-cheek sculpin, *Eurymen gyrinus* Gilbert and Burke, caught at 98 m in southern part of Funka Bay, Hokkaido on 21 July 1982. The dissected parts of holotype female (USNM 1027288) and allotype male (USNM 1027289) were mounted separately in Hoyer's solution on two slides and deposited in the National Museum of Natural History, Smithsonian Institution in Washington, D.C.

Female: Body (Figs. 1A, B) subtriangular, 5.79 mm long and 3.04 mm wide across posterior part of trunk. Head slightly wider than long, 1.36 × 1.43 mm, and bearing a small posterolateral protrusion. First pediger narrower than head and without outgrowth. Second pediger with a short blunt lateral process and appearing wider than head. Third and fourth pedigers fused to form a trapezoidal trunk with a pair of short lateral processes and another pair of large, blunt posterolateral process. Dorsal surface of pedigers 2, 3, and 4 slightly protruded (Fig. 1A). Egg sac shorter than body, containing many rows of small eggs.

Antennule (Fig. 1C) fleshy and cylindrical, with an armature of 1-1-1-2-2-8. Antenna (Fig. 1D) 2-segmented, with usual recurved terminal hook. Labrum (Fig. 1E) with smooth posterior margin and a small protrusion on lateral margin. Mandible (Fig. 1F) bearing 44 teeth on convex side and 38 teeth on concave side. Paragnath (Fig. 1G) with denticles on distal-inner surface. Maxillule (Fig. 1H) a fleshy lobe tipped with 2 terminal elements. Maxilla (Fig. 1I) 2-segmented; proximal segment large but unarmed and distal segment a process bearing a row of 17 teeth in addition to a spiniform seta and small simple seta in basal region. Maxilliped as usual in chondracanthid.

Leg 1 (Fig. 1J) smaller than leg 2 (Fig. 1K), both bilobate, with small, simple outer seta on protopod, and large patch of fine denticles on distal surface of both endopod and exopod.

Male: Body (Fig. 2A) 810 μm long, with inflated cephalothorax. Metamerism on body indistinct. Genital somite and abdomen indistinguishably fused (Fig. 2B). Caudal ramus (Fig. 2C) a spiniform process with bilaterally pinnate tip and 3 setae plus 1 small knob in basal region.

Antennule (Fig. 2D) filiform, armature being 1-1-2-2-8. Antenna (Fig. 2E) 2-segmented as in female, but terminal hook short and stout and bearing 1 medial seta and 1 outer knob in basal region. Labrum (Fig. 2F) as in female except having spinules on posterior margin. Mandible (Fig. 2G) with 18 teeth on convex margin and 16 teeth on concave margin. Maxillule (Fig. 2H) different from female in being spinulose. Maxilla (Fig. 2I) with only 2 teeth on terminal process. Maxilliped (Fig. 2J) generally as in female except having shorter second segment.

Leg 1 (Fig. 2K) similar to leg 2 (Fig. 2L), both with a large outer seta, a small exopod tipped with 2 or 3 setae, and a simple, unarmed endopod.

Etymology: The species *parvus* is a Latin for "little." It alludes to the possession of a pair of small posterolateral knobs on the head.

Remarks: Using Ho's (1991) key to the species of *Chondracanthus* the present species from Funka Bay was keyed out to *Chondracanthus deltoideus* Fraser, 1920, which is a parasite of kelp greenling, *Hexagrammos decagrammus* (Pallas), and known so far only from British Columbia, Canada (Fraser, 1920). The resemblance between the two species is chiefly seen in the structures of the cephalic appendages and legs, shape of the trunk, and the number of lateral outgrowths in the trunk region. However, the new species differs from *Ch. deltoideus* in having only one pair (vs. two pairs) of small knobs on the head and carrying a pair of lateral processes (vs. none) in the neck region on the second pediger.

Chondracdanthus yabei n. sp.

(Figs. 3–4)

Material examined: 173 ♀♀ (each carrying a ♂) on inner surface of operculum of 36 (out of 115) spinyhead sculpins, *Dasycottus setiger* Bean, examined; all fishes collected in 1979 from eastern Bering Sea: 26 ♀♀ on 4 fishes caught at 315 m on 12 June, 28 ♀♀ on a fish caught at 210 m on 12 June, 40 ♀♀ on 4 fishes caught at 370 m on 16 June, 2 ♀♀ on 2 fishes caught at 440 m on 18 June, 1 ♀ on 1 fish caught at 610 m on 18 June, 8 ♀♀ on 4 fishes caught at 230 m on 23 June, 1 ♀ on 1 fish caught at 500 m on 23 June, 3 ♀♀ on 1 fish caught at 740 m on 23 June, 1 ♀ on 1 fish caught at 470 m on 27 June, 3 ♀♀ on 2 fishes caught at 124 m on 6 July, 1 ♀ on 1 fish caught at 510 m on 7 July, 1 ♀ on 1 fish caught at 151 m on 11 July, 3 ♀♀ on 1 fish caught at 88 m on 21 July, 7 ♀♀ on 1 fish caught at 107 m on 21 July, 1 ♀ on 1 fish caught at 159 m on 22 July, 4 ♀♀ on 2 fishes caught at 123 m on 26 July, 2 ♀♀ on 1 fish caught at 154 m on 28 July, 4 ♀♀ on 1 fish caught at 122 m

