JOURNAL OF CRUSTACEAN BIOLOGY, 16(2): 406–417, 1996

ARCHIDACTYLINA MYXINICOLA, NEW GENUS, NEW SPECIES (SIPHONOSTOMATOIDA), IN A NEW FAMILY OF COPEPODA PARASITIC ON HAGFISHES (AGNATHA: MYXINIFORMES) FROM JAPAN

Kunihiko Izawa

ABSTRACT

A parasitic copepod, *Archidactylina myxinicola*, new genus, new species (Siphonostomatoida: Archidactylinidae, new family), is described based on specimens of both sexes obtained from the gill pouches of hagfishes (Agnatha: Myxiniformes) collected from the continental slopes of the Sea of Kumano, Japan. This is the first record of parasitic copepods from Agnatha. Although this new taxon generally exhibits eudactylinid facies, it apparently possesses more primitive features than those found in the Eudactylinidae. This new siphonostomatoid is characterized by possessing the following features: (1) a sternal suture on the cephalothorax between the maxillipedal and the first pedigerous somites; (2) incomplete prosome-urosome differentiation; (3) a free genital somite; (4) ventral copulatory pores isolated from the lateral genital apertures in the female; (5) no cuticular ornamentation characteristic of the eudactylinids; (6) an indistinctly 18-segmented antennule in both sexes, geniculate bilaterally in the male; (7) uniramous, 5-segmented antenna; (8) maxilliped on a discrete pedestal and lacking myxal process on the corpus; and (9) a setation formula of III,I,5 on the third exopodal segment of legs 2–4 of both sexes.

Although fishes are known to carry many species of parasitic copepods, members of the Agnatha are yet to be reported as hosts for parasitic copepods. Therefore, a search for parasitic copepods on Japanese hagfishes (Agnatha: Myxiniformes) was conducted and a new form of siphonostomatoid was obtained from the gill pouches of two species of hagfishes occurring on the continental slopes of the Sea of Kumano, Japan. Although this new taxon possesses eudactylinid facies (see Kabata, 1979), it appears to be more primitive than the Eudactylinidae, which has been considered one of the most primitive families of the siphonostomatoids (Huys and Boxshall, 1991). The Eudactylinidae comprises 10 genera, eight of which are parasitic on the gill or nasal lamellae of elasmobranchs and the other two on the gills of teleosts (Deets and Ho, 1988). In addition to the description of the new parasitic copepod of hagfishes, a discussion on the morphological features and comparisons with the eudactylinids are provided. The words "cyclopiform" and "caligiform" siphonostomatoids used in the discussion refer to the unmodified siphonostomatoids associated with invertebrates and to the parasitic siphonostomatoids belonging to the Caligidae and related families, respectively.

MATERIALS AND METHODS

The specimens (140 females and 38 males in all) were obtained from the gill pouches of 33 *Eptatretus okinoseanus* (Dana) and 3 *Myxine garmani* Jordan and Snyder. Hosts were collected over an eleven year period 1983–1994, during the cruises of the training ship *Seisui-Maru* of Mie University. The fishes were caught in net-traps set on the upper part of the continental slopes in the Sea of Kumano, at depths ranging 300–600 m located between 33°50′N, 136°10′E and 34°18′N, 137°10′E off the Pacific coast of Japan. The specimens, fixed with Formalin and preserved in alcohol, were examined in lactic acid with a differential interference contrast microscope (Olympus BH–2). Drawings were made with the aid of a drawing tube. The terminology is based on Kabata (1979) and Huys and Boxshall (1991). Hierarchy of higher categories of fishes follows Nelson (1994).

DESCRIPTION

Archidactylina, new genus

Diagnosis.—Female: Body slender, eudactylinid facies, but lacking cuticular ornamentation on body surface and appendages. Major body articulation probably between fifth pedigerous and genital somites. Rostrum fused to cephalothorax. Dorsal shield and terga of somites bearing legs 2–4 weakly developed. Cephalothorax, including first pediger, retaining sternal suture separating maxillipedal and first pedigerous somites. Genital somite small, separate from fifth pedigerous and first abdominal somites. Cop-

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

ulatory pores ventral, separated from lateral genital apertures, each covered by operculum. Abdomen 4-segmented. Caudal ramus carrying 6 elements, with long curled pinnate setae. Antennule on broad pedestal, indistinctly 18-segmented. Antenna uniramous, uncinate, and 5-segmented. Mandible and maxillule eudactylinid. Maxilla brachiform, with simple terminal claw. Maxilliped shorter than antennule and antenna, mounted on discrete pedestal, uncinate, without myxal process on corpus. Legs 1–4 biramous; rami 3-segmented, without coxal setae. Third exopodal segments of legs 2–4 with setation formula of III,I,5. Fifth leg modified as posterolateral process on somite.

Male: Cyclopiform, slender, with distinct dorsal shield; terga of pedigers 2–4 without cuticular ornamentation. Fifth pediger reduced. Genital somite large, with lateral genital opercula. Antennule bilaterally geniculate, indistinctly 18-segmented. Other appendages mostly as in female. Setation formulae of legs 1–4 as in female.

Parasitic in the gill pouches of hagfishes (Agnatha: Myxiniformes).

Type species.—*Archidactylina myxinicola,* new species.

Etymology.—The generic name is a combination of the Greek *arch* (*i*) (=beginning, primitive) and dactylina, a part of the family name, with which the new form bears close affinities.

Gender.—Feminine.

