

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/47500630>

Pseudohatschekiidae, a new family for *Pseudohatschekia* branchiostegi Yamaguti, 1939 (Crustacea: Copepoda: Siphonostomatoida) from *Branchiostegus* spp. (Teleostei: Perciformes: Malac...

Article in *Systematic Parasitology* · November 2010

DOI: 10.1007/s11230-010-9269-4 · Source: PubMed

CITATIONS

6

READS

356

4 authors:



Danny Tang

Orange County Sanitation District

45 PUBLICATIONS 258 CITATIONS

SEE PROFILE



Kunihiko Izawa

4 PUBLICATIONS 21 CITATIONS

SEE PROFILE



Daisuke Uyeno

Florida Museum of Natural History

81 PUBLICATIONS 312 CITATIONS

SEE PROFILE



Kazuya Nagasawa

Hiroshima University

565 PUBLICATIONS 6,331 CITATIONS

SEE PROFILE

Pseudohatschekiidae, a new family for *Pseudohatschekia branchiostegi* Yamaguti, 1939 (Crustacea: Copepoda: Siphonostomatoida) from *Branchiostegus* spp. (Teleostei: Perciformes: Malacanthidae) in Japanese waters, with descriptions of the early developmental stages of *P. branchiostegi*

Danny Tang · Kunihiko Izawa · Daisuke Uyeno · Kazuya Nagasawa

Received: 6 April 2010 / Accepted: 29 June 2010
© Springer Science+Business Media B.V. 2010

Abstract The siphonostomatoid copepod *Pseudohatschekia branchiostegi* Yamaguti, 1939 is re-described in detail based on specimens of both sexes collected from the gill filaments of three species of *Branchiostegus* Rafinesque (Teleostei: Malacanthidae) captured in Japanese waters. Descriptions of two naupliar stages and the infective copepodid stage of *P. branchiostegi* are also provided for the first time, and *P. mebaru* Yamaguti, 1939 is recognised herein as a junior synonym of *P. branchiostegi*. The latter copepod species represents a new family, the Pseudohatschekiidae fam. nov., of the Siphonostomatoida characterised by the following apomorphies: (a) two free pedigerous somites present between the cephalothorax and the genital complex; (b) a chelate antenna bearing two digitate processes and a thin cuticular covering; (c) a unilobate maxillule, with the palp completely fused to the endite and represented by a surface seta; (d) a rounded process furnished with pectinate membranes on the apex of the

maxillary basis; (e) 2-segmented rami on legs 1–3; and (f) the absence of leg 4. It is also now evident that *P. branchiostegi* is a relatively common and abundant parasite of *Branchiostegus* spp. in the Far East.

Introduction

The copepod genus *Pseudohatschekia* Yamaguti, 1939 was established by Yamaguti (1939a) in the siphonostomatoid family Dichelesthidae Milne Edwards, 1840 to accommodate two new species, *P. branchiostegi* Yamaguti, 1939 obtained from the gills of the red tilefish *Branchiostegus japonicus* (Houttuyn) caught in the western North Pacific Ocean, off Kochi, Japan, and *P. mebaru* Yamaguti, 1939 collected from the gills of the darkbanded rockfish *Sebastes inermis* (Cuvier) (= a junior synonym of *Sebastes inermis* Cuvier: see Kai & Nakabo, 2008) caught in the Seto Inland Sea, off Tarumi, Japan. Among the other four genera recognised in the Dichelesthidae at that time, i.e. *Dichelesthium* Hermann, 1804, *Lamproglena* von Nordmann, 1832, *Hatschekia* Poche, 1902 and *Pseudocongericola* Yü, 1933, Yamaguti (1939a) explicitly stated that *Pseudohatschekia* differs from *Hatschekia* in having a cheliform antenna, two pairs of maxillipeds (= maxilla and maxilliped), the first thoracic somite fused with the head and the second and the third thoracic somites free. Yamaguti (1963)

D. Tang (✉) · D. Uyeno · K. Nagasawa
Laboratory of Aquaculture, Department of Bioresource Science, Graduate School of Biosphere Science, Hiroshima University, 1-4-4 Kagamiyama, Higashi-Hiroshima 739-8528, Japan
e-mail: copepods@gmail.com

K. Izawa
Izawa Marine Biological Laboratory,
795-16 Kannonji, Tsu, Mie 514-0062, Japan

subsequently retained *Pseudohatschekia* in the Dichelesthioidea when he arbitrarily raised it to superfamily level as the Dichelesthioidea Milne Edwards, 1840 to encompass the Dichelesthioidea along with the Catlaphillidae Tripathi, 1960 and three erroneous new families, the Anthosomatidae C. B. Wilson, 1922, Eudactylinidae C. B. Wilson, 1922 and Pseudocycnidae C. B. Wilson, 1922. Kabata (1979) questioned Yamaguti's (1963) Dichelesthioidea, and particularly the inclusion of the Catlaphillidae, a taxon that was founded on a poorly described species, *Catlaphilla elongata* Tripathi, 1960. This species, along with *Catlaphilla lingi* Manohar, Seenappa, Venkateshappa & Shetty, 1981, was later relegated to the cyclopoid family Lernaeidae Cobbold, 1879 by Ho (1998). Kabata (1979) further recognised the lack of affinity between various groups of genera within the former Dichelesthioidea *sensu lato*, and consequently evaluated the body tagmosis and structure of the antenna, maxilla and maxilliped among the dichelesthioid genera to untangle this undeniably heterogeneous group. As a result of Kabata's skilful efforts, some genera were reshuffled among the Eudactylinidae, Dichelesthioidea, Pseudocycnidae and his three newly-proposed families, Kroyeriidae Kabata, 1979, Hatschekiidae Kabata, 1979 and Lernanthropidae Kabata, 1979. More importantly, Kabata concluded that more information on *Pseudohatschekia* was needed before a valid decision could be made on its familial position. Indeed, *Pseudohatschekia* has continued to be regarded as a *genus inquirendum* by present authorities (Kazachenko, 2001; Boxshall & Halsey, 2004). In this paper we provide a detailed redescription of *P. branchiostegi* based on new material collected from several species of *Branchiostegus* Rafinesque captured in Japanese waters in order to clarify the morphological details and systematic position of this historically problematical copepod species. Descriptions of the early developmental stages of *P. branchiostegi* are also provided for the first time.

Materials and methods

Pseudohatschekia branchiostegi samples were obtained from the following sources: (a) specimens collected from *Branchiostegus japonicus* and *B. albus* Dooley, respectively, captured off the Tsushima

Islands and Okinawa-jima Island, Japan, by Dr Masaaki Machida were borrowed from the National Museum of Nature and Science (NSMT), Tokyo, Japan; (b) from *B. japonicus* caught in Tanabe Bay, Wakayama Prefecture, Japan; (c) from *B. japonicus* captured in the Sea of Japan, off Hagi, Yamaguchi Prefecture, Japan, and subsequently purchased at Shimonoseki Fish Market, Yamaguchi Prefecture, Japan; (d) from specimens of an undescribed species of *Branchiostegus* (known in Japan as "Hana-amadai") purchased in 1997 and 2000 at Awase Fish Market, Okinawa-jima Island, Japan, and subsequently lodged at the Faculty of Science of the University of the Ryukyus (URM), Japan; and (e) from "Hana-amadai" samples purchased in 2010 at Awase Fish Market, Okinawa-jima Island, Japan. Type-material of *P. branchiostegi* (identified by the prefix SY, an abbreviation of Satyu Yamaguti) was also borrowed from the Meguro Parasitological Museum, Tokyo, Japan, for comparative purposes.

Larvae used in this study were reared from egg-sacs that were manually separated from ovigerous females of *P. branchiostegi* at the Seto Marine Biological Laboratory, Kyoto University, Japan, from 16 to 22 May, 1971. Detached egg-sacs were distributed into Petri dishes each containing about 30 ml of filtered seawater and placed in a water bath at 18–19°C. Neither aeration nor water circulation was applied to the culture system, but the filtered seawater was renewed two or three times each day. Samples of each larval stage that had developed during the 7-day rearing period were fixed in 4% formalin and then preserved in 70% ethanol.

Some larval and adult specimens were, respectively, stained with chlorazol black E in lactic acid and cleared in lactic acid prior to being measured using a calibrated eyepiece micrometer. Measurements given are in micrometres and represent the range followed by the mean in parentheses unless stated otherwise. A subsample of the stained larvae and cleared adult specimens (intact and dissected) was transferred to a wooden slide (see Humes & Gooding, 1964) and examined using, respectively, an Olympus BH-2 and Olympus BX51 compound microscope each equipped with Phase Contrast. All drawings were made with the aid of a drawing tube. SEM material was dehydrated in a graded ethanol series, critical point-dried, sputter-coated with platinum, mounted on brass stubs and examined using a

JEOL JSM-6390LV scanning electron microscope at 5–20 kV. Morphological terminology follows Kabata (1979) and Huys & Boxshall (1991), and fish names conform to FishBase (Froese & Pauly, 2010).