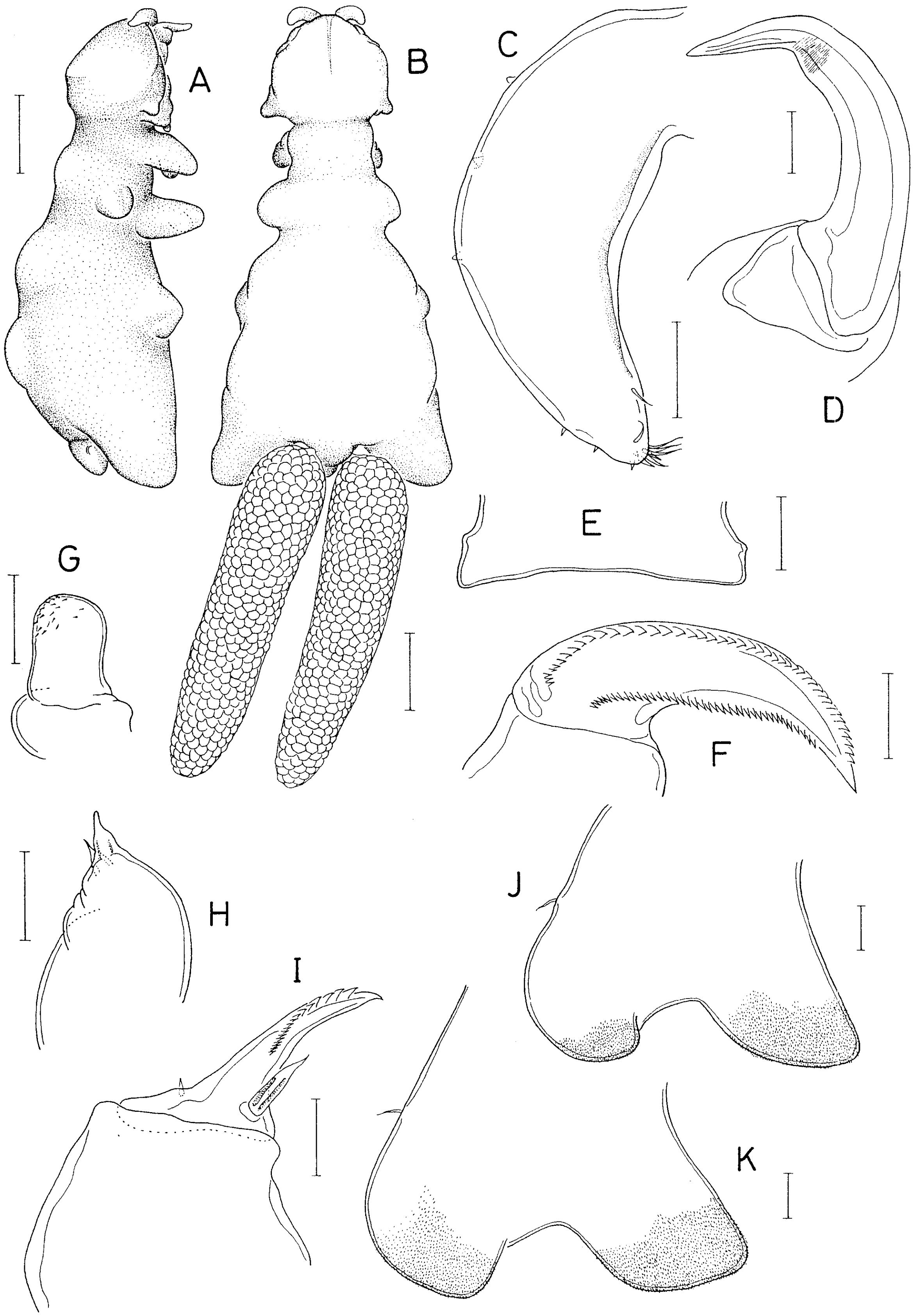

Fig. 1. *Chondracanthus parvus* n. sp., holotype female. A, habitus, lateral. B, same, dorsal. C, antennule. D, antenna. E, labrum, ventral. F, mandible. G, paragnath. H, maxillule. I, maxilla. J, leg 1. K, leg 2. Scale bars: 1 mm in A, B; 0.1 mm in C-E, J, K; 0.05 mm in F-I.

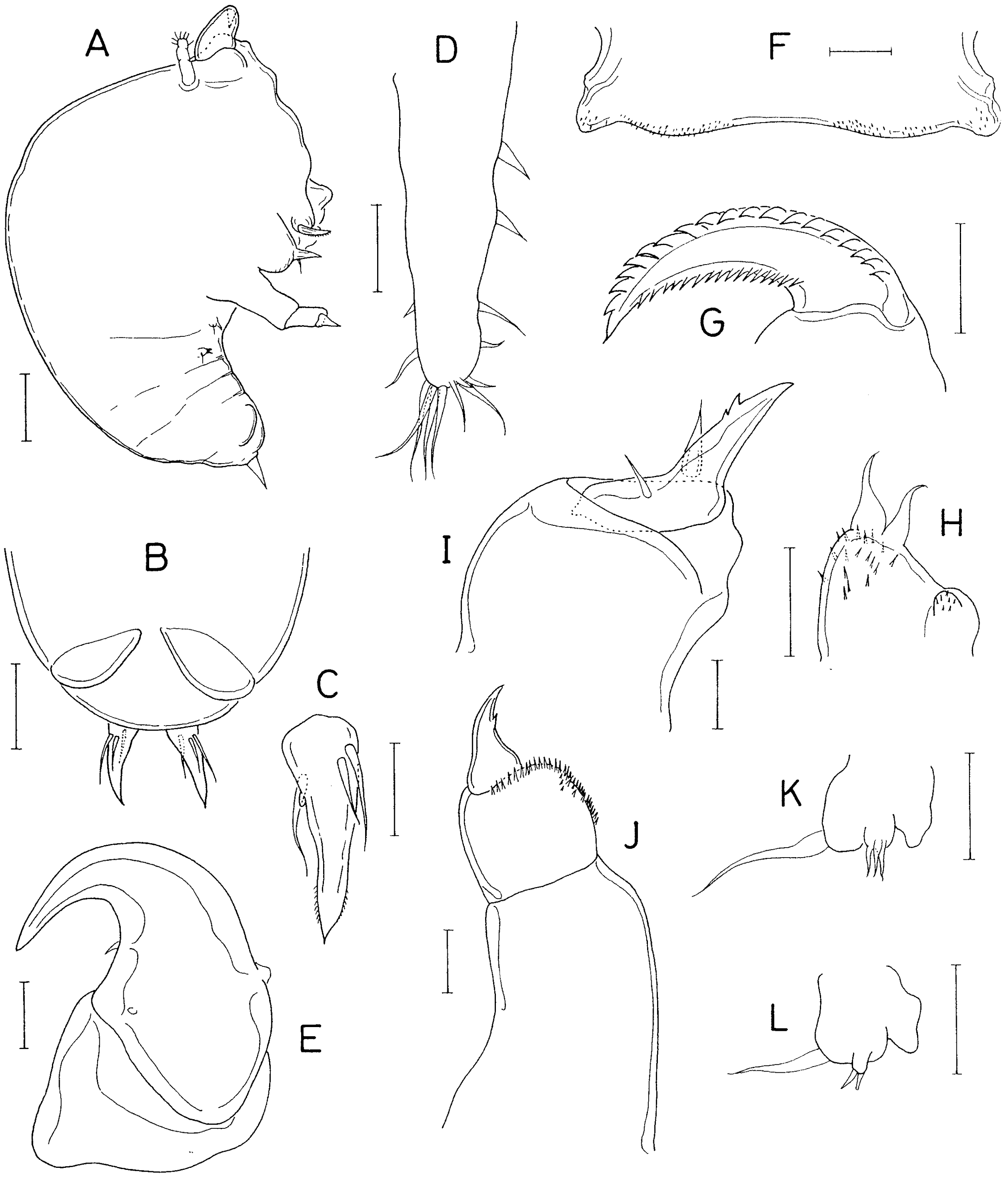

Fig. 2. *Chondracanthus parvus* n. sp., allotype male. A, habitus, lateral. B, posterior part of body, ventral. C, caudal ramus, ventral. D, antennule. E, antenna. F, labrum, ventral. G, mandible. H, maxillule. I, maxilla. J, maxilliped. K, leg 1. L, leg 2. Scale bars: 0.1 mm in A; 0.05 mm in B; 0.02 mm in C-L.

on 28 July, 1 ♀ on 1 fish caught at 133 m on 31 July, 15 ♀♀ on 2 fishes caught at 324 m on 4 August, and 21 ♀♀ on 3 fishes caught at 360 m on 4 August. Another 68 ♀♀ (each carrying a ♂) on inner surface of operculum of 26 (out of 137) darkfin sculpins, *Malacocottus zonurus* Bean, examined; fishes were collected from the following localities: Sea of Okhotsk, 5 ♀♀ on 1 fish caught at 410 m on 2 January 1970; off Kamchatka, 3 ♀♀ on 2 fishes caught at 441 m on 16 May 1975; eastern Bering Sea: 6 ♀♀ on 2 fishes caught at 230 m on 23 June 1979, 3 ♀♀ on 1 fish caught at 295 m on 24 July 1979, 3 ♀♀ on 1 fish caught at 154 m on 28 July 1979, 1 ♀ on 1 fish caught at 132 m on 1 August 1979, 1 ♀ on 1 fish caught at 515 m on 13 July 1981, and 1 ♀ on 1 fish caught at 205 m on 5 August 1981; western North Pacific, 2 ♀♀ on