Archidactylina myxinicola, new species
Figs. 1–5

Material Examined.—From *Eptatretus okinoseanus*: 12 ♀ ♀, 3 ♂ ♂ from 4 fishes, 20 May 1983; 46 ♀ ♀, 23 ♂ ♂ from 5 fishes, 21 January 1986; 14 ♀ ♀, 4 ♂ ♂ from 5 fishes, 17 October 1986; 6 ♀ ♀ from 11 fishes, 15 October 1987; 1 ♀, 1 ♂ from 1 fish, 15 October 1988; 55 ♀ ♀, 7 ♂ ♂ from 7 fishes, 1 June 1994. From *Myxine garmani:* 6 ♀ ♀ from 3 fishes, 22 October 1983. Holotype ♀ (NSMT-Cr 11550), 20 paratypes (10 ♀ ♀, 10 ♂ ♂) (NSMT-Cr 11551) from *E. okinoseanus,* 21 January 1986, are deposited in the National Science Museum, Tokyo. The remaining specimens are retained temporarily in the laboratory of Mie University.

Female (Figs. 1–3)—Total length about 2.5 mm. Body (Fig. 1A, B) elongate, about 6.5 times as long as wide, gently bent ventrally. Anterior portion of body from cephalothorax to fifth pediger almost equal in width. Posterior portion less than half of anterior portion in width and length. Although indistinct, major body articulation apparently between fifth pedigerous and genital somites. Dorsal shield and terga of pedigers 2–4 weakly developed. No cuticular ornamentation on surfaces of body and appendages.

Cephalothorax longer than wide, with sternal suture separating maxilliped-bearing and first pedigerous somites. Rostrum fused to cephalothorax, with round tip, bearing pair of sensilla dorsally. Free somites bearing legs 2–4 wider than long. Fifth pedigerous somite somewhat larger than cephalothorax, hunched up at about posterior one-third. Genital somite (Fig. 1C, D) small; copulatory pores ventrally located in narrow transverse depression at posterior margin of somite, and each lateral genital aperture covered by operculum. Abdomen (Fig. 1C) 4-segmented, diminishing in size posteriorly. First abdominal somite swollen on ventral side, with longitudinal ventrolateral ridges. Caudal ramus (Fig. 1E) 2.5 times as long as wide, with row of fine setules medially and 6 setae distally; 4 terminal pinnate setae curled ventrally and 2 subterminal naked setae. Egg sacs about 1.2 mm in length, eggs uniseriate.

Antennule (Fig. 1F) mounted on pedestal almost as long as the first antennular segment, indistinctly 18-segmented, and flexed posteriorly at compound segment IX–XII. Fusion pattern and armature elements of ancestral segments as follows: I–1, II–III–3, IV–V–3, VI–2, VII–1, VIII–1, IX–XII–4, XIII–2, XIV–2, XV–XVI–2, XVII–1, XVIII–1, XIX–0, XX–1, XXI–2 + aesthetasc, XXII–XXIII–1, XXIV–2, XXV–XXVIII–9 + aesthetasc. Suture lines between XXI and XXII–XXIII, and XXIV and XXV–XXVIII weak.

Antenna (Fig. 1G) about 0.3 mm in length, longer than antennule, uniramous, and 5-segmented; first 3 segments stout, unarmed; fourth segment longer than wide, with ridgelike sclerite from which an internal tendonlike structure connecting to fifth segment. Fifth segment small, with 2 medial setules and terminal claw. Articulation between third and fourth segments forming main flexing point of limb.

Oral cone (Fig. 2A, B) short, with narrow membranes around mouth. Mandible (Fig. 2A, C) 2-segmented; basal segment broad,