Pseudohatschekia branchiostegi Yamaguti, 1939

Material examined: 26 adult ♀ types, all mounted on 1 slide (SY 3697), ex *Branchiostegus japonicus* (Houttuyn), western North Pacific Ocean, off Kochi (33°23'N, 133°28'E), Kochi Prefecture, Japan, 17 August 1936, leg. S. Yamaguti; 3 adult ♀, ex *B. japonicus*, northern East China Sea, off the Tsushima Islands (34°22'N, 129°19'E), Nagasaki Prefecture, Japan, 30 July 1969, leg. M. Machida; 8 adult ♀ (1 dissected and mounted on a glass slide), ex *B. japonicus*, western North Pacific Ocean, Tanabe Bay (33°41'N, 135°20'E), Wakayama Prefecture, Japan, 16 May 1971, leg. K. Izawa; 87 adult ♀ (4 damaged; 3 dissected and mounted on 1 glass slide each) and 2 adult ♂ (1 damaged), ex 4 *B. japonicus* (SL = 26.0–35.6 cm), Sea of Japan, off Hagi (34°25'N, 131°23'E), Yamaguchi Prefecture, Japan, 28 October 2009, leg. D. Tang and K. Nagasawa; 12 adult ♀ (1 dissected and mounted on 1 glass slide), ex *B. albus* Dooley, East China Sea, off Nago (26°35'N, 127°58'E), Okinawa-jima Island, Okinawa Prefecture, Japan, 22 May 1993, leg. M. Machida; 37 adult ♀ (11 damaged), ex 1 *Branchiostegus* sp. (URM-38976; SL = 27.9 cm), Awase Fish Market (26°19'N, 127°50'E), Okinawa-jima Island, Okinawa Prefecture, Japan, 7 December 1997, leg. D. Uyeno and D. Tang; 59 adult ♀ (10 damaged; 4 young adults) and 2 adult ♂, ex 1 *Branchiostegus* sp. (URM-40872; SL = 30.0 cm), Awase Fish Market (26°19'N, 127°50'E), Okinawa-jima Island, Okinawa Prefecture, Japan, 6 September 2000, leg. D. Uyeno and D. Tang; 52 adult ♀ (3 young adults), ex 4 *Branchiostegus* sp. (SL = 25.2–31.5 cm), Awase Fish Market (26°19'N, 127°50'E), Okinawa-jima Island, Okinawa Prefecture, Japan, 22 April 2010, leg. D. Tang and K. Nagasawa.

Attachment site: The parasite uses its chelate antennae to clasp the host's secondary gill lamella (Fig. 1A,B).

Voucher specimens: Specimens collected by M. Machida from the Tsushima Islands (3 adult ♀; NSMT–Cr 21132) and Okinawa-jima Island (12 adult

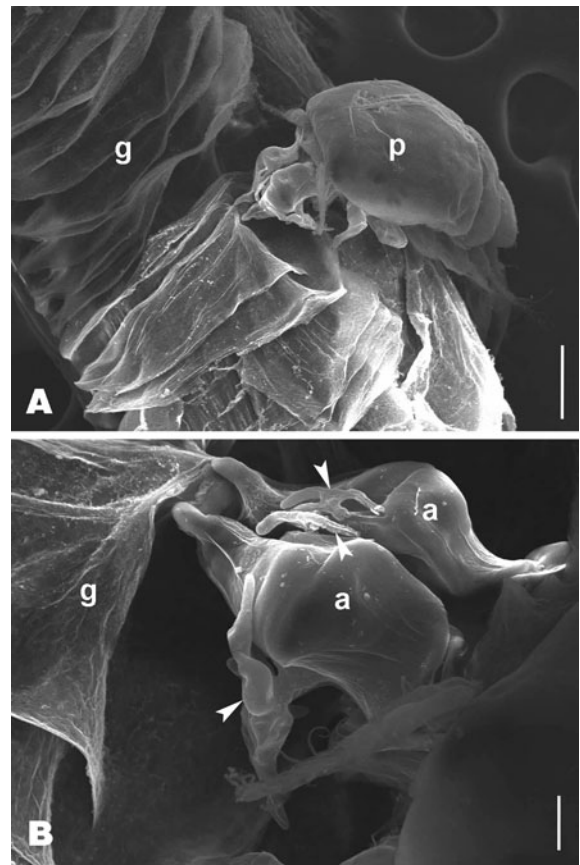


Fig. 1 *Pseudohatschekia branchiostegi* Yamaguti, 1939, SEM photographs. A, adult female (p) *in situ* on the host's gill filament (g); B, anterolateral view of antennae (a) showing clasp of secondary gill lamella (g) and digitate processes (arrowheads). Scale-bars: A, 100 µm; B, 20 µm

♀; NSMT–Cr 21133), Japan, along with 15 adult ♀ and 1 adult ♂ (NSMT–Cr 21134) collected from hosts caught off Hagi, Yamaguchi Prefecture, Japan, are deposited at the National Museum of Nature and Science (NSMT), Tokyo, Japan. An additional 21 adult ♀ and 1 adult ♂ (USNM 1138871) collected from hosts caught off Hagi, Yamaguchi Prefecture, Japan, are deposited at the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. The remaining specimens are kept in the personal collection of the authors.

Description (Figs. 2–6)

Adult female

Body (Fig. 2A) 572–810 (715) long (from anterior margin of cephalothorax to posterior margin of

caudal rami; $n = 11$), composed of cephalothorax, 2 free pedigerous somites, genital complex and abdomen. Cephalothorax orbicular, incorporating first pedigerous somite, wider than long [210–285 (250) \times 285–335 (309)], representing *c.*35% of body length, with posterolateral corners protruded over anterolateral corners of succeeding somite. First free pedigerous somite (= second pedigerous somite) wider than long [75–110 (91) \times 240–290 (266)], with rounded lateral margins. Second free pedigerous somite (= third pedigerous somite) distinctly narrower than preceding somite, 60–90 (79) \times 122–150 (140), with posterior margin typically extending over proximal margin of genital complex. Fourth pedigerous somite incorporated into anterior region of genital complex (Fig. 2B); latter large, suborbicular, representing *c.*43% of body length, slightly longer than wide [230–380 (308) \times 235–325 (281)], with genital apertures (Fig. 2C) situated ventrally near junction of abdomen. Abdomen 1-segmented, short, quadrate and 35–55 (42) \times 40–50 (44). Caudal ramus (Fig. 2D) longer than wide [10–15 (14) \times 7.5–12.5 (10.7)], with 6 setae (seta I absent; seta VII displaced towards apical margin); setae III and IV unipinnate; seta VI longest and bipinnate; all other setae naked. Egg-sac (Fig. 2E) uniseriate, straight and containing 3–6 eggs.

Rostrum (Fig. 2F) short, subtriangular. Antennule (Fig. 2G) indistinctly 5-segmented (articulation between first and second segments visible on dorsal surface only), with armature of 9, 8, 2, 1 and 13+ aesthetasc (segmental homology of ultimate segment probably XXI–XXVIII; others indeterminate); all setae naked; 2 posterodistal setae on terminal segment share common base. Antenna (Figs. 1B, 2H, 3A) chelate, partly surrounded by additional thin cuticular covering and 4-segmented, comprising coxa, basis and 2-segmented endopod; coxa unarmed; basis with large, fleshy digitate process arising laterally from weakly sclerotised surface; proximal endopodal segment bears small, fleshy digitate process arising proximally from inner surface and anterodistal beak-like process opposing terminal segment; distal endopodal segment unarmed, incorporating distal claw; claw and beak-like process furnished with surface striations distally (Fig. 3B). Oral siphon (Fig. 3C,D) with membranous tip on labrum and 2 ventrodistal folds flanking flaccid midsection on labium. Mandible (Figs. 2I, 3D)

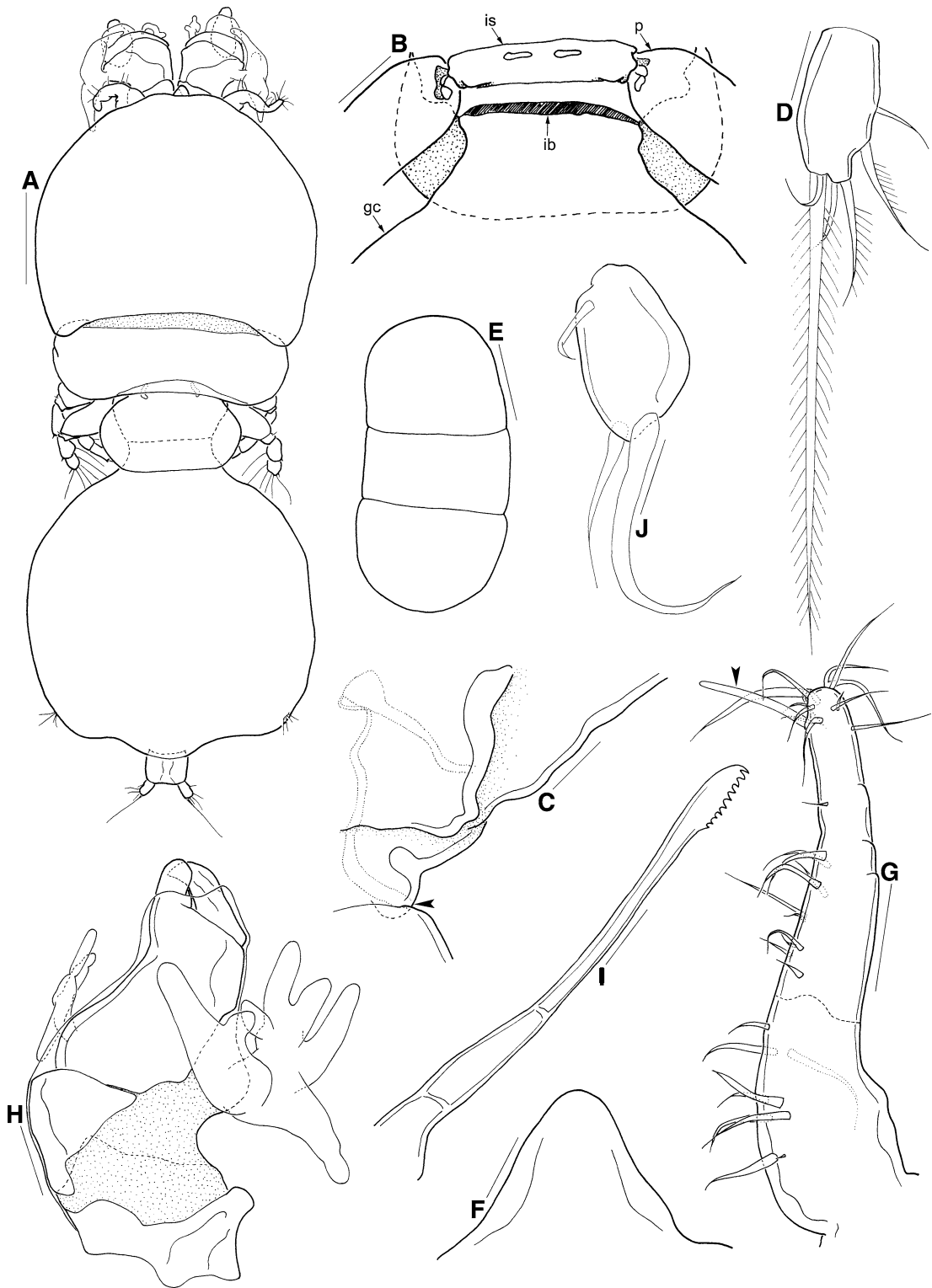
Fig. 2 *Pseudohatschekia branchiostegi* Yamaguti, 1939, adult female. A, habitus, dorsal; B, leg 3 intercoxal sclerite (is) and protopod (p), third interpodal bar (ib) and anterior region of genital complex (gc), ventral; C, genital apertures (copulatory opening indicated by arrowhead), ventral; D, right caudal ramus, dorsal; E, egg-sac, dorsal; F, rostrum, dorsal; G, left antennule (aesthetasc indicated by arrowhead), ventral; H, right antenna, lateral; I, right mandible, posterior; J, left maxillule, ventrolateral. Scale-bars: A, 100 μ m; B, H, 25 μ m; C–D, I, 10 μ m; E, 50 μ m; F, J, 5 μ m; G, 20 μ m