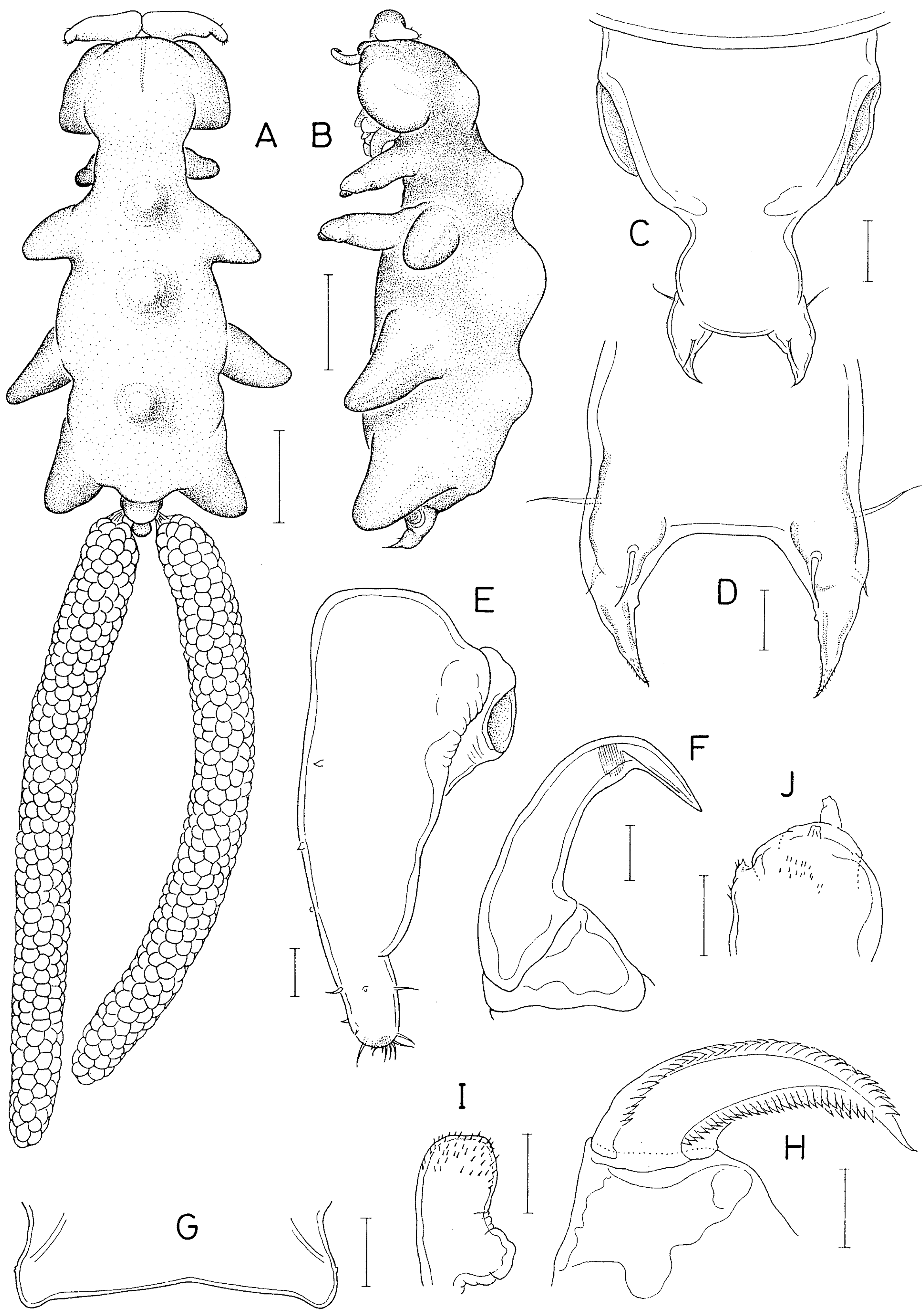

Fig. 3. *Chondracanthus yabei* n. sp., paratype female. A, habitus, dorsal. B, same, lateral. C, genito-abdomen, dorsal. D, abdomen and caudal rami, dorsal. E, antennule. F, antenna. G, labrum, ventral. H, mandible. I, paragnath. J, maxillule. Scale bars: 1 mm in A, B; 0.1 mm in E-G; 0.05 mm in D, H-J.

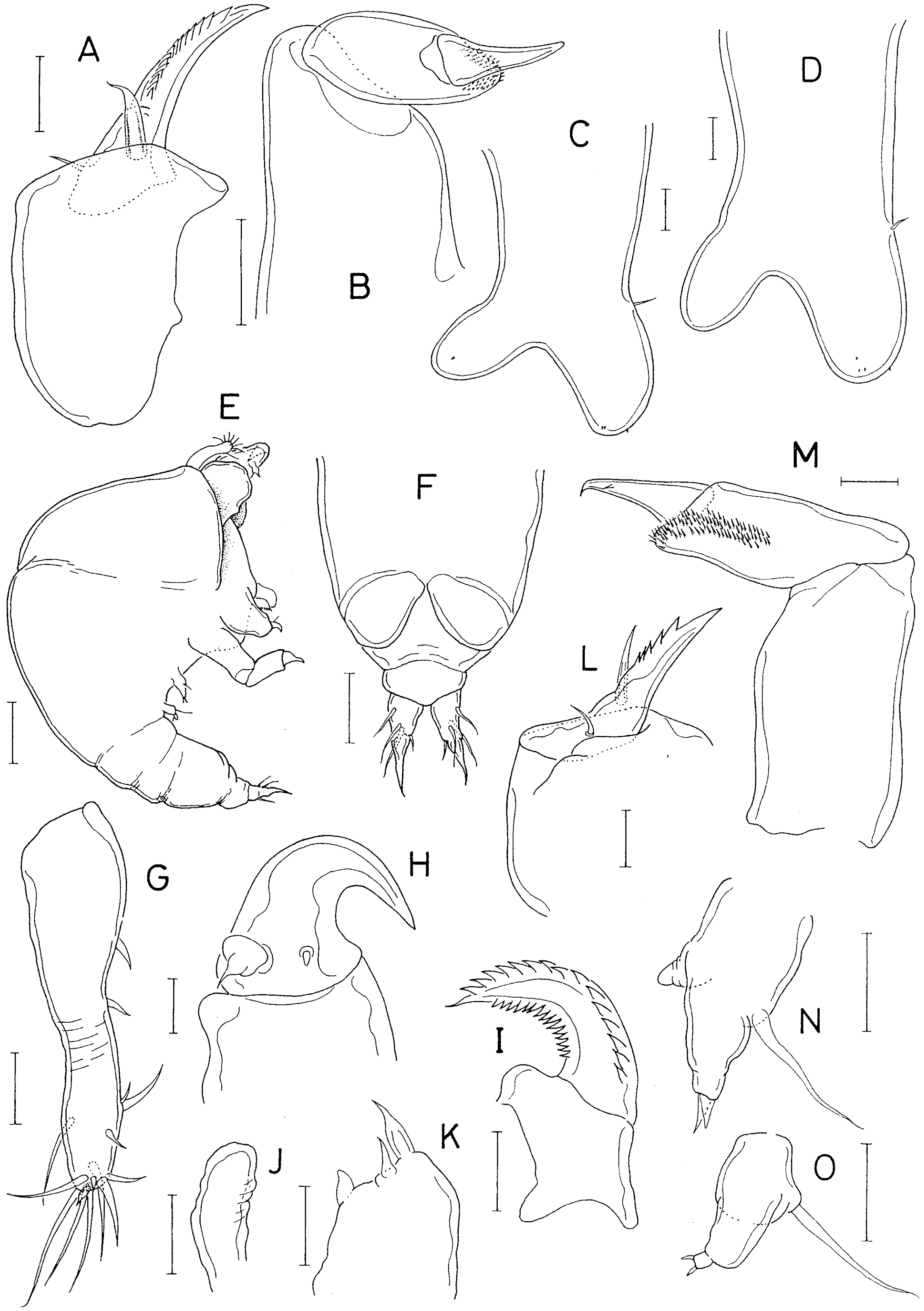

Fig. 4. *Chondracanthus yabei* n. sp., paratype female. A, maxilla. B, maxilliped. C, leg 1. D, leg 2. Paratype male: E, habitus, lateral. F, posterior part of body, ventral. G, antennule. H, antenna. I, mandible. J, paragnath. K, maxillule. L, maxilla. M, maxilliped. N, leg 1. O, leg 2. Scale bars: 0.05 mm in A, F; 0.1 mm in B-E; 0.02 mm in G-O.