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

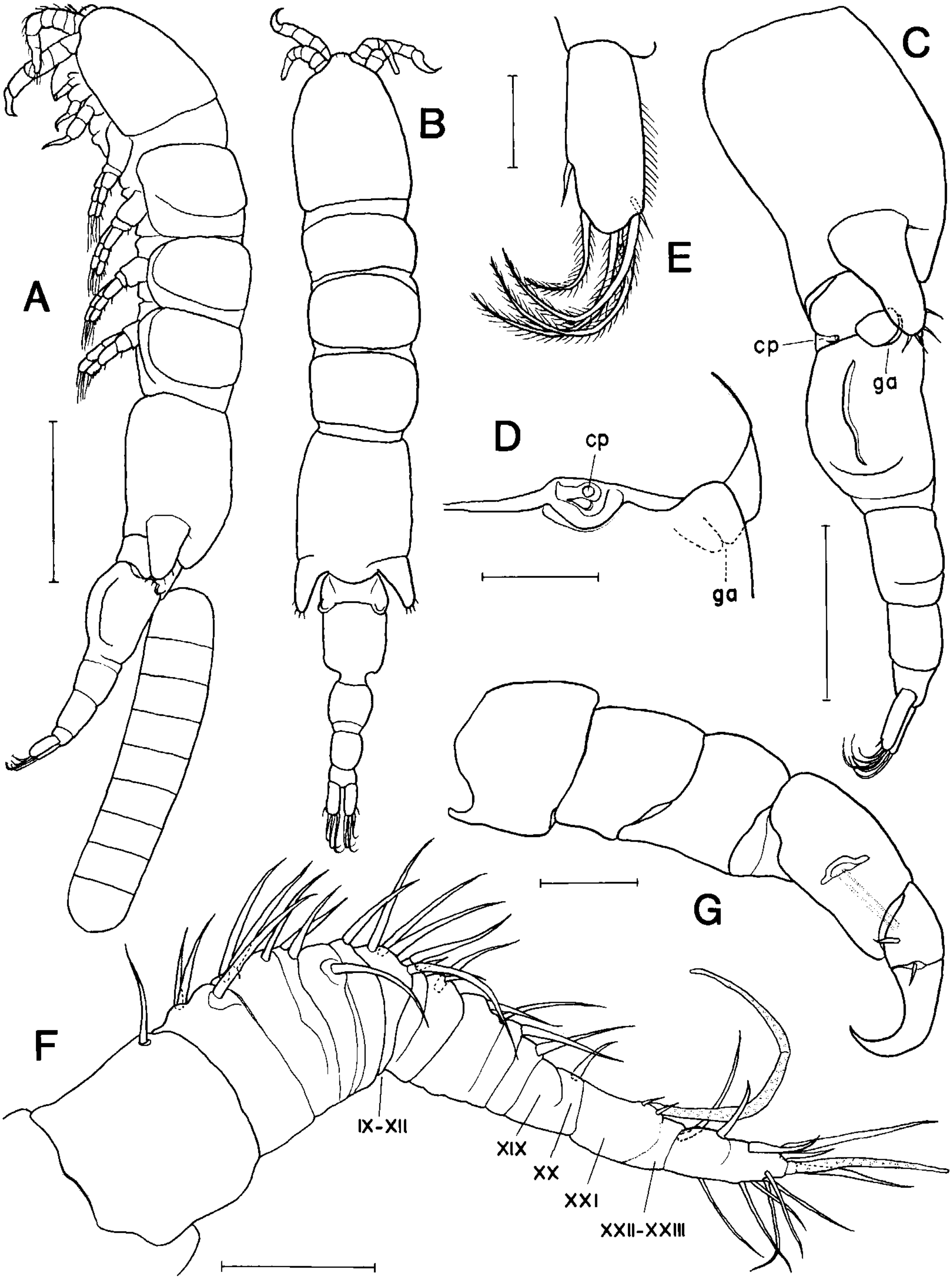

Fig. 1. *Archidactylina myxinicola,* new genus, new species, female. A, habitus, lateral; B, same, dorsal; C, fifth pedigerous and posterior somites, lateral; D, copulatory pore and genital aperture, ventral; E, caudal ramus, ventral; F, antennule, dorsal; G, antenna, medial. cp = copulatory pore; ga = genital aperture. Scales: 0.5 mm for A, B; 0.3 mm for C; 0.05 mm for D–G.

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

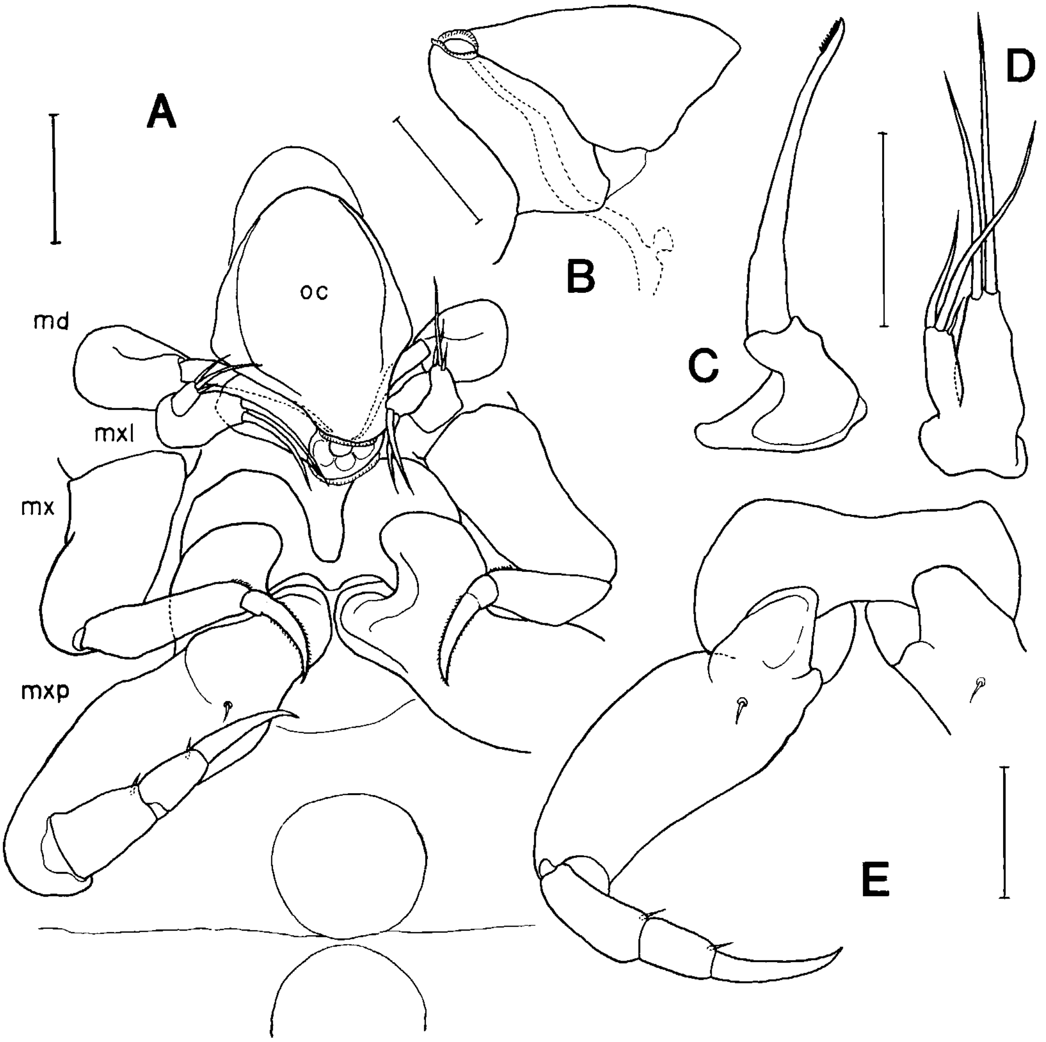

Fig. 2. *Archidactylina myxinicola*, new genus, new species, female. A, oral area, ventral; B, oral cone, lateral; C, mandible; D, maxillule; E, maxilliped. md = mandible; mx = maxilla; mxl = maxillule; mxp = maxilliped; oc = oral cone. Scales: 0.05 mm for A–E.

tapered distally; second segment styliform, with cutting blade armed with fine teeth.