modified into elongate stylet bearing 10 inner distal teeth. Maxillule (Fig. 2J) small, unilobate, with outer proximal surface seta (representing palp) and 2 unequal apical elements on endite. Maxilla (Figs. 4A, 5A) 2-segmented, composed of syncoxa and basis; syncoxa unarmed, with large tube pore near its base; basis slimmer than syncoxa, with crescentic row of minute spinules dorsodistally, spiniform element ventrodistally and rounded terminal process furnished with rows of pectinate membranes. Maxilliped (Fig. 4B) subchelate, 4-segmented, comprising syncoxa, basis and 2 free endopodal segments; basal segments unarmed; proximal endopodal segment compound, representing first and second segments, with seta near centre of posterior surface; terminal (third) endopodal segment forming claw armed with proximal seta on posterior surface.

Legs 1–3 (Figs. 4C–D, 5B–D, 6A) biramous and bimerous. Armature on rami of legs 1–3 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-1	I-1; II,I,5	0-1; 1,5
Leg 2	0-0	1-0	I-1; II,5	0-1; 1,4
Leg 3	0-0	1-0	I-1; I,5	0-1; 3

Leg 1 (Figs. 4C, 5B,C) intercoxal sclerite naked, wider than long, with small rounded lobe at distolateral corners. Coxa and basis ornamented with minute spinules on anterior surface. Exopod with inner row of setules on proximal segment, outer fringe of minute spinules on each segment and several spinules at base of each spine; apical spine on terminal segment with filiform tip; all spines with finely spinulate margins. Endopod with outer row of spinules on proximal segment, 2 spiniform processes on terminal segment and row of setules along lateral



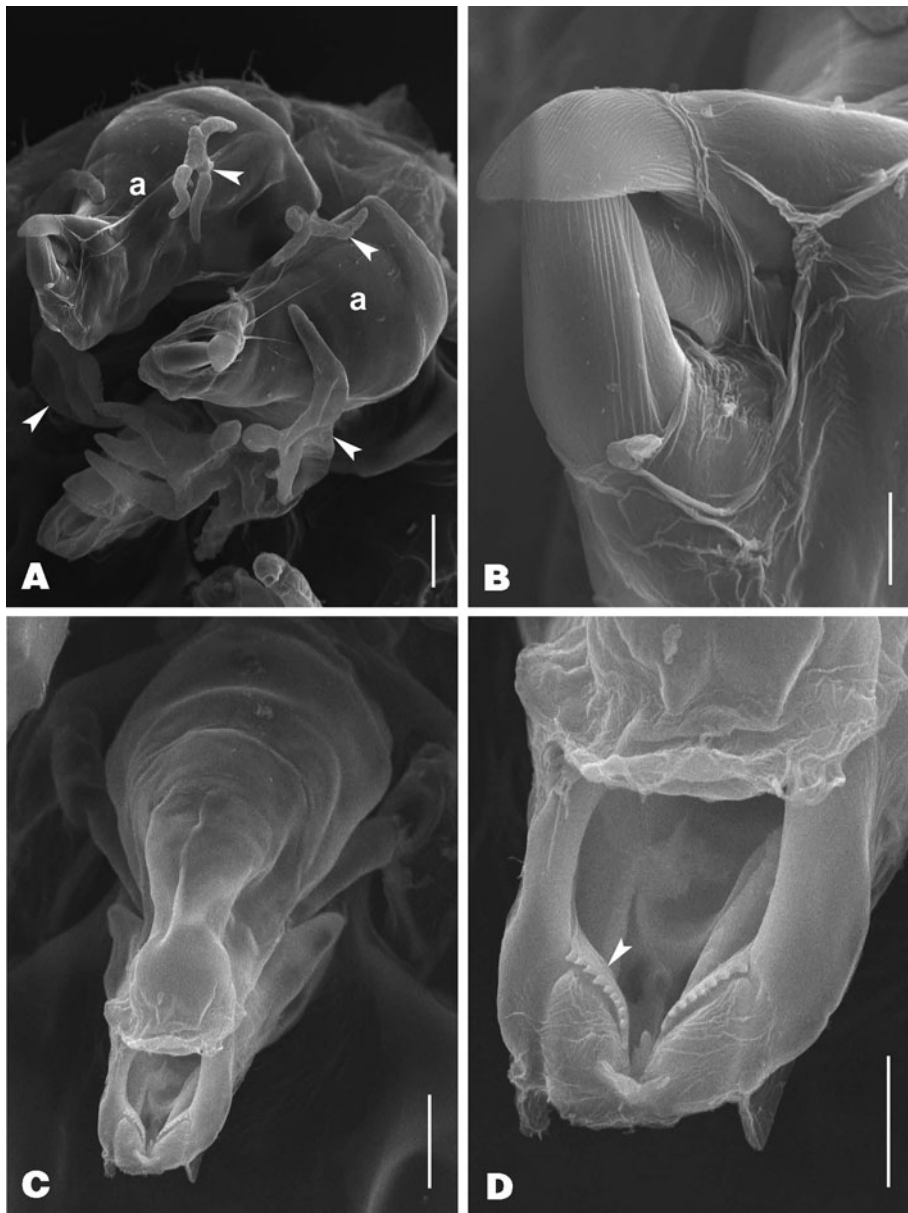


Fig. 3 *Pseudohatschekia branchiostegi* Yamaguti, 1939, SEM photographs. A, anterior view of antennae (a) showing digitate processes (arrowheads); B, distal end of right antenna showing cuticular covering as well as surface striations on beak-like process of proximal endopodal segment and terminal claw, inner view; C, oral siphon, anteroventral view; D, distal end of oral siphon showing mandible tip (arrowhead), anteroventral view. *Scale-bars*: A, 20 μ m; B, D, 5 μ m; C, 10 μ m

margin of each segment as well as inner margin of terminal segment. Leg 2 (Figs. 4D, 5D) similar to leg 1, except with relatively wider intercoxal sclerite, naked coxa, finely spinulate lateral margin on outermost seta of terminal exopodal segment and 1 less armature element on basis as well as terminal segment of each ramus. Leg 3 (Fig. 6A) similar to leg 2, except

without spinules on coxa, basis and proximal endopodal segment, and with 1 less spine on terminal exopodal segment and 2 fewer setae and just 1 spiniform process on terminal endopodal segment.

Leg 4 absent. Leg 5 (Figs. 2A, 6B) vestigial, represented by 4 naked setae on posterolateral surface of genital complex. Leg 6 (Fig. 2C) rudimentary,