2 fishes caught at 180 m on 5 June 1977; eastern North Pacific in 1977: 1 ♀ on 1 fish caught at 220 m on 7 June, 1 ♀ on 1 fish caught at 340 m on 8 June, and 13 ♀♀ on 3 fishes caught at 128 m on 12 June; Aleutian Islands, 1 ♀ on 1 fish caught at 180 m on 6 July 1980; and Gulf of Alaska in 1984: 5 ♀♀ on 1 fish caught at 120 m on 16 July, 3 ♀♀ on 1 fish caught at 235 m on 22 July, 12 ♀♀ on 2 fishes caught at 265 m on 9 August, and 3 ♀♀ on 1 fish caught at 450 m on 1 August. Holotype female (USNM 1027290), allotype male (USNM 1027291) and 8 paratype females (USNM 1027292, with each carrying a pygmy male) have been deposited in the National Museum of Natural History, Smithsonian Institution in Washington, D.C.

Female: Body (Figs. 3A,B) stocky, thick, and measuring 5.40 mm long. Head large, wider than long, 1.03 (excluding antennule) × 1.83 mm, and with a pair of broad, lateral expansions. Neck comprising only first pediger, distinctly narrower than head. Second, third, and fourth pedigers fused to form a rectangular, thick trunk with two pairs of lateral processes in addition to a pair of posterolateral processes. Dorsal surface of trunk raised in each of three pedigers. Genitoabdomen (Fig. 3C) longer than wide, 500 × 462 μm. Caudal ramus (Fig. 3D) fused to abdomen; swollen basal region with 3 simple setae and attenuated terminal process with spinules distally. Egg sacs (Fig. 3A) long, about 1.5 times length of body.

Antennule (Fig. 3E) fleshy, with large inflated base; armature formula 1-1-1-3-2-9. Antenna (Fig. 3F) 2-segmented, with usual recurved terminal hook. Labrum (Fig. 3G) with smooth posterior margin and a minute protrusion on lateral margin. Mandible (Fig. 3H) bearing a single row 32 to 36 teeth on convex side, but concave side with 24 to 34 teeth in a row and a separate row of 3 teeth in subterminal region. Paragnath (Fig. 3I) a fleshy lobe with spinules on terminal surface. Maxillule (Fig. 3J) with subterminal, spinule-bearing protrusion in addition to 2 terminal elements. Maxilla (Fig. 4A) 2-segmented; proximal segment large but unarmed; distal segment a process bearing a row of 13 to 15 teeth in addition to a spiniform seta and small simple seta in basal region. Maxilliped (Fig. 4B) 3-segmented; basal segment largest and unarmed; second segment with mediodistal corner protruded and spinulose; third segment a claw

Leg 1 (Fig. 4C) shorter than leg 2 (Fig. 4D), both with long protopod bearing a small outer seta and an endopod smaller than exopod.

Male: Body (Fig. 4E) 792 μm long, with inflated cephalothorax. Metamerism on body indistinct. Genital somite and abdomen indistinguishably fused (Fig. 4F). Caudal ramus (Fig. 4F) a spiniform process carrying 4 setae in basal region. Antennule (Fig. 4G) filiform, armature being 1-1-2-2-9. Antenna (Fig. 4H) 2-segmented as in female, but terminal hook short and stout and bearing 1 medial seta and 1 outer knob in basal region. Mandible (Fig. 4I) with 12 to 15 larger teeth on convex margin and same number but smaller teeth on concave margin. Paragnath (Fig. 4J) a simple, fleshy lobe. Maxillule (Fig. 4K) different from female in lacking spinules. Maxilla (Fig. 4L) with only 4 to 5 teeth on terminal process. Maxilliped (Fig. 4M) generally as in female.

Leg 1 (Fig. 4N) larger than leg 2 (Fig. 4O), both with a large outer seta, a small exopod tipped with 2 tiny setae. Endopod on leg 1 a simple process but lacking entirely on leg 2.

Etymology: The species is named after Dr. Mamoru Yabe, who collected the fathead sculpins kept in HUMZ.

Remarks: This species resembles *Ch. yanezi* Atria, 1980 in having two pairs of lateral processes on the trunk and lacking a medio-ventral process in the same part of the body. The resemblance between the two is also seen in the structure of the head (with lateral expansions), genito-abdomen, and most appendages except for the maxillule. The maxillule in *Ch. yanezi* is tipped with two terminal elements (Ho, 1982: Fig. 1J), but in *Ch. yabei* there is a subterminal process in addition to the two terminal elements (see Fig. 3J). The new species can also be distinguished from the latter by possession of three, low protrusions on the mid-dorsal surface of the trunk (see Figs. 3A, B).

Family Caligidae Burmeister, 1834

Caligus similis n. sp.

(Figs. 5–7)

Material examined: 22 ♀♀ and 7 ♂♂ on gill filaments or inner surface of operculum of 7 (out of 8 examined) dark toadfishes, *Neophrynichthys latus* (Hutton), collected in New Zealand in 1981: 2 ♀♀ and 1 ♂ on 2 fishes caught at 177m on 16 February, 18 ♀♀ and 5 ♂♂ on 4 fishes caught at 123 m on 20 February, and 2 ♀♀ and 1 ♂ on 1 fish caught at 157 m on 20 February. Holotype female (USNM 1027293), allotype male (USNM 1027294) and 4 paratype females (USNM 1027295) have been deposited in the National Museum of Natural History, Smithsonian Institution in Washington, D.C.

Female: Body (Fig. 5A) 4.95 mm long, excluding setae on caudal rami. Cephalothoracic shield suborbicular, 2.53 × 2.40 mm, excluding lateral, hyaline membranes. Prominent lunule on frontal plate. Fourth pediger wider than long. Genital complex subquadrate with rounded corners, 1.32 × 1.29 mm. Abdomen (Fig. 5B) small, 665 × 458 μm, and 1-segmented. Caudal ramus (Fig. 5C) attached obliquely to abdomen, longer than wide (196 × 138 μm), and armed with a dorsal papilla carrying a setule and a row of setules on medial margin in addition to 3 short and 3 long plumose setae on distal margin. Egg sac slightly shorter than body.

Antennule (Fig. 5D) 2-segmented; proximal segment with 27 pilose and 2 naked setae on anterodistal surface, distal segment with 1 subterminal seta on posterior margin and 11 setae plus 2 aesthetascs on distal margin. Antenna (Fig. 5E) 3-segmented; proximal segment armed with bluntly pointed posteromedial process; middle segment largest and armed with a small adhesion pad; distal segment strongly bent claw bearing thick seta in proximal region and thin seta in middle region. Postantennal process (Fig. 5F) bluntly