Maxillule (Fig. 2A, D) bilobate, segmentation indistinct; inner lobe extending along oral cone and bearing 2 long naked apical setae; outer lobe tipped with 3 unequal naked setae.

Maxilla (Fig. 2A) brachiform, 3-segmented; first segment short and almost fused to sternal surface; second segment stout, unarmed; third segment slim, with patch of fine spinules mediodistally; claw indistinctly 2-jointed, with rows of fine spinules on medial and lateral sides of distal joint.

Maxilliped (Fig. 2A, E) shorter than antennule, mounted on discrete pedestal, uncinate. First segment (corpus maxillipedis), about 3 times as long as wide, bifurcate proximal end articulated to pedestal, without myxal process, but with setule on syncoxal portion. Second and third segments each with setule mediodistally. Terminal claw simple. Two rounded sternal expansions situated one behind another on midline posterior to maxillipeds, with sternal suture between them indicating separation between maxilliped-bearing and first pedigerous somites (Fig. 2A). Similar sternal expansions and sutures located at intersomatic portion between legs 2–4.

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

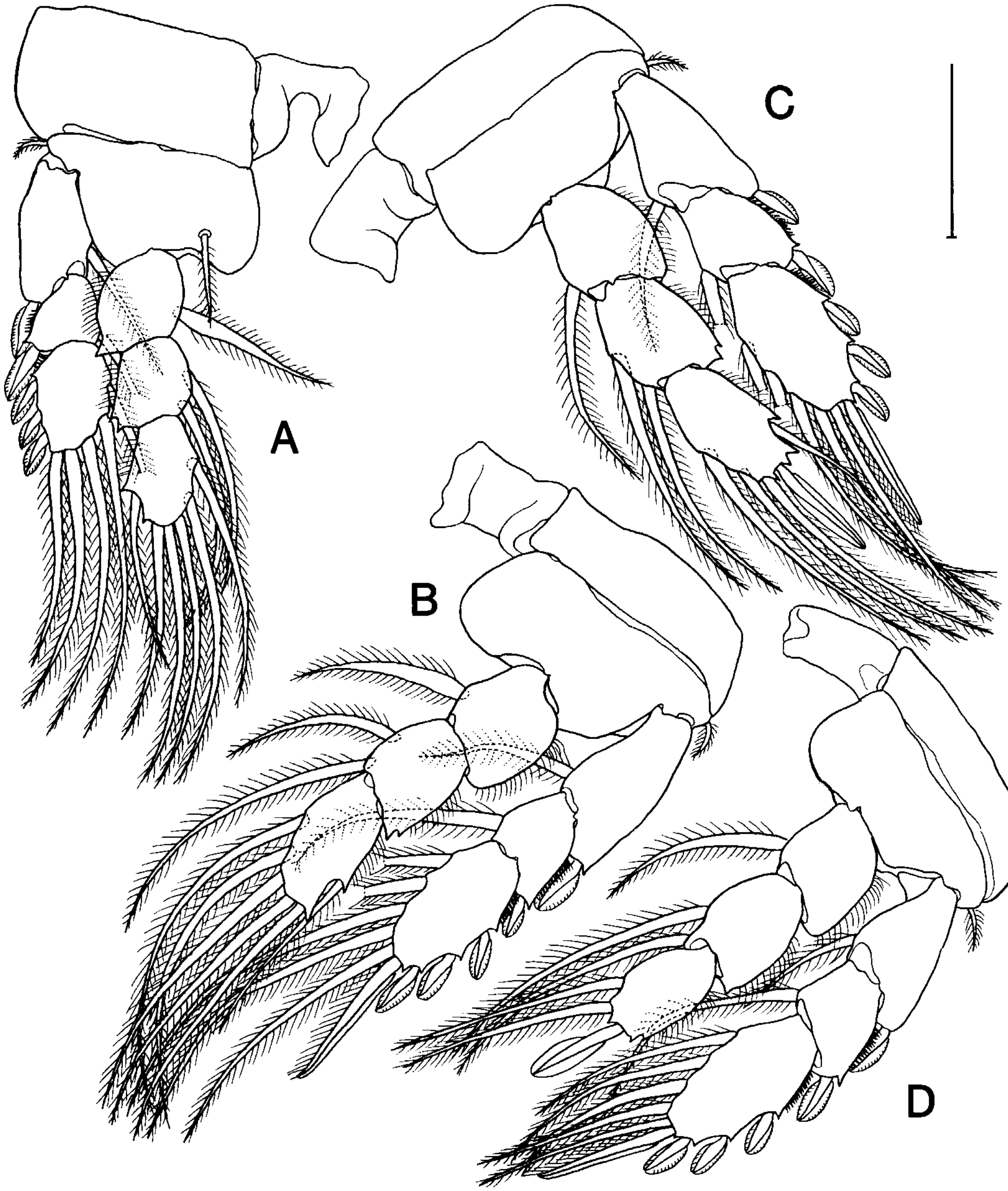

Fig. 3. *Archidactylina myxinicola*, new genus, new species, female. A, leg 1, ventral; B, leg 2, ventral; C, leg 3, ventral; D, leg 4, ventral. Scale: 0.1 mm for A–D.