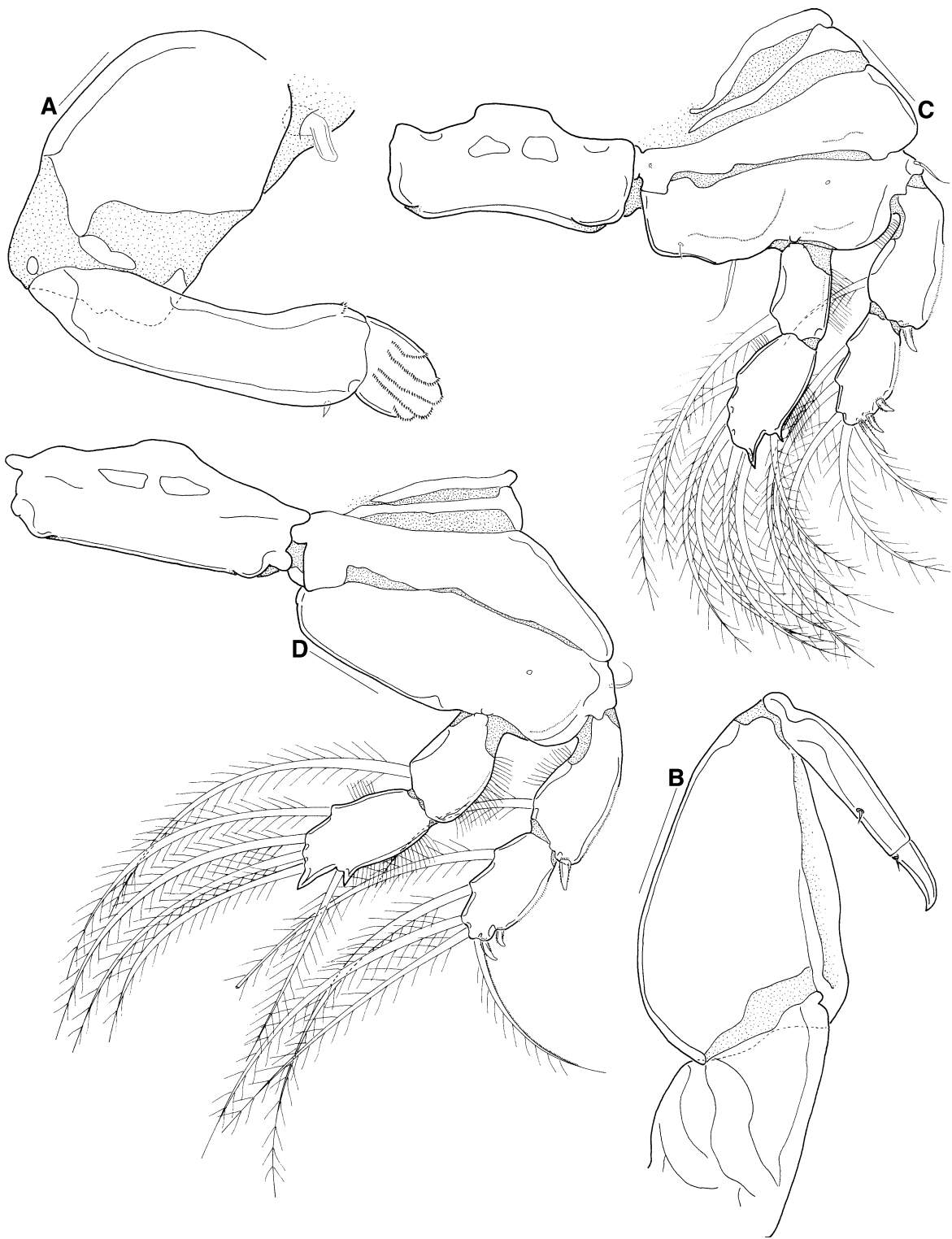


Fig. 4 *Pseudohatschekia branchiostegi* Yamaguti, 1939, adult female. A, right maxilla, anterior; B, right maxilliped, posterior; C, left leg 1, anterior; D, left leg 2, anterior. Scale-bars: A, 10 μ m; B–D, 20 μ m

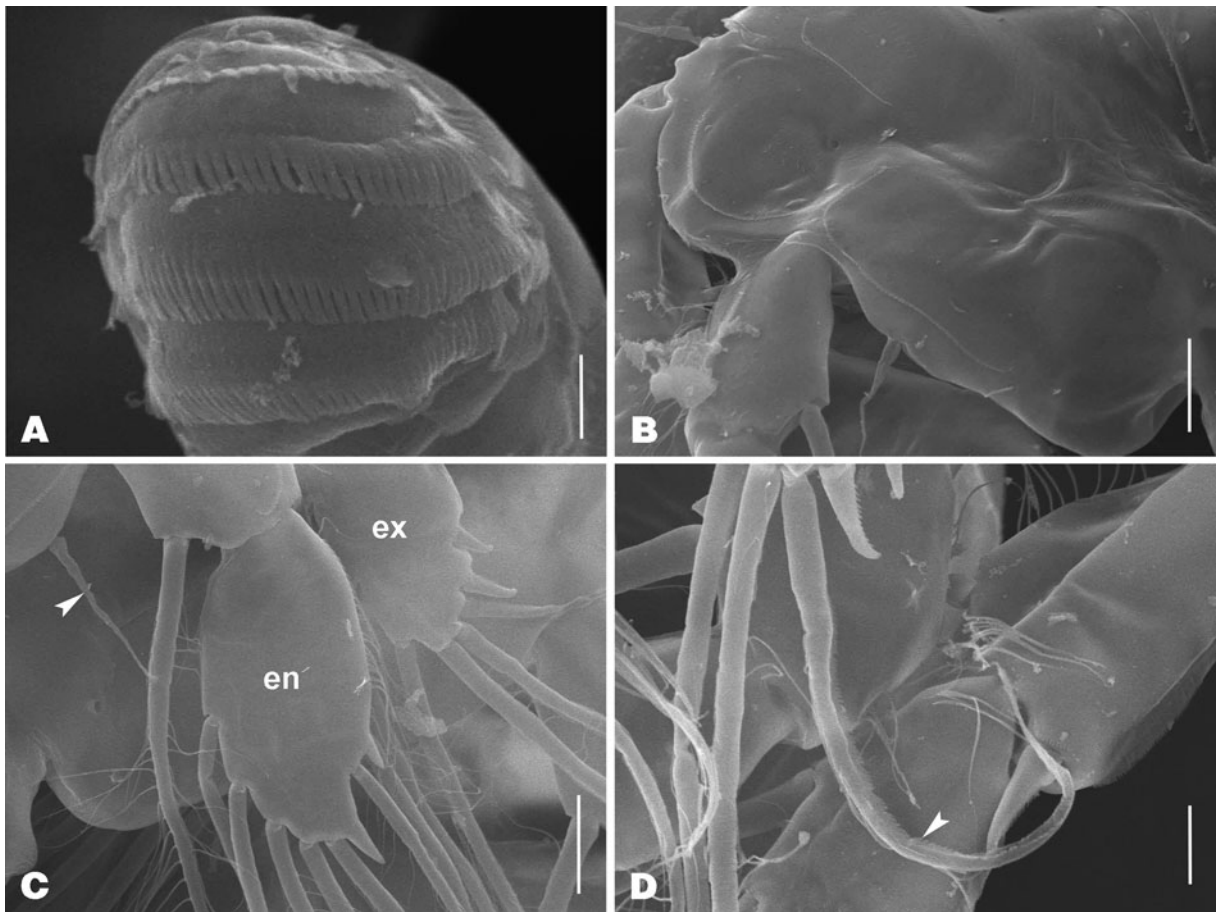


Fig. 5 *Pseudohatschekia branchiostegi* Yamaguti, 1939, SEM photographs. A, distal end of left maxilla, ventral view; B, protopodal segments of right leg 1, anterior view; C, inner seta on basis (arrowhead), terminal segment of exopod (ex) and both segments of endopod (en) of left leg 1, anterior view; D, terminal armature elements of left leg 2 exopod showing spinulate lateral margin (arrowhead) on outermost seta, anterior view. Scale-bars: A, 2 μ m; B–D, 10 μ m

represented by unarmed genital operculum at oviduct opening.

Variability of adult female. Six of 8 adult female specimens from the western North Pacific Ocean, off Tanabe Bay, Wakayama Prefecture, Japan, with comparatively more compact body as well as quadrate genital complex (Fig. 6C). Measurements of 1 of these specimens as follows: body 510 long; cephalothorax 195 \times 315; first free pedigerous somite 105 \times 300; second free pedigerous somite 65 \times 145; genital complex 200 \times 247.5; abdomen 30 \times 42.5; caudal ramus 15 \times 10.

Adult male

Body (Fig. 6D) and appendages as in female, except genital complex considerably smaller and abdomen

composed of 2 somites. Measurements of 1 specimen as follows: body 545 long; cephalothorax 235 \times 270; first free pedigerous somite 80 \times 220; second free pedigerous somite 72.5 \times 115; genital complex 120 \times 120; first abdominal somite 10 \times 35; second abdominal somite 30 \times 37.5; caudal ramus 12.5 \times 10.

Development

The first nauplii hatch from eggs within 1 day after the onset of rearing, and almost all the second nauplii moult further into copepodid I without feeding within 4 days.

Nauplius I

Body (Fig. 7A) ovoid, of typical nauplius shape, 110–130 (130) long and 80–90 (90) wide ($n = 8$),