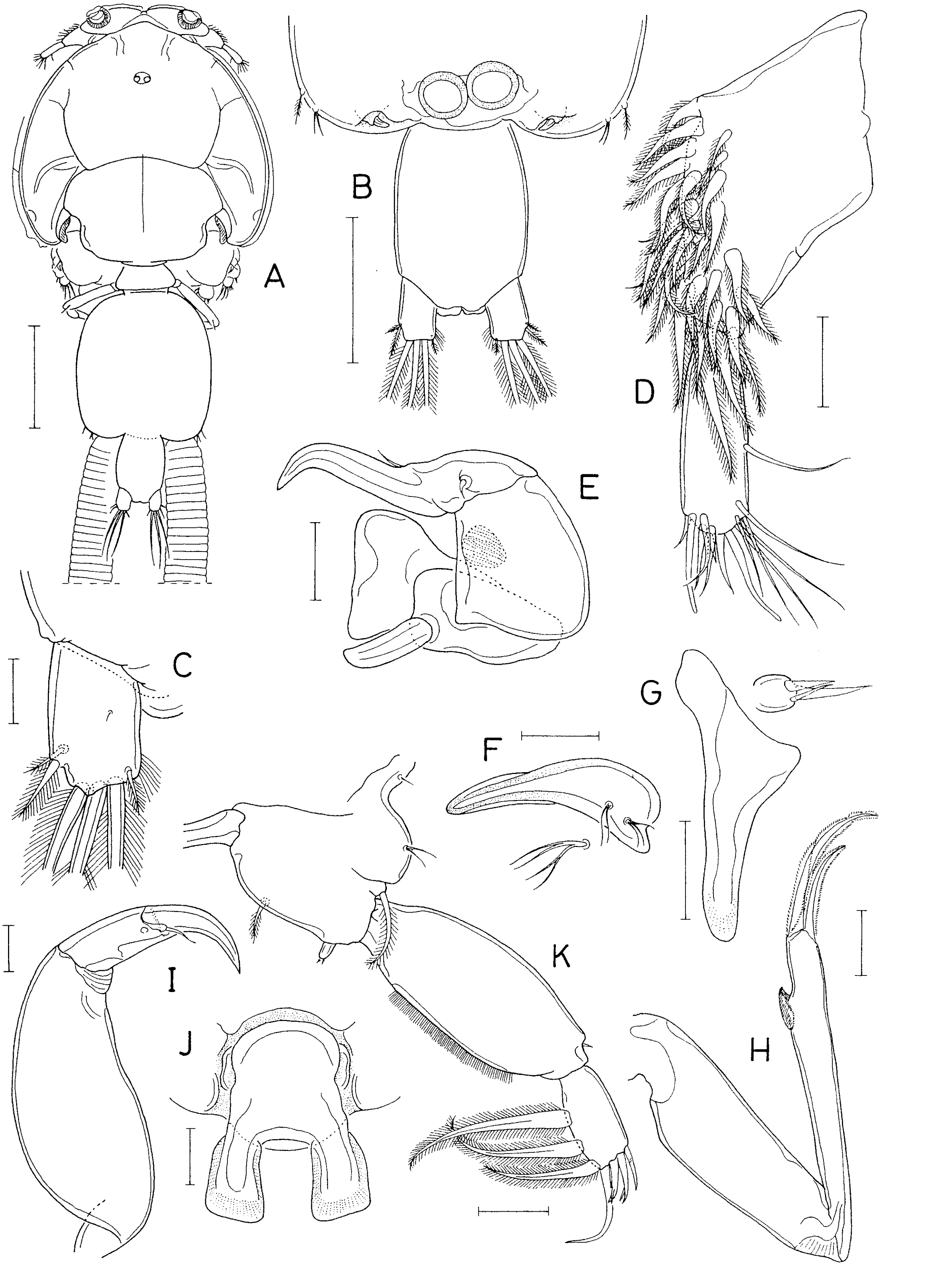

Fig. 5. *Caligus similis* n. sp., paratype female. A, habitus, dorsal. B, abdomen, ventral. C, caudal ramus, dorsal. D, antennule. E, antenna. F, postantennal process, ventral. G, maxillule, ventral. H, maxilla. I, maxilliped. J, sternal furca, ventral. K, leg 1, ventral. Scale bars: 1 mm in A; 0.5 mm in B; 0.1 mm in C-K.

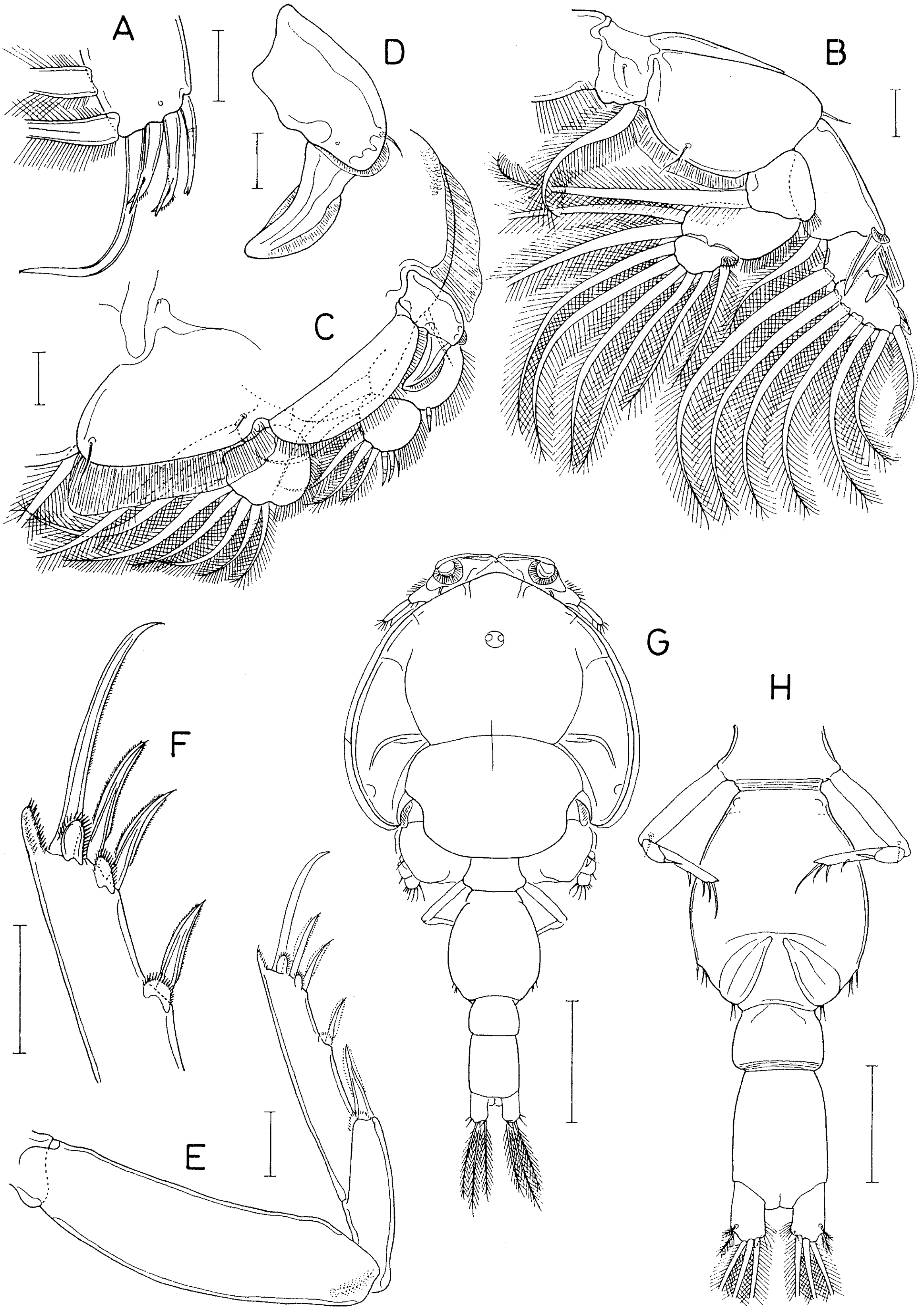

Fig. 6. *Caligus similis* n. sp., paratype female. A, distal part of leg 1 exopod, ventral. B, leg 2, ventral. C, leg 3, ventral. D, proximal segment of leg 3 exopod, ventral. E, leg 4. F, distal part of leg 4 exopod. Male: G, habitus, dorsal. H, urosome, ventral. Scale bars: 0.05 mm in A, D; 0.1 mm in B, C, E, F; 1 mm in G; 0.5 mm in H.