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

Legs 1–4 (Fig. 3A–D) biramous, with 2-segmented protopod and 3-segmented rami, lacking cuticular ornamentation on surfaces. Setae of rami long and pinnate. Formula for spines (Roman numerals) and setae (Arabic numerals) on legs 1-4 as follows:

leg 1	Prp 0–0;	1–1	Exo	I–1;	I–1;	III,2,3
			Enp	0–1;	0–2;	1,2,3
leg 2	Prp 0–0;	1–0	Exo	I–1;	I–1;	III,I,5
			Enp	0–1;	0–2;	1,2,3
leg 3	Prp 0–0;	1–0	Exo	I–1;	I–1;	III,I,5
			Enp	0–1;	0–2;	1,I,3
leg 4	Prp 0–0;	1–0	Exo	I–1;	I–1;	III,I,5
			Enp	0–1;	0–2;	I,2

Rarely with formula of II,I,5 on third exopod segment of leg 2. Leg 5 (Fig. 1C) uni-

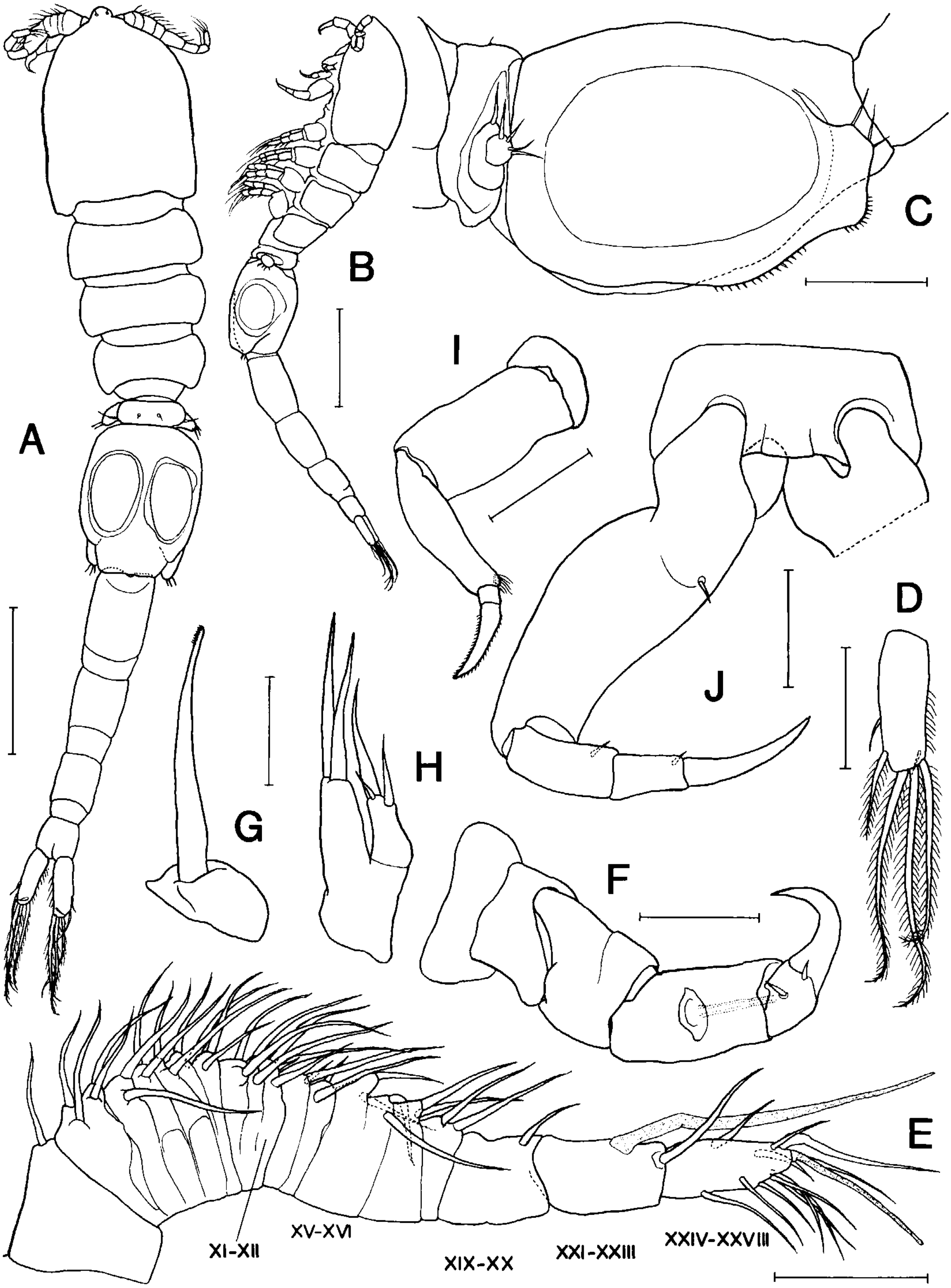

Fig. 4. *Archidactylina myxinicola,* new genus, new species, male. A, habitus, dorsal; B, same, lateral; C, fifth pedigerous and genital somites, lateral; D, caudal ramus, ventral; E, antennule, ventral; F, antenna, posteromedial; G, mandible; H, maxillule; I, maxilla; J, maxilliped. Scales: 0.3 mm for A, B; 0.1 mm for C, D; 0.03 mm for G, H; 0.05 mm for E, F, I, J.