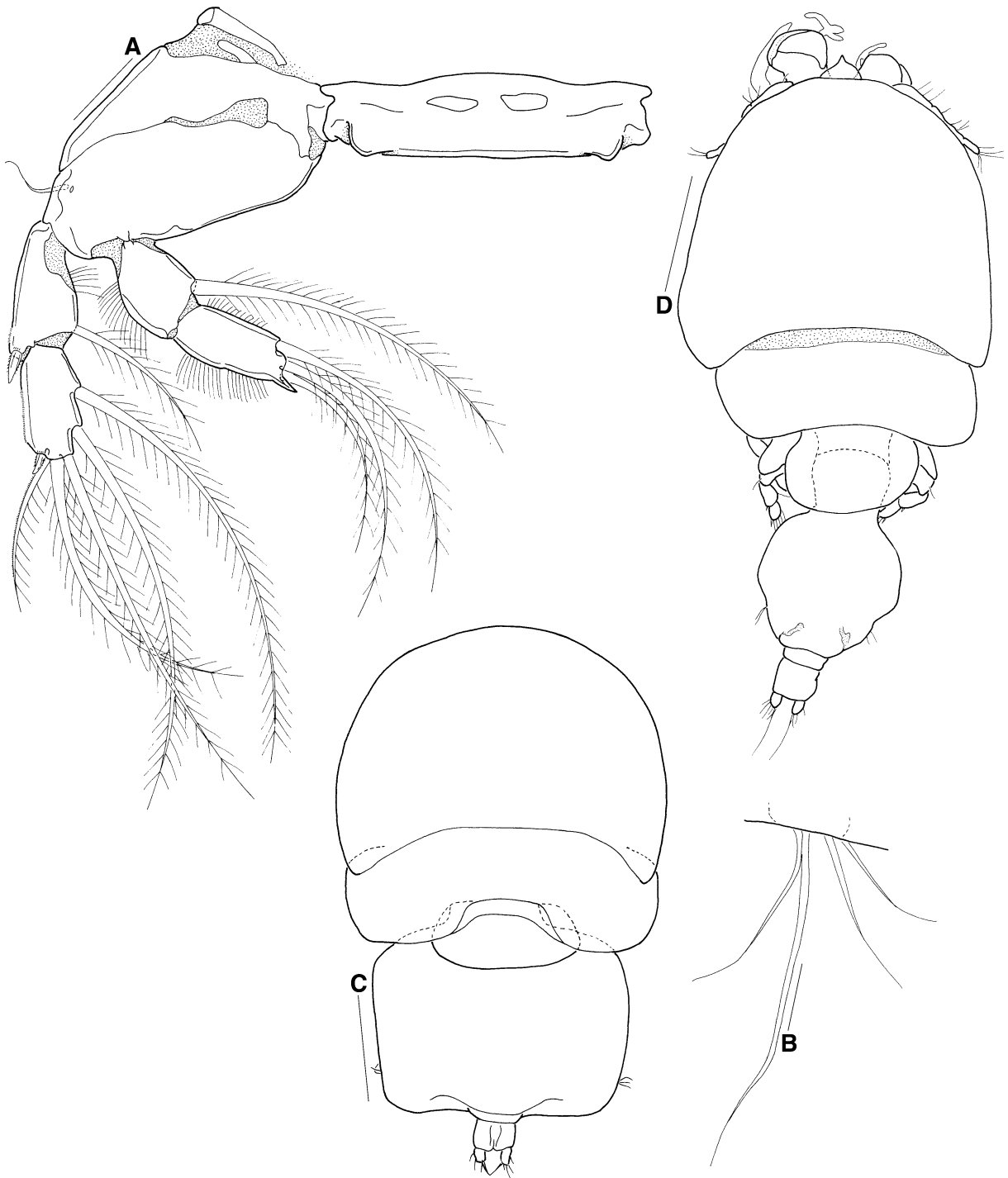


Fig. 6 *Pseudohatschekia branchiostegi* Yamaguti, 1939, adult female (A–C) and adult male (D). A, right leg 3, anterior; B, left leg 5, dorsal; C, habitus, dorsal; D, habitus, dorsal. Scale-bars: A, 20 μm ; B, 5 μm ; C–D, 100 μm

bears 3 ventrolateral pairs of appendages along anterior third of body and posterolateral pair of setiform balancers. Labrum represented by ventromedian round

swelling. Antennule uniramous, indistinctly 3-segmented; first segment short and unarmed, second unarmed and third with 2 terminal setae. Antenna

biramous. Exopod 4-segmented; first 3 segments each with mediobasal seta, last with distal seta. Endopod 2-segmented; first segment unarmed, second with 2 distal setae. Mandible biramous. Exopod similar to that of antenna. Endopod unimerous, with 2 distal setae.

Nauplius II

Body (Fig. 7B) elongate in comparison to preceding stage, 150–160 (150) long and 80 wide ($n = 3$), bears additional limb buds along posteroventral portion of body and pair of spines medial to balancers. Antennule as in preceding stage, except with newly added anterodistal seta and posterodistal seta on distal segment. Antenna as in preceding stage, except with newly added inner seta on first endopodal segment. Mandible unchanged from previous stage.

Copepodid I

Body (Fig. 7C,D) comprised of cephalothorax (incorporating first pedigerous somite) and posterior portion of 4 free somites; first 2 free somites bears leg 2 and rudimentary leg 3, respectively, third naked and fourth with caudal rami. Body length (not including caudal rami) 210–300 (220) ($n = 14$). Cephalothorax occupies *c.*55% of body length, with mean length of 120 and mean width of 100. Caudal ramus (Fig. 7D) as long as wide, with 6 setae (seta I absent); seta V longest and pinnate; all other setae naked.

Rostrum distinct. Antennule (Fig. 8A) indistinctly 4-segmented, mounted on pedestal and deflected at nearly right angle at articulation between first 2 segments; armature formula of 1, 1, 1 and 12+ aesthetasc. Antenna (Fig. 8B,C) chelate, robust, 4-segmented; coxa and basis broad; latter with digitate, fleshy process arising from lateral surface. Proximal endopodal segment with beak-like anterodistal process receiving tip of distal endopodal segment (claw); latter recurved, stout, with midventral seta. Oral siphon (Fig. 8B,C) short. Mandible (Fig. 8B,C) modified into elongate blade, with rod-shaped, fleshy process on its base representing palp. Maxillule (Fig. 8B,C) lobate, bears 2 distal setae. Maxilla (Fig. 8D) brachiform, 3-segmented; praecoxa short; coxa broad, unarmed; basis elongate, with distal seta and claw. Maxilliped (Fig. 8D) prehensile, 4-segmented; basis unarmed and longer than distal 3 endopodal segments combined; distal endopodal segment forms claw.

Legs 1–2 (Fig. 8E,F) biramous and unimerous. Armature on rami of legs 1–2 as follows (Roman numerals = spines; Arabic numerals = setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	IV,1,3	7
Leg 2	0-0	1-0	III,1,3	6

Outermost seta on exopod of both legs with pinnate inner margin and membrane along outer margin; all other setae pinnate along both margins. Endopod of both legs with spiniform projection between bases of 2 outermost setae.

Leg 3 (Fig. 7D) vestigial, represented by 2 unequal posterolateral setae on second free pedigerous somite.

Discussion

Systematics

Nearly all of the 26 adult female type-specimens of *Pseudohatschekia branchiostegi* examined in this study were completely or partly dried out, due in large part to the coverslip being left unsealed for more than 60 years. Fortunately, all the appendages, except the antennules, maxillules and caudal rami, of one specimen were satisfactorily preserved, which permitted us to conclude after careful examination that: (a) our specimens are conspecific with *P. branchiostegi*; and (b) Yamaguti (1939a) overlooked the digitate processes on the antenna and misinterpreted the spiniform process(es) on the terminal endopodal segment of all three legs as an armature element(s). Yamaguti also misinterpreted the structure of the maxillule as a bilobate structure; judging from his description and figure of this appendage the “inner ramus with a long seta, which appears as if segmented near its middle” is in actuality the mandible. Yamaguti illustrated a proximal seta on the maxilliped basis, but no such element was observed in our specimens. According to Yamaguti (1939a), *P. branchiostegi* can be distinguished from its congener, *P. mebaru*, only by differences in body shape and size ratios of the body somites and

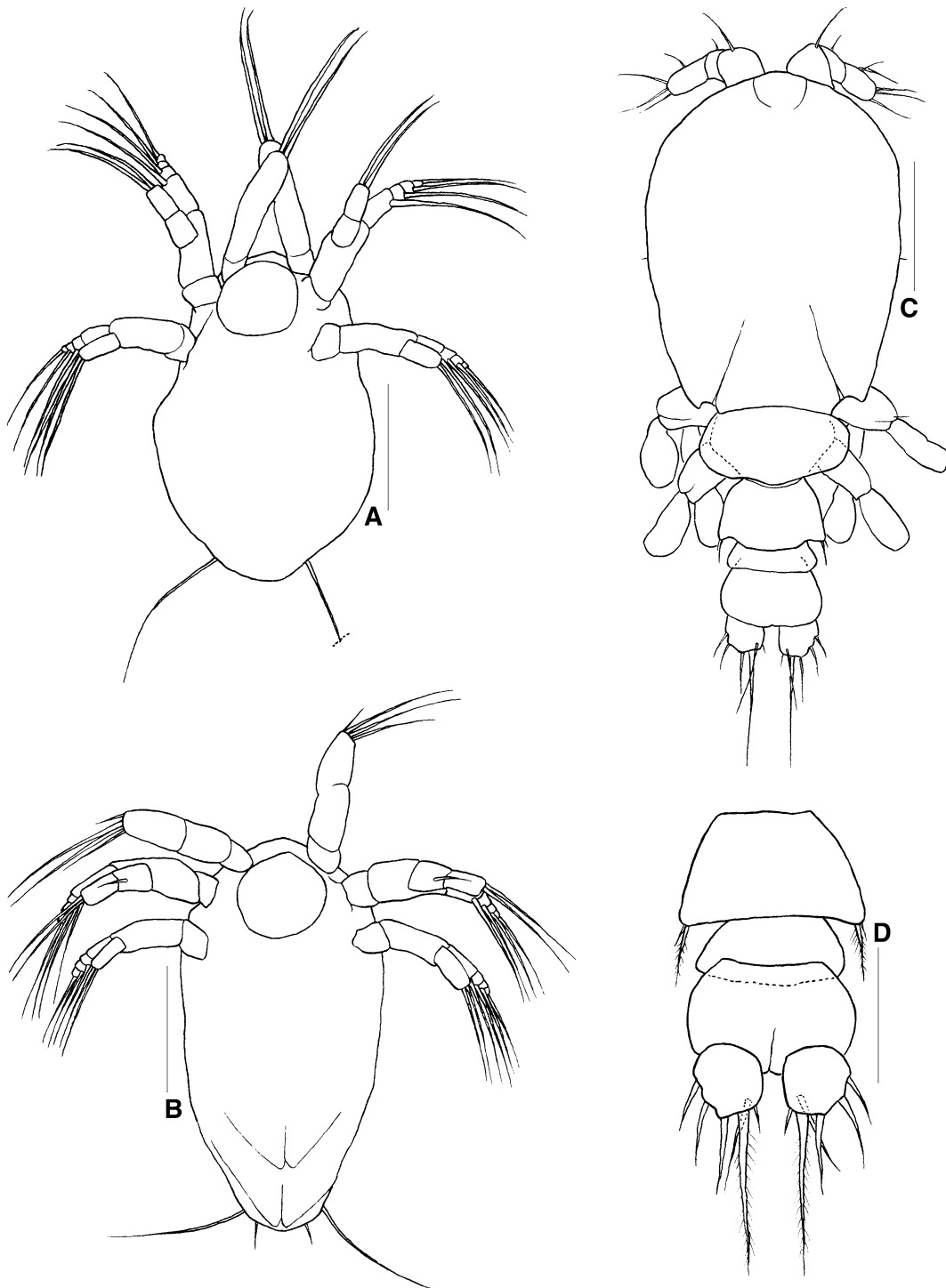


Fig. 7 *Pseudohatschekia branchiostegi* Yamaguti, 1939, free-living stages. A, nauplius I, ventral; B, nauplius II, ventral; C, copepodid I, dorsal; D, posterior region of copepodid I, ventral. Scale-bars: A–C, 50 μ m; D, 30 μ m