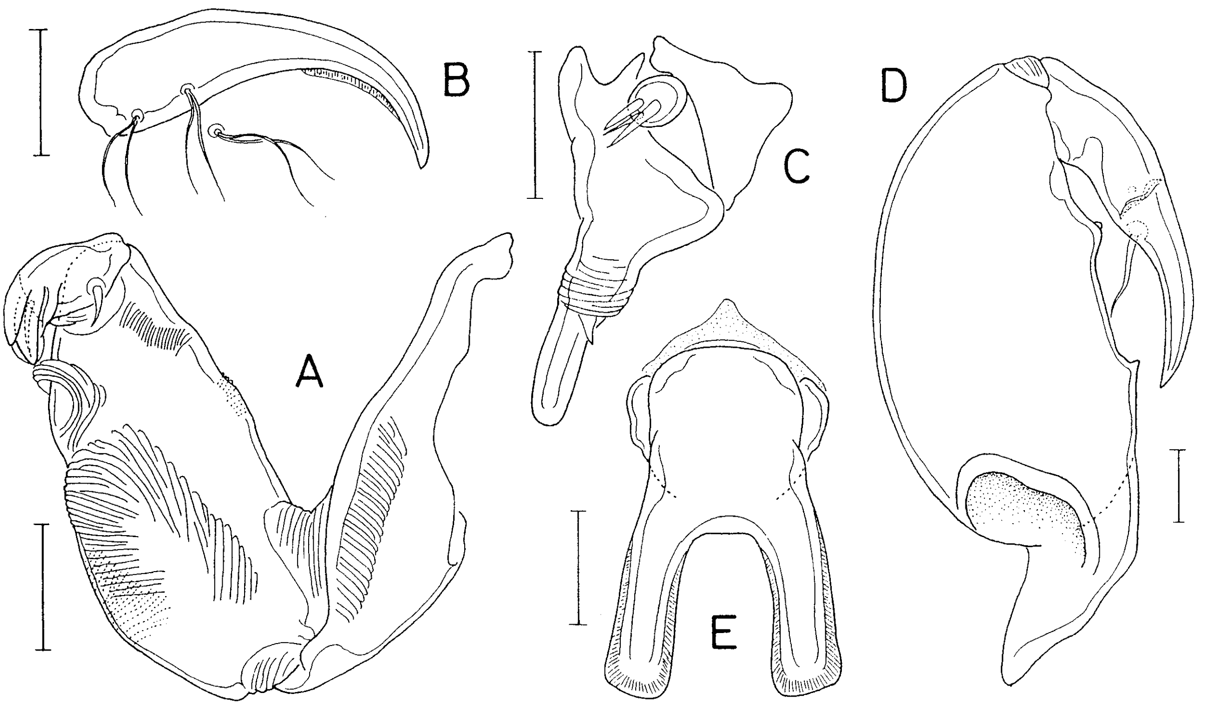

Fig. 7. *Caligus similis* n. sp., paratype male. A, antenna. B, postantennal process, ventral. C, maxillule, ventral. D, maxilliped. E, sternal furca, ventral. Scale bars: 0.1 mm in all drawings.

pointed carrying 2 basal papillae with each bearing 2–3 setules; another similar papilla located nearby on sternum bearing 2 bifurcate setule. Mandible 4-segmented; with 12 teeth on medial margin of distal blade. Maxillule (Fig. 5G) comprising bluntly pointed, dentiform process and small basal papilla tipped with 3 short setae. Maxilla (Fig. 5H) 2-segmented; proximal segment (lacertus) unarmed; slender, longer, distal segment (brachium) carrying subterminal, marginal membrane on outer edge; canna (167 μm) slightly over tow-thirds length of calamus (245 μm). Maxilliped (Fig. 5I) 2-segmented; proximal segment (corpus) long but unarmed; subchela two-third length of corpus and armed with long barbell in mid-region. Box of sternal furca (Fig. 5J) with ear-like outgrowth, tines fringed with transparent rim and showing truncate tip.

Armature on rami of legs 1–4 as follows (Roman numerals indicating spines and Arabic numerals, setae):

	Exopod	Endopod
Leg 1	1-0; III,1,3	(vestigial)
Leg 2	I-1; I-1; II,I,5	0-1; 0-2; 6
Leg 3	I-1: I-1; III,4	0-1; 6
Leg 4	I-0; IV	(absent)

Leg 1 (Fig. 5K) protopod with plumose outer and inner seta; vestigial endopod tipped with 2 tiny setae; first segment of exopod with row of spinules on posterior edge and short spiniform seta at outer distal corner; middle 2 of 4 terminal elements on last segment of exopod serrated on outer margin and with accessory process (Fig. 6A). Leg 2 (Fig. 6B) coxa small, with setule-bearing papilla on anterior surface and large, plumose, inner seta on posterior edge; basis with small, simple, outer seta; posterior margin of basis with long, narrow membrane and a setule-bearing papilla on the base in the middle region of this membrane; anterodistal surface of coxa and first segment of exopod with outer marginal membrane. Leg 3 (Fig. 6C) protopod (apron) with small, outer and large, inner plumose seta; outer and posterior edge fringed with marginal membrane; setule-bearing papilla near both ends of posterior membrane; velum large, fringed with marginal setule; proximal segment of exopod carrying a setule and fringed with narrow membrane (Fig. 6D). Leg 4 (Fig. 6E) protopod with plumose seta at outerdistal corner; pecten at base of each outer spine on exopod. Leg 5 represented by 2 papillae on posterolateral corner of genital complex (Fig. 5B), with anterior (outer) one carrying 1 setule and posterior (inner) one, 2 setule.

Male: Body (Fig. 6G) 4.72 mm long, excluding setae on caudal rami. Cephalothoracic shield suborbicular, 2.50 × 2.31 mm, excluding frontal and lateral, hyaline membranes. Fourth pediger wider than long. Genital complex (Fig. 6H) small, longer than wide, 917 × 771 μm. Abdomen (Fig. 6H) 2-segmented, with small first segment (258 × 425 μm) about half size of posterior segment (525 × 417 μm). Caudal ramus (Fig. 6H) longer than wide (223 × 142 μm), and armed as in female.

Antenna (Fig. 7A) 3-segmented; with various size of corrugated, adhesion pads on first 2 segments; terminal segment with 2 flat processes and 2 basal setae. Postantennal process (Fig. 7B) carrying 2 basal papillae with each bearing 2 long setules. Dentiform process of maxillule (Fig. 7C) striated in midregion and carrying here a small seta.

Myxal area of corpus of maxilliped (Fig. 7D) slightly protruded at 2 places. Sternal furca (Fig. 7E) generally as in female, except for slightly longer tines. Leg 5 (Fig. 6H) on posterolateral margin of genital complex and constructed generally as in female. Leg 6 (Fig. 6H) represented by 2 setae at the of posterolateral ridge of genital complex.

Etymology: The species name *similis* is a Latin word meaning "like, resembling". It alludes to its closeness with three species of *Caligus*.

Remarks: Characteristic features of the present new species are found in the possession of (1) a short abdomen (shorter than one/third length of the cephalothoracic shield), (2) a postantennal process with tooth-like protrusion in the basal region, (3) an accessory process on each of the middle two terminal elements on the exopod of leg 1, and (4) a 2-segmented exopod of leg 4 with an armature of I; IV. The combination of these four features is shared with three species of *Caligus*, namely, *C. dieuzeidei* Brian, 1933; *C. glandifer* Shiino, 1954; and *C. willungae* Kabata, 1965. However, according to Brian (1933) *C. dieuzeidei* differs from the new species in having an accessory tine on the dentiform process of the maxillule and a pair of bluntly pointed tines on the sternal furca; based on Shiino (1954) *C. glandifer* is distinguishable in having its genital complex as large as the cephalothoracic shield; and according to Kabata (1965) *C. willungae* is separable by the possession of marginal indentation on the cephalothoracic shield, a relatively longer caudal ramus, and a pair of bluntly pointed tines on the sternal furca.

Phylogenetic relationships of *Chondracanthus* parasites

So far as we are aware, five of the 39 species of *Chondracanthus* are known exclusively from the fatheads. The two species that were not found in our above study of the fatheads of Hokkaido University are *Ch. cottunculi* Rathbun, 1886 and *Ch. multituberculatus* (Markewitsch, 1956). The former is known to occur on *Cottunculus microps* Collet and *C. thomsoni* (Günther) occurring in the western North Atlantic (Rathbun, 1886; Ho, 1971) and the latter, on *Dasycottus setiger* Bean, in the Bering Sea (Markewitsch, 1956).