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

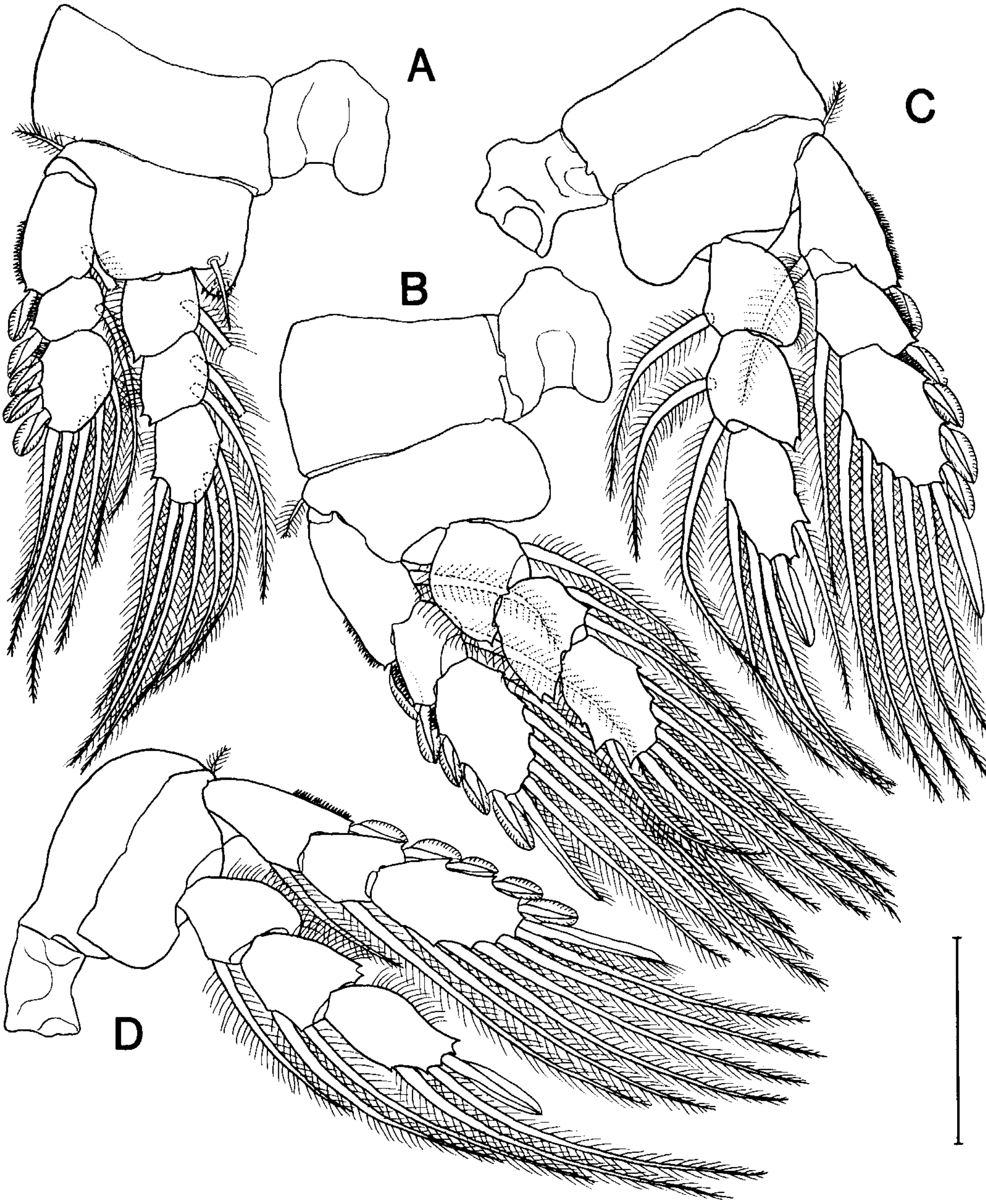

Fig. 5. *Archidactylina myxinicola*, new genus, new species, male. A, leg 1, ventral; B, leg 2, ventral; C, leg 3, ventral; D, leg 4, ventral. Scale: 0.1 mm for A–D.

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

ramous, reaching posterior border of genital somite; bearing setule dorsally at base and 4 setules distally.

Male (Figs. 4, 5).—Total length approximately 1.7 mm. Body (Fig. 3A, B) cyclopiform, slim, about 6 times as long as wide. Dorsal shield of cephalothorax and terga of somites of legs 2–4 moderately developed. Cephalothorax retaining sternal suture as in female, with slight ventrolateral indentations of dorsal shield at level of maxillipeds. Fifth pedigerous somite much reduced, with small uniramous legs laterally and paired sensilla dorsally. Genital somite large next to cephalothorax, with lateral genital opercula bearing row of spinules along ventrodistal margins and 3 setules dorsodistally (Fig. 4C). Abdomen 4-segmented. Body constricting anterior to fifth pedigerous somite, but highly flexible articulation located between genital and first abdominal somites. Caudal ramus (Fig. 4D) 2.8 times as long as wide; armature as in female.

Antennule (Fig. 4E) indistinctly 18-segmented, geniculate between ancestral segments XX and XXI. Fusion pattern and armature elements of ancestral segments as follows: I–1, II–III–4, IV–2, V–2, VI–2, VII–2, VIII–2, IX–2, X–2, XI–XII–4, XIII–2, XIV–2, XV–XVI–4, XVII–2, XVIII–2, XIX–XX–1, XXI–XXIII–1 + aesthetasc, XXIV–XXVIII–12 + aesthetasc. One of 2 setae on segment XV arising from pedestal.