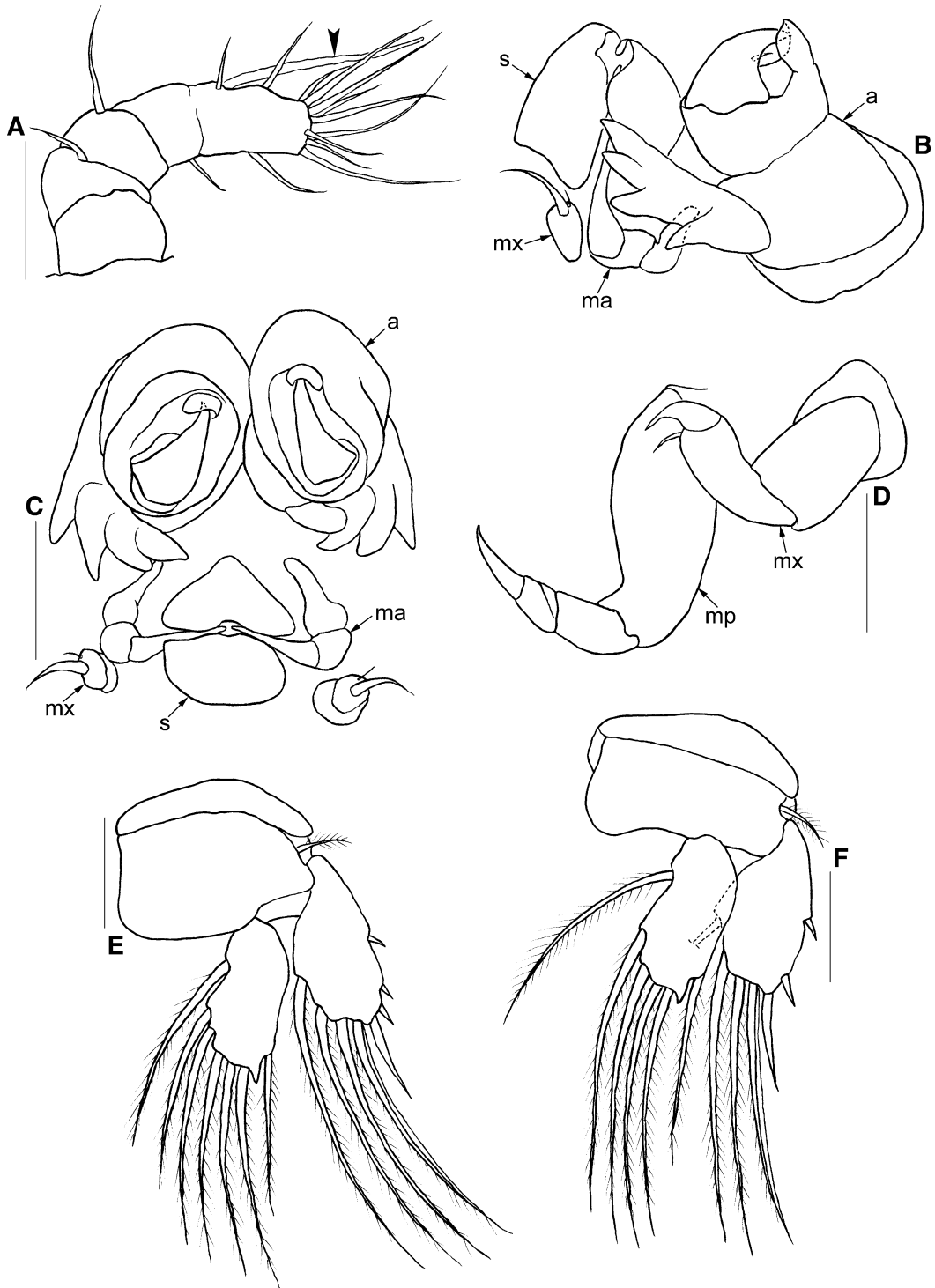


Fig. 8 *Pseudohatschekia branchiostegi* Yamaguti, 1939, copepodid I. A, right antennule (aesthetasc indicated by arrowhead), dorsolateral; B, antenna (a), oral siphon (s), mandible (ma) and maxillule (mx), lateral; C, same, ventral; D, left maxilla (mx) and left maxilliped (mp), ventrolateral; E, left leg 1, anterior; F, left leg 2, anterior. Scale-bars: A–F, 20 μ m

egg-sacs. The validity of *P. mebaru* is, in our opinion, questionable, particularly considering that two different female body forms of *P. branchiostegi* were observed in this study and the size of a copepod egg-sac naturally varies according to the number of eggs extruded into the egg-sac by the adult female. Furthermore, the occurrence of *P. mebaru* on *Sebastes inermis* may represent a fortuitous association, as *Pseudohatschekia* has not been collected again from members of the *S. inermis* species complex (see Kai & Nakabo, 2008) despite extensive sampling of this fish group from 2005 to 2006 in the Seto Inland Sea (K. Nagasawa, unpublished data). The type-specimens of *P. mebaru* (four adult females all mounted on a single, unsealed slide; SY3667) deposited at the Meguro Parasitological Museum, Tokyo, Japan, are completely dried out, which precluded us from making any comparisons between them and our material of *P. branchiostegi*. Despite this, *P. mebaru* is here regarded as a junior synonym of *P. branchiostegi* until there is evidence to the contrary. Since Yamaguti's (1939a, 1963) diagnoses of *Pseudohatschekia* are inaccurate, a revised diagnosis is provided below.

***Pseudohatschekia* Yamaguti, 1939**

Amended diagnosis. Body comprising cephalothorax (incorporating first pedigerous somite), 2 free pedigerous somites, genital complex (incorporating fourth pedigerous somite) and abdomen. Genital complex orbicular in female, pyriform in male. Genital apertures situated ventrally near junction of abdomen in both sexes. Abdomen 1-segmented in female, 2-segmented in male. Caudal ramus with 6 setae (seta I absent). Egg-sacs uniseriate, straight, each containing 3–6 eggs. Rostrum short and subtriangular. Antennule indistinctly 5-segmented. Antenna chelate, surrounded by thin cuticular covering and 4-segmented, comprising coxa, basis and 2-segmented endopod; basis with large, fleshy digitate process; proximal endopodal segment bears small, fleshy digitate process proximally and beak-like process distally; distal endopodal segment unarmed, incorporating distal claw. Oral siphon well developed. Mandible styliform, bears distal teeth; palp absent. Maxillule small, unilobate, with outer proximal surface seta (representing palp) and 2 unequal apical elements on endite. Maxilla 2-segmented, composed of syncoxa and basis; latter with rounded terminal process furnished with rows of pectinate membranes.

Maxilliped subchelate, 4-segmented, comprising syncoxa, basis and 2 free endopodal segments; basal segments unarmed; endopodal segments each with 1 seta. Legs 1–3 unmodified, each connected by intercoxal sclerite and with 2-segmented rami. First exopodal segment of all 3 leg pairs with inner seta. Distal endopodal segment of legs 1 and 2 with 2 spiniform projections; leg 3 with 1 spiniform projection. Leg 4 absent. Leg 5 vestigial, represented by 4 naked setae on posterolateral surface of genital complex. Leg 6 rudimentary, represented by unarmed genital operculum. Type-species: *P. branchiostegi* Yamaguti, 1939.

It is commonly recognised that the Siphonostomatoida Burmeister, 1835 is a monophyletic group and the siphonostomes parasitic on vertebrate hosts were derived from siphonostomes associated with invertebrates (Kabata, 1979; Huys & Boxshall, 1991). This premise has gained support from Benz's (1993) morphology-based phylogenetic analysis of all siphonostomatoid families parasitic on vertebrates, except the Archidactylinidae Izawa, 1996 and Amaterasidae Izawa, 2008, and more recently from Huys et al.'s (2007) molecular analysis of gymnoplean and podoplean copepod representatives, including siphonostomes associated with invertebrates and vertebrates. Although Benz's analysis did not fully resolve the interfamilial relationships of the siphonostomes parasitic on vertebrates, six discrete clades were identified: the Eudactylinidae is a sister taxon to an unresolved group containing the Kroyeriidae, the dichelesthiiform complex (Dichelesthiidae, Pseudocycnidae, Hatschekiidae, Lernanthropidae and Hyponeoidae Heegaard, 1962), the Pennellidae Burmeister, 1835, the lernaepodiform complex (Lernaepodidae Milne Edwards, 1840, the Sphyriidae C. B. Wilson, 1919 and Tanyleuridae Kabata, 1969) and the caligiform complex (Caligidae Burmeister, 1835, Pandaridae Milne Edwards, 1840, Cecropidae Dana, 1849, Trebiidae C. B. Wilson, 1905 and Dissonidae Yamaguti, 1939). The Archidactylinidae and Amaterasidae are probably the sister group to the Eudactylinidae and Pandaridae, respectively (Boxshall & Halsey, 2004; Izawa, 2008). Among these 18 families, *Pseudohatschekia* shares the apomorphic chelate antenna with the Kroyeriidae and Pennellidae. However, species of *Pseudohatschekia* cannot be accommodated in either family due to its

non-vermiform facies and possession of two digitate processes, one of which may represent the exopod (see below), and a thin cuticular covering on the adult antenna and a rounded process furnished with pectinate membranes on the apex of the maxillary basis. The pennellid *Exopenna crimmeni* Boxshall, 1986 also possesses an irregular anteroventral process arising from the antennal basis (see Boxshall, 1986), which may perhaps represent the exopod, but information on the larval development of this species is needed to determine the homology of this structure. The dichelesthiiid *Anthosoma crassum* (Abildgaard, 1794) also possesses a cuticular covering on the antenna, but this sheath is confluent with the ventral surface of the cephalothorax, extends around the first segment (coxa) and is functionally coupled with the retractile nature of the antenna (Ingram, 2004). Species of *Pseudohatschekia* can be further distinguished from the Kroyeriidae by the absence of leg 4 and presence of only two free pedigerous somites, 2-segmented rami on legs 1–3 and a unilobate maxillule, with the palp completely fused to the endite and represented by a surface seta, and from the Pennellidae by the presence of maxillipeds and a non-telescoping oral siphon. *Pseudohatschekia* is here recognised as the type-genus of a new monotypic family, the Pseudohatschekiidae fam. nov., with the diagnosis for the family as for the type-genus given above.