In total 2339 trees (cladograms) were obtained from our new cladistic analysis. All with a tree length of 109 steps, a consistency index (CI) of 33, and a retention index (RI) of 59. The command "mhennig*" constructed several initial cladograms and saved only one shortest tree after limited branch-swapping. This shortest tree has the same CI and RI with those 2339 trees produced after extended branch-swapping. It is selected to represent the phylogenetic relationships of the species of *Chondracanthus* and reproduced in Fig. 8. The most remarkable point of this new analysis is finding the monophyletic occurrence of four species, *yabei, yanezi*, *cottunculi* and *lepidionis* as shown in a partial topology in a rectangle in Fig. 8, throughout the obtained trees. While *parvus* maintains a close affinity to this 4-taxa monophyly, the fifth species of the psychrolutid chondracanthids, *Ch. multituberculatus*, always appears distantly located in a

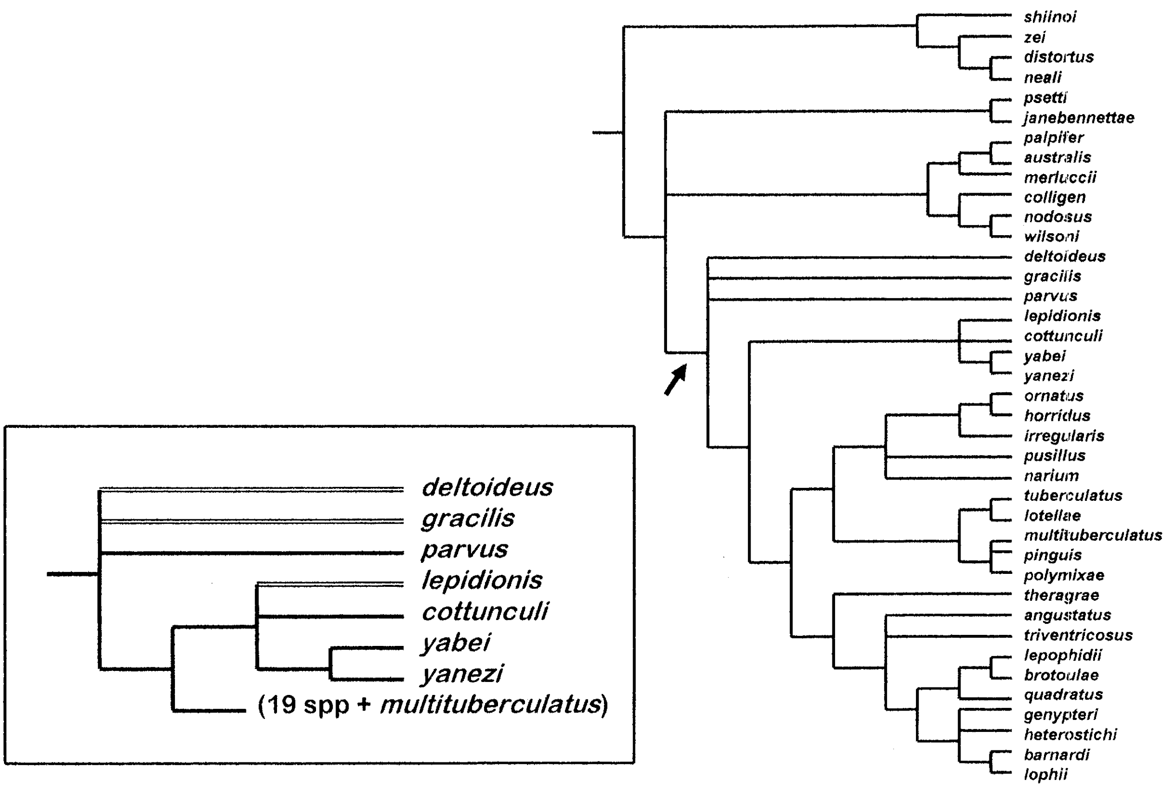

Fig. 8. Phylogeny of *Chondracanthus* produced through analysis of 37 binary characters. The clade containing the five species found on the psychrolutids is indicated by an arrow and shown in the rectangle.

lineage separated from this tightly clustered clade of four taxa.

DISCUSSION

Occurrence of parasites

The phylogenetic scheme of the Psychrolutidae proposed by Jackson and Nelson (1998) is reproduced in Fig. 9, with notation of the eight species of copepod parasites found in this study (see Table 1). The genus *Gilbertidia* listed in the website of FishBase (Froese and Pauly, 2004) was not included in Jackson and Nelsons study.

It is clear from this host-parasite scheme that *Neobrachiella amphipacifica* Ho (◆ in Fig. 9) is the most common parasite and the host genus *Malacocottus* carries the heaviest burden of the copepod parasites. The eight species of parasites belong to six genera (in six rows in Fig. 9) and the genus *Chondracanthus* is most highly represented, with three species occurring in four genera of the psychrolutids kept in the Hokkaido University Museum of Zoology. Taking into account all species of *Chondracanthus* reported from the psychrolutid fishes, we found that there are five species of this genus of parasites occurring on six genera of the fatheads studied by Jackson and Nelson (1998). A summary

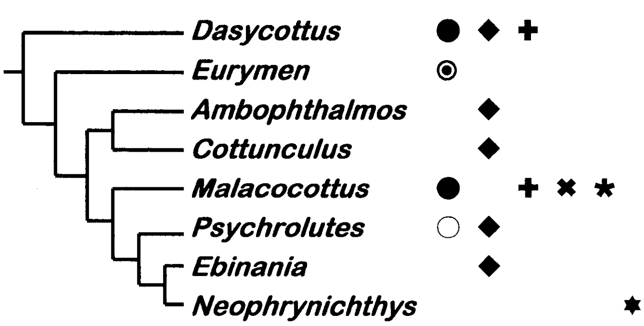

Fig. 9. The cladogram of psychrolutid genera produced by Jackson and Nelson (1998) with indication of the parasitic copepods found in this study. The symbols are: ★ for *Bobkabata kabatabobbus*, ✦ for *Caligus similis*, ⦿ for *Chondracanthus parvus*, ● for *Ch. yabei*, ○ for *Ch. yanezi*, ✖ for *Clavella adunca*, ◆ for *Neobrachiella amphipacifica*, and ✚ for *Naobranchia occidentalis*.

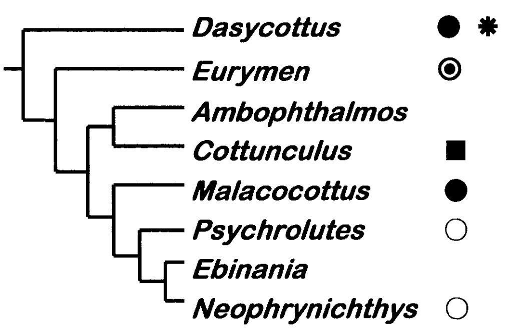

Fig. 10. The five species of *Chondracanthus* known on the fatheads (Psychrolutidae). The symbols are: ■ for *Ch. cottunculi*, ✱ for *Ch. multituberculatus*, ⦿ for *Ch. parvus*, ● for *Ch. yabei*, and ○ for *Ch. yanezi*.

cladogram showing this occurrence of *Chondracanthus* parasites is given in Fig. 10. Both *Ch. yabei* (●) and *Ch. yanezi* (○) infect two genera of fatheads, but each of the other three species of parasites, *Ch. multituberculatus* (✱), *Ch. parvus* (⦿) and *Ch. cottunculi* (■), infects only one genus of fish hosts.