Antenna (Fig. 4F), mandible (Fig. 4G), maxillule (Fig. 4H), maxilla (Fig. 4I), and maxilliped (Fig. 4J) generally as in female, except for maxilla with plume on third segment (brachium) instead of patch of spinules and maxilliped with additional medial sensilla on corpus, about at midlength.

Legs 1–4 (Fig. 5A–D) as in female, except for basis of leg 1 with spinulose expansion on mediodistal corner. Setation formula as in female. Rarely with formula of III,I,4 for third exopod segment found on leg 4.

Etymology.—The specific name is a combination of Myxini, a class to which the hosts belong, and the Latin *cola* (=inhabiting).

DISCUSSION

Although eudactylinid in general appearance, the new form is distinguishable from the family Eudactylinidae (Kabata, 1979) by the following features: (1) the sternal suture separating the maxillipedal and first pedigerous somites is retained; (2) the cuticular ornamentation which is characteristic of the eudactylinids on the surfaces of body and appendages, especially the swimming legs, is absent. The eudactylinid *Heterocladius abyssetes* Deets and Ho, 1988, is also devoid of cuticular ornamentation (Deets, personal communication); (3) the copulatory pores are ventral and isolated from the lateral genital apertures in the female; (4) the antenna is 5-segmented; (5) the maxilliped retains the discrete pedestal and lacks a myxal process on the corpus; and (6) the setation formula of III,I,5 for the third exopodal segment is retained on legs 2–4 of both sexes. Thus, a new family, Archidactylinidae, is proposed to accommodate this new genus and species. The new family is also distinct from all other siphonostomatoid families by having eudactylinid facies and a combination of the above mentioned features.

Archidactylina has the genital and abdominal somites separated in the female, as do *Bariaka alopiae* Cressey, 1966, and *Jusheyus shogunus* Deets and Benz, 1987, which are monotypic eudactylinids parasitic on the gills of gnathostome fishes; *Bariaka* was reported from a thresher shark (Lamniformes) and *Jusheyus* from a sea bass (Perciformes). Boxshall (1990) and Huys and Boxshall (1991) mentioned that *Bariaka* and *Jusheyus* were the only two siphonostomatoid genera that possess a free genital somite, whereas in all other siphonostomatoids the genital and first abdominal somites are fused to form a genital double-somite in the female. As mentioned by Boxshall (1990), the genital double-somite of the siphonostomatoids is characterized by the location of the female genital apertures in about the middle of the double-somite, corresponding to the posterior margin of the original genital somite, and by the presence of a maximum of three free abdominal somites. Boxshall (1990) and Huys and Boxshall (1991) regarded *Bariaka* as the most primitive eudactylinid genus in having a separate female genital somite and primitive antennules. Deets and Ho (1988) considered the monotypic *Protodactylina pamelae* Laubier, 1966, obtained from one of the most primitive extant elasmobranchs (Hexanchiformes) as the most primitive one based on their cladistic analysis of the 10 eudactylinid genera.

The number of female abdominal segments in *Protodactylina* has been described in two different ways: 3-segmented (Laubier, 1966; Schirl, 1978), and 4-segmented (Cressey, 1977, as *Bariaka pamelae*). Aside from this discrepancy in the number of abdominal segments, these authors agreed with each other in that the genital apertures are located near the posterior margin of the genital segment. This is the case in *Bariaka* and *Jusheyus* mentioned above, and in *Eu-*

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

dactylinodes niger (Wilson) which has a 3-segmented abdomen (Deets and Ho, 1988) and *Carnifossorius siamensis* Deets and Ho, 1988, which has an unsegmented abdomen. Moreover, the genital apertures sit near the anterior margin of the elongate genital segment in *Eudactylinella alba* Wilson which has a 2-segmented abdomen (Deets and Ho, 1988) and at the middle in *Heterocladius abyssetes* Deets and Ho, 1988, which has a 2-segmented abdomen. In the last two species, the genital segment is undoubtedly fused to the first abdominal somite.

A female genital segment with posterior genital apertures is not found in the siphonostomatoids associated with invertebrates, but it is usual in the majority of the siphonostomatoids parasitic on fishes. By having a pair of rudimentary fifth legs, it is clear that the genital segment is fused to the fifth pedigerous somite in the latter case. Thus, the female genital segment with posterior genital apertures found in the eudactylinids and some other siphonostomatoids does not incorporate the first abdominal somite regardless of the number of abdominal segments. Reduction of the abdominal segments can result from two different processes: formation of a genital double-somite and suspension of somite division, apart from a secondary disappearance of the segment boundary (Izawa, 1991).

The female genital system of *Archidactylina* resembles some siphonostomatoids, such as *Asterocheres reginae* Boxshall and Huys, 1994, and *Brychiopontius falcatus* Humes (see Huys and Boxshall, 1991). The copulatory pores are located ventrally on both sides at the middle of the genital double-somite. The genital apertures, each closed off by an operculum, are located laterally or dorsolaterally on the same border. Recognizing that *Bariaka alopiae* is one of the most primitive siphonostomatoids, Huys and Boxshall (1991) have inferred that the ancestral siphonostomatoid probably had paired ventral genital apertures in the female, each aperture containing a copulatory pore and a gonopore as in *Bariaka.* They interpreted that the female genital system of some siphonostomatoids is derived from this ancestral type by lateral migration of the genital apertures, leaving the copulatory pores in the original position. The female genital system of *Bariaka,* however, differs from the ancestral genital system in that the genital operculum is not discernible and both copulatory and genital pores open in a common duct (Huys and Boxshall, 1991; fig. 2.9.29A). In the ancestral female genital system, the copulatory pore and the gonopore have been considered to open separately at medial and lateral margins, respectively, within the genital aperture (Huys and Boxshall, 1991). Therefore, the female genital system of *Bariaka* is referable to the secondary transformation by lateral migration of the copulatory pore and fusion with the gonopore into a common duct. *Archidactylina* is considered to retain the primitive female genital system of the siphonostomatoids, as in some siphonostomatoids associated with invertebrates.