Prior to this study, we were under the false impression that *P. branchiostegi* was an extremely rare species, considering that it has been reported only once since its original discovery (Kim, 1998). It is now evident that this species is a relatively common inhabitant of *Branchiostegus* spp. and occurs in relatively high numbers on a single host. For example, of the four *B. japonicus* specimens examined from off Hagi, Yamaguchi Prefecture, on 28 October 2009 and four *Branchiostegus* sp. examined from Awase Fish Market, Okinawa Prefecture, on 22 April 2010, all were infected by *P. branchiostegi* at a mean intensity of 22.2 (range of 16–30 parasites) and 13 (range of 4–20 parasites), respectively. Four other parasitic copepods, all siphonostomes, have been reported from *B. japonicus*: the hatschekiids *Hatschekia branchiostegi* Yamaguti, 1939 and *H. longibrachium* Yamaguti, 1939, the lernaeopodid *Clavellotis branchiostegi* (Yamaguti, 1939) and the pennellid *Phrixecephalus umbellatus*

Shiino, 1956 (Yamaguti, 1939a,b; Choi et al., 2000). *Branchiostegus* contains 16 species, most of which occur in the Indo-West Pacific in depths ranging from 20 to 600 m (Dooley & Kailola, 1988). Species of *Pseudohatschekia* have been found thus far on three species of *Branchiostegus* from waters of the Far East (Yamaguti, 1939a; Kim, 1998; Present study), but sampling of *Branchiostegus* species elsewhere may reveal that *Pseudohatschekia* is more widely distributed than the present data suggest.

Developmental stages

Among the Siphonostomatoida infecting fishes, free-living stages experimentally reared from egg-sacs have been previously described for the Eudactylinidae, Kroyeriidae, Lernanthropidae, Pennellidae, Lernaeopodidae, Caligidae and Pandaridae. The number of naupliar stages preceding copepodid I is two in Pseudohatschekiidae (Present study), Lernanthropidae (see Cabral et al., 1984) and Caligidae (see Ho & Lin, 2004; Ohtsuka et al., 2009), one in the Eudactylinidae (see Kabata, 1976), one or none in the Lernaeopodidae (see Kabata & Cousens, 1973; Kabata, 1976; Ho et al., 2007; Piasecki & Kuźmińska, 2007), two, one or none in the Pennellidae (see Sproston, 1942; Kabata, 1976; Schram, 1979; Perkins, 1983), three in the Kroyeriidae (see Izawa, 2009) and five in the Pandaridae (see Izawa, 2010). It is worth noting here that a single nauplius stage has been experimentally reared from detached egg-sacs for the Dissonidae Yamaguti, 1963, but it differs from the above in that immediately after hatching it remains attached to the egg membrane by a pair of fine threads arising from the posterior end of its body and the paired limbs are unsegmented, uniramous and aetose (Anderson & Rossiter, 1969; Bennett, 1999).

Copepodid I of *Pseudohatschekia branchiostegi* is unique in having a fleshy digitate process on the lateral surface of the antennal basis. This structure may represent the exopod as it is positionally homologous to the 1-segmented, setose exopod on the antenna of copepodid I of plesiomorphic and derived siphonostome families, such as the Asteroceridae Burmeister, 1835 (see Ivanenko & Ferrari, 2003) and Lernaeopodidae (see Kabata & Cousens, 1973; Kabata, 1976; Ho et al., 2007; Piasecki & Kuźmińska, 2007), respectively, as well as the vestigial, irregularly wrinkled, aetose exopod on

the antenna of copepodid I of the pennellid *Haemobaphes diceraus* Wilson, 1917 (see Kabata, 1976). This digitate structure may, alternatively, represent an extension of the arthrodial membrane between the coxa and basis. Further studies are needed (e.g. muscular anatomy) to determine the homology of this structure. The smaller, fleshy digitate process arising proximally from the inner surface of the proximal endopodal segment of the antenna in adult *P. branchiostegi* (Figs. 1B, 2H, 3A) is regarded instead as a secondary addition in this species, as this antennal segment is always unarmed in siphonostomes (Huys & Boxshall, 1991). Additional studies on the life-history of *P. branchiostegi* are needed to corroborate this and to determine at which developmental stage this structure appears first on the antenna.

The exopodal armature pattern of the two leg pairs of copepodid I is IV, 1, 3 in leg 1 and III, 1, 3 in leg 2 for the Pseudohatschekiidae (Present study), Caligidae (see Benz, 1989; Kim, 1993; Lin et al., 1996; Ohtsuka et al., 2009), Dichelesthidae (see Kabata & Khodorevski, 1977), Pandaridae (see Izawa, 2010) and Amaterasidae (see Izawa, 2008). This differs from that of copepodid I of the Kroyeriidae (III, 1, 3 in both legs, or I, 1, 3 in leg 1 and III, 1, 3 in leg 2) (see Benz et al., 2001; Izawa, 2009), Lernanthropidae (IV, 1, 3 in leg 1 and II, 1, 3 in leg 2) (see Cabral et al., 1984), Pennellidae (III, 1, 3 in both legs, or III, 1, 3 in leg 1 and II, 1, 3 in leg 2) (see Ho, 1966; Kabata, 1976; Schram, 1979; Izawa, 1997) and Lernaepodidae (III, 1, 3 in first leg and II, 1, 3 in second leg, I, 1, 3 in leg 1 and II, 1, 3 in leg 2, or I, 1, 3 in both legs) (see Kabata & Cousens, 1973; Kabata, 1976; Ho et al., 2007; Piasecki & Kuźmińska, 2007). On the other hand, the endopodal setation pattern of seven and six in legs 1 and 2, respectively, is identical in the copepodid I of all families, except the Lernanthropidae and Lernaepodidae, mentioned above. Copepodid I of *Lernanthropus kroyeri* van Beneden, 1851 bears six setae on both legs (see Cabral et al., 1984) and *Achtheres percarum* von Nordmann, 1832 is unusual among lernaepodids in that the endopod bears four and five setae on the first and second legs, respectively (see Piasecki & Kuźmińska, 2007). Nevertheless, the endopod of both legs in copepodid I of *P. branchiostegi* has a small spiniform projection between the bases of the two outermost setae similar to that reported in copepodid I of some siphonostome families associated with invertebrate hosts (see Ivanenko,

1998; Ivanenko et al. 2001; Ivanenko & Ferrari, 2003). In contrast, a similar spiniform projection is either situated lateral to the outermost seta on the endopod of legs 1 and 2 of copepodid I of the Dichelesthidae (see Kabata & Khodorevski, 1977), Caligidae (see Benz, 1989; Kim, 1993; Lin et al., 1996; Ohtsuka et al., 2009), Amaterasidae (see Izawa, 2008) and Pandaridae (see Izawa, 2010), or absent altogether in the Kroyeriidae (see Benz et al., 2001; Izawa, 2009), Lernanthropidae (see Cabral et al., 1984), Pennellidae (see Ho, 1966; Kabata, 1976; Izawa, 1997) and Lernaepodidae (see Kabata & Cousens, 1973; Kabata, 1976; Ho et al., 2007; Piasecki & Kuźmińska, 2007).

Acknowledgements We thank Jun Araki (Meguro Parasitological Museum, Japan) and Toshiaki Kuramochi (National Museum of Nature and Science, Japan) for kindly arranging loans of copepod material, Tetsuo Yoshino (University of the Ryukyus) for allowing us to collect copepods from preserved fish specimens, Takeshi Sasaki (University of the Ryukyus Museum) for providing laboratory support during our stay in Okinawa-jima Island, and two anonymous reviewers for their constructive comments. This research was made possible through financial support from the Ocean Exposition Commemorative Park Management Foundation, Okinawa, to K.N. and the Japan Society for Promotion of Science Postdoctoral Fellowship (Grant No. 21-09117) to D.T.