Coevolution

Dasycottus setiger Bean is the only species of fatheads recorded to be infected by two species of *Chondracanthus*, *Ch. multituberculatus* (✱) and *Ch. yabei* (●) (Fig. 10). Close examination of the phylogenetic tree of *Chondracanthus* (Fig. 8) shows that these two species of parasites are 6 nodes away from each other. Such a distant relation would indicate that the two species of *Chondracanthus* must have established life on the same species of host at different time. As *Ch. yabei* is 6 nodes away from the base of the genus and *Ch. multituberculatus*, 8 nodes away from the same base, the former species of parasite must have colonized the genus *Dasycottus* before the latter species. Since *Ch. yabei* is also found on *Malacocottus zonurus* Bean, it raises the question of which genus is the original host of this species of parasite, when *Dasycottus* and *Malacocottus* are distantly related (see Fig. 10).

Based on the Principle of Parsimony, it seems *Malacocottus* is the original host of *Ch. yabei*, because a hypothesis of *Dasycottus* as the original host would invoke making six assumptions that the parasite *Ch. yabei* was lost in all subsequent lineages of the fatheads evolution, except for the one led to the development of *Malacocottus*. On the other hand, if *Malacocottus* is accepted as the original host, then, just one simple biological phenomenon of colonization would explain the occurrence of the same parasite on *Dasycottus*. The later hypothesis finds also its support from the phylogeny of *Chondracanthus* shown in Fig. 8. As shown in the inserted partial topology in Fig. 8, *Ch. yabei* and *Ch. yanezi* are in sister-taxa relationship that signifies the closeness between their hosts, *Malacocottus* and *Psychrolutes*. Furthermore, as *Ch. cottunculi* is shown as a sister taxon of *Ch. yabei* + *Ch. yanezi* in Fig. 8, it corroborates that the host of *Ch. cottunculus* must have evolved from a lineage in sister-taxa relationship with *Malacocottus* and *Psychrolutes*. Such affinity is exactly what Jackson & Nelson (1998) had worked out (see Fig. 10).

The new cladogram of *Chondracanthus* supports further that the genus *Eurymen* should occupy a basal node on the evolution of the fatheads, as its parasite, *Ch. parvus*, is a direct descendent of the first lineage of the parasites occurring on the psychrolutids (see the partial topology in Fig. 8).

As depicted in Fig. 11, we found coevolution occurring between *Chondracanthus* and their psychrolutid hosts. The arrow in Fig. 11 indicates that the chondracanthid parasites succeeded in living on the fatheads after the divergence of *Dasycottus*. The subsequent divergence of *Eurymen* led to the development on it of *Ch. parvus* (⦿) and the split of psy-

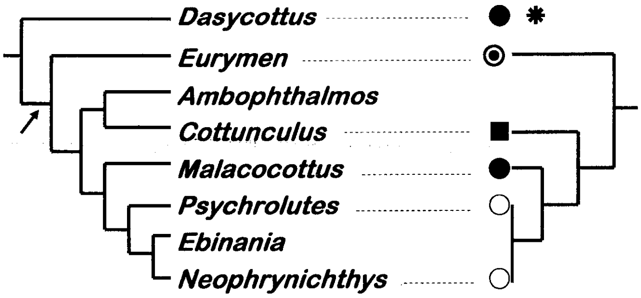

Fig. 11. Cladograms of Psychrolutidae (after Jackson and Nelson, 1998) and *Chondracanthus* showing matching phylogeny. For the symbols of chondracanthid parasites refer to the legend in Fig. 10. The arrow on the host cladogram indicates the lineage on which the species of *Chondracanthus* had established in their coevolution on the fatheads. For the occurrence of ● and ✱ on the *Dasycottus* see explanation in the text.

chrolutids into the clade containing *Ambophthalmos* + *Cottunculus* on one hand and *Malacocottus* + *Psychrolutes* + *Neophrynichthys* + *Ebinania* on the other hand invoked the evolution of *Ch. cottunculi* (■) on the former lineage and *Ch. yabei* (●) and *Ch. yanezi* (○) on the latter lineage. In other words, the new cladistic analysis of *Chondracanthus* supports Jackson and Nelson's (1998) hypothesis on the phylogeny of the psychrolutids.

According to Kabata (1970), *Chondracanthus lepidionis* Kabata, 1970 is a parasite of morid cod, *Lepidion schmidti* Svetovidov, occurring in the North Atlantic, where *Ch. cottunculi* was found (Ho, 1971). Another species of morid cod, *Pseudophycis bachus* (Forster), is known to carry another species of *Chondracanthus, Ch. lottelae* Thomson, 1889 (Ho, 1975). Since the cldogram in Fig. 8 does not show closeness between these two species of parasites, it is logical to assume that there is no coevolution between *Chondracanthus* and the morid cods. Then, the occurrence of *Ch. lepidionis* on a non-psychrolutid fish can be dismissed as a result of colonization by a descendent of the psychrolutid *Chondracanthus*.

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Appendix 1. Character matrix adapted from Ho (1991) with the addition of character states for the two new species of Chondracanthus, Ch. parvus and Ch. yabei. Question mark "?" indicates unknown character state.

Species	Characters							
	5	10	15	20	25	30	35	37
outgroup	00000	00000	00000	00000	00000	00000	00000	01
angustatus	10000	00010	00001	00000	00000	01000	10000	01
australis	00000	00000	00001	00000	00000	00000	01001	01
barnardi	10010	01010	01000	10000	10110	00001	00010	11
brootulae	00000	00000	00001	00000	10000	00000	10101	01
colligens	00000	00010	00001	00100	00010	00000	10000	0?
cottunculi	00000	00010	00001	00000	00000	00010	00000	00
deltoideus	00000	00000	00001	00000	00000	00010	00000	0?
distortus	01000	00000	10000	00000	01100	00001	00010	10
genypteri	00000	00010	00001	00100	00000	00001	00010	11
gracilis	00000	00000	00001	00010	00000	00010	00000	01
heterostichi	10000	00010	01001	00010	00000	00000	10010	10
horridus	10000	10010	01001	00000	10100	00100	00000	0?
irregularis	00000	10010	01001	00010	10000	00010	00000	01
janebennettae	10000	00000	00001	00000	00000	10000	10000	01
lepidionis	00000	00010	00000	00000	00000	00010	00000	00
lepophidii	10000	00010	00001	00100	00000	00001	00101	01
lophii	10000	01001	00100	10101	00110	00001	00010	10
lotellae	00010	10010	01001	00000	00100	00010	00000	00
merluccii	10000	00000	00001	00000	00010	00000	01000	11
multituberculatus	10010	10010	01001	00010	00000	00010	00000	0?
narium	00000	10010	01001	00010	00000	00010	00000	01
neali	01000	10000	10010	01110	10100	10001	00010	10
nodosus	00100	00010	00000	01100	01010	00100	00000	01
ornatus	00100	10010	01001	00010	10000	00100	00000	01
palpifer	00000	00000	00001	00000	00010	00000	01001	01
parvus	10000	00000	00001	00000	00000	00010	00000	01
pinguis	10010	10010	01001	00010	00000	00010	00000	00
polymixiae	10010	10010	01001	00010	00000	00010	00000	01
psetti	00000	00000	00001	00000	00000	00000	10000	01
pusillus	00000	10010	01001	00010	00000	00010	00000	01
quadratus	10000	00000	00001	00000	00000	00001	00011	0?
shiinoi	00000	00001	00000	10000	01100	00010	00000	01
theragrae	10000	00010	00001	00000	00000	00010	00000	01
triventricosus	10000	00010	00001	00000	00000	10000	00000	00
tuberculatus	10010	10010	00010	10000	10101	0001	00000	01
wilsoni	00000	00010	00000	10100	10000	00100	00000	0?
yabei	00100	00010	00001	00000	00000	00010	00000	00
yanezi	00100	00010	00001	00000	00000	00010	00000	00
zei	00001	00100	10000	01000	00100	00100	00000	00