References

- Anderson, D. T., & Rossiter, G. T. (1969). Hatching and larval development of *Dissonus nudiventris* Kabata (Copepoda, Fam Dissonidae), a gill parasite of the Port Jackson shark. *Proceedings of the Linnean Society of New South Wales*, 93, 476–481.
- Bennett, S. M. (1999). Egg development, hatching and early life-history of *Dissonus manteri* (Copepoda), parasitic on the gills of coral trout *Plectropomus leopardus*. *International Journal for Parasitology*, 29, 267–274.
- Benz, G. W. (1989). Developmental stages of *Alebion lobatus* Cressey, 1970 (Copepoda: Euryphoridae) found parasitic on the sandbar shark (*Carcharhinus plumbeus* (Nardo, 1827)) in the western North Atlantic, and a phylogenetic analysis of the genus *Alebion* Krøyer, 1863. *Canadian Journal of Zoology*, 67, 1578–1598.
- Benz, G. W. (1993). *Evolutionary biology of Siphonostomatoida (Copepoda) parasitic on vertebrates*. PhD Thesis, The University of British Columbia, 173 pp.
- Benz, G. W., Smith, B. E., & Bullard, S. A. (2001). *Kroeyerina deetsorum* n. sp. (Copepoda: Kroyeriidae) from the olfactory sacs of Atlantic sharpnose sharks (Rhizoprionodon terraenovae) captured in the Gulf of Mexico and northwestern Atlantic and first report of copepodids

- representing Kroyeriidae. *Journal of Parasitology*, 87, 1279–1290.
- Boxshall, G. A. (1986). A new genus and two new species of Pennellidae (Copepoda: Siphonostomatoida) and an analysis of evolution within the family. *Systematic Parasitology*, 8, 215–225.
- Boxshall, G. A., & Halsey, S. H. (2004). *An introduction to copepod diversity*. London: The Ray Society, 966 pp.
- Cabral, P., Coste, F., & Raibaut, A. (1984). Cycle évolutif de *Lernanthropus kroyeri* van Beneden, 1851, Copépode branchial hématophage du Loup *Dicentrarchus labrax* (Linné, 1758) dans des populations naturelles et en élevage. *Annales de Parasitologie Humaine et Comparée*, 59, 189–207.
- Choi, S. D., Lee, C. H., Chang, D. S., & Ha, D. S. (2000). *PhrEXOcephalus umbellatus* (Copepoda: Lernaecidae) from marine fish, *Branchiostegus japonicus* of the Korean southern sea. *Journal of Aquaculture*, 13, 9–12.
- Dooley, J. K., & Kailola, P. J. (1988). Four new tilefishes from the northeastern Indian Ocean, with a review of the genus *Branchiostegus*. *Japanese Journal of Ichthyology*, 35, 247–260.
- Froese, R., & Pauly, D. (2010). *FishBase*. World Wide Web electronic publication. <http://www.fishbase.org/>, version (1/2010).
- Ho, J.-s. (1966). Larval stages of *Cardiodectes* sp. (Caligoida: Lernaecoceriformes), a copepod parasitic on fishes. *Bulletin of Marine Science*, 16, 159–199.
- Ho, J.-s. (1998). Cladistics of the Lernaecidae (Cyclopoida), a major family of freshwater fish parasites. *Journal of Marine Systems*, 15, 177–183.
- Ho, J.-s., & Lin, C.-L. (2004). *Sea lice of Taiwan*. Keelung: The Sueichan Press, 388 pp.
- Ho, J.-s., Cheng, Y.-R., & Lin, C.-L. (2007). The development of *Parabrachiella lata* (Song & Chen, 1976), a lernaecopodid copepod parasitic on the black porgy, *Acanthopagrus schlegelii* (Bleeker, 1854), of Taiwan. *Crustaceana*, 80, 40–66.
- Humes, A. G., & Gooding, R. U. (1964). A method for studying the external anatomy of copepods. *Crustaceana*, 6, 238–240.
- Huys, R., & Boxshall, G. A. (1991). *Copepod evolution*. London: The Ray Society, 468 pp.
- Huys, R., Llewellyn-Hughes, J., Conroy-Dalton, S., Olson, P. D., Spinks, J. N., & Johnston, D. A. (2007). Extraordinary host switching in siphonostomatoid copepods and the demise of the Monstrilloida: Integrating molecular data, ontogeny and antennular morphology. *Molecular Phylogenetics and Evolution*, 43, 368–378.
- Ingram, A. L. (2004). Muscular anatomy and aspects of the structure of the antennae of *Anthosoma crassum* (Dichelesthiidae: Siphonostomatoidae: Copepoda). *Journal of Parasitology*, 90, 175–177.
- Ivanenko, V. N. (1998). Deep-sea hydrothermal vent Copepoda (Siphonostomatoida, Dirivultidae) in plankton over the Mid-Atlantic Ridge (29°N), morphology of their first copepodid stage. *Zoologicheskii Zhurnal*, 77, 1249–1256.
- Ivanenko, V. N., & Ferrari, F. D. (2003). Redescription of adults and description of copepodid development of *Dermatomyzon nigripes* (Brady & Robertson, 1876) and of *Asterocheres lilljeborgi* Boeck, 1859 (Copepoda: Siphonostomatoida: Asterocheridae). *Proceedings of the Biological Society of Washington*, 116, 661–691.
- Ivanenko, V. N., Ferrari, F. D., & Smurov, A. V. (2001). Nauplii and copepodids of *Scottomyzon gibberum* (Copepoda: Siphonostomatoida: Scottomyzontidae, a new family), a symbiont of *Asterias rubens* (Asteroidea). *Proceedings of the Biological Society of Washington*, 114, 237–261.
- Izawa, K. (1997). The copepodid of *Peniculisa shiinoi* Izawa, 1965 (Copepoda, Siphonostomatoida, Pennellidae), a single free-swimming larval stage of the species. *Crustaceana*, 70, 911–919.
- Izawa, K. (2008). *Amaterasia amanoiwatoi* nov. gen., nov. sp. (Copepoda, Siphonostomatoida, Amaterasidae nov. fam.), with gall-forming juveniles parasitic on the fins of a balistid actinopterygian fish. *Crustaceana*, 81, 1331–1346.
- Izawa, K. (2009). Free-living stages of the parasitic copepod, *Kroyeria elongata* Pillai, 1967 (Siphonostomatoida, Kroyeriidae) reared from eggs. *Crustaceana*, 82, 439–447.
- Izawa, K. (2010). Free-living stages of the parasitic copepod, *Gangliopus pyriformis* Gerstaecker, 1854 (Siphonostomatoida, Pandaridae) reared from eggs. *Crustaceana*, 83, 829–837.
- Kabata, Z. (1976). Early stages of some copepods (Crustacea) parasitic on marine fishes of British Columbia. *Journal of the Fisheries Research Board of Canada*, 33, 2507–2525.
- Kabata, Z. (1979). *Parasitic Copepoda of British fishes*. London: The Ray Society, 468 pp.
- Kabata, Z., & Cousens, B. (1973). Life cycle of *Salmincola californiensis* (Dana 1852) (Copepoda: Lernaecopodidae). *Journal of the Fisheries Research Board of Canada*, 30, 881–903.
- Kabata, Z., & Khodorevski, O. A. (1977). The copepodid stage of *Dichelesthium oblongum* (Abilgaard, 1794), a copepod parasite of acipenserid fishes. *Parazitologiya*, 11, 236–240. [in Russian]
- Kai, Y., & Nakabo, T. (2008). Taxonomic revision of the *Sebastes inermis* species complex (Scorpaeniformes: Scorpaenidae). *Ichthyological Research*, 55, 238–259.
- Kazachenko, V. N. (2001). *Opredelitel' semejstv i rodov paraziticheskikh kopepod (Crustacea: Copepoda) ryb: Monografiia*. Vladivostok: Dal'nevostochnyi Gosudarstvennyi Tekhnicheskii Rybokhoziaistvennyi Universitet, 253 pp. [in Russian]
- Kim, I.-H. (1993). Developmental stages of *Caligus punctatus* Shiino, 1955 (Copepoda: Caligidae). In Boxshall, G. A. & Defaye, D. (Eds) *Pathogens of wild and farmed fish: sea lice*. New York: Ellis Horwood, pp. 16–29.
- Kim, I.-H. (1998). *Illustrated encyclopedia of fauna and flora of Korea. Vol. 38. Cirripedia, symbiotic Copepoda, Pycnogonida*. Korea: Ministry of Education, 1038 pp.
- Lin, C.-L., Ho, J.-s., & Chen, S.-N. (1996). Developmental stages of *Caligus epidemicus* Hewitt, a copepod parasite of tilapia cultured in brackish water. *Journal of Natural History*, 30, 661–684.
- Ohtsuka, S., Takami, I., Maran, B. A. V., Ogawa, K., Shimono, T., Fujita, Y., Asakawa, M., & Boxshall, G. A. (2009). Developmental stages and growth of *Pseudocaligus fugu* Yamaguti, 1936 (Copepoda: Siphonostomatoida: Caligidae) host-specific to Puffer. *Journal of Natural History*, 43, 1779–1804.

- Perkins, P. S. (1983). The life history of *Cardiodectes medusaeus* (Wilson), a copepod parasite of Lanternfishes (Myctophidae). *Journal of Crustacean Biology*, 3, 70–87.
- Piasecki, W., & Kuźmińska, E. (2007). Developmental stages of *Achtheres percarum* (Crustacea: Copepoda), parasitic on European perch, *Perca fluviatilis* (Actinopterygii: Perciformes). *Acta Ichthyologica et Piscatoria*, 37, 117–128.
- Schram, T. A. (1979). The life history of the eye-maggot of the sprat, *Lernaeenicus sprattae* (Sowerby) (Copepoda, Lernaeoceridae). *Sarsia*, 64, 279–316.
- Sproston, N. G. (1942). The developmental stages of *Lernaeocera branchialis* (Linn.). *Journal of the Marine Biological Association of the United Kingdom*, 25, 441–466.
- Yamaguti, S. (1939a). Parasitic copepods from fishes of Japan. Part 5. Caligoida, III. *Volume Jubilare pro Professore Sadao Yoshida*, 2, 443–487, pls. 14–33.
- Yamaguti, S. (1939b). Parasitic copepods from fishes of Japan. Part 6. Lernaeopodoida, I. *Volume Jubilare pro Professore Sadao Yoshida*, 2, 529–578, pls. 34–58.
- Yamaguti, S. (1963). *Parasitic Copepoda and Branchiura of fishes*. New York: Interscience Publishers, 1104 pp.