The podoplean tagmosis is not discernible in *Archidactylina.* The major body articulation is located between the fifth pediger and the genital somite in the female and between the genital and first abdominal somites in the male in *Archidactylina.* However, it seems reasonable to consider that the prosome-urosome differentiation is incomplete or the prosome-urosome tagma boundary has not been fixed yet in *Archidactylina.* This condition is considered similar to the ancestral copepod condition without prosome-urosome differentiation (Huys and Boxshall, 1991). The podoplean tagmosis is also not discernible in the Dichelesthiidae including the fossil form *Kabatarina pattersoni* Cressey and Boxshall, 1989, and in the Eudactylinidae. In the "caligiform families" the prosome-urosome articulation exists between the third and fourth pedigerous somites exclusively. These may indicate that the siphonostomatoids parasitic on fishes formerly considered the Caligoida were not derived from the ancestry with podoplean tagmosis, but derived independently from the ancestral condition with their own tagmosis. In other words, the tagmosis of "caligoids" cannot be referred to as a modification of the podoplean tagmosis.

Antennules of *Archidactylina* are indistinctly 18-segmented in both sexes, though the fusion pattern and setation differ between the two. The female antennule of *Archidactylina* is comparable to that of *Protodactylina* and *Bariaka.* It is almost 18-

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

segmented in *Protodactylina pamelae* (Cressey, 1977, as *Bariaka pamelae*; Schirl, 1978; Huys and Boxshall, 1991), and in *Bariaka alopiae* (Cressey, 1966; Huys and Boxshall, 1991). The features shared by the female antennules of *Archidactylina, Protodactylina,* and *Bariaka* are: (1) segments I, XIII, and XIV free; (2) segments IX–XII form a compound segment; (3) segments XIX and XXII naked; (4) possession of an aesthetasc each on XXI and XXVIII. Formation of compound segments (IX–XII, XXI–XXIII and XXIV–XXVIII) and possession of a prominent aesthetasc on XXI are common to most siphonostomatoids (Huys and Boxshall, 1991). Possession of the naked segments XIX and XXII is the same in the male of *Archidactylina.* The naked segment XIX is noticed also in the females of *Eudactylinodes keratophagus* Deets and Benz, 1986, *Jusheyus shogunus* Deets and Bents, 1987, and *Eudactylinodes niger* Wilson, *Eudactylinella alba* Wilson, and *Heterocladius abyssetes* Deets and Ho, 1988. This segment, however, bears a seta in the males of *Protodactylina pamelae* Laubier (see Schirl, 1978) and *Eudactylinella alba* (see Deets and Ho, 1988; Huys and Boxshall, 1991). No naked segment is found in the siphonostomatoids associated with invertebrates, as in *Asterocheres reginae* (see Huys and Boxshall, 1991). Though it cannot always be verified in eudactylinids with simplified antennules, such as species of *Eudactylina* and *Nemesis* (see Kabata, 1970, 1979), possession of naked segment(s) is considered a common feature of *Archidactylina* and the eudactylinids at least in the females. The naked antennular segments XVII, XIX and XXII have been reported in both sexes in the Platycopioida (see Huys and Boxshall, 1991). The male antennule of *Archidactylina* is comparable to the 16- or 17-segmented male antennule of *Protodactylina* (see Schirl, 1978), but the former retains many more setae (51 elements including aesthetascs) than the latter (39 elements). This setation is closer to those primitive siphonostomatoids, such as *Asterocheres reginae,* apart from the naked segments. The modified joint between XIII and XIV, which is possessed by the males of the "cyclopiform" siphonostomatoids (Huys and Boxshall, 1991), is not discernible in *Archidactylina,* as in the eudactylinids.

The 5-segmented antenna of *Archidactylina* is interpreted to be composed of the coxa, basis, and three endopodal segments. In eudactylinid antennae, a reduction of segments has taken place. The antenna is usually 3- or 4-segmented; the coxa is reduced in size and usually almost fused to the sternal surface, and the third endopodal segment characteristically having two setules is fused to the terminal claw. Some confusion exists on segment identification. The first two segments of the 3-segmented antenna of *Eudactylinella alba* have been interpreted as the coxa and basis, and a seta on the second segment as the rudimentary exopod by Huys and Boxshall (1991, fig. 2.9.17D). Its third segment is naked, and the basal portion of the terminal claw bears two setules. These portions clearly correspond to the fourth and fifth segments of the 5-segmented antenna of *Archidactylina,* respectively. From this, their coxa and basis can be interpreted as the basis and first endopodal segment, respectively. In Deets and Ho (1988, figs. 3B, 5C) a segmentlike portion has been depicted proximally in the 3-segmented antenna of *Eudactylinella alba,* though no reference to it has been made by them. This portion can be interpreted as the coxa. A similar proximal portion regarded as the coxa has also been depicted in other eudactylinids, such as *Heterocladius abyssetes* and *Carnifossorius siamensis* (see Deets and Ho, 1988), and *Eudactylinodes keratophagus* (see Deets and Benz, 1986). The antenna is usually 4-segmented in the species of *Eudactylina* and *Nemesis,* such as *E. acuta* van Beneden, *E. acanthii* A. Scott, and *N. lamna vermi* A. Scott (see Kabata, 1979). The portion distal to the first segment of the 4-segmented antenna corresponds to the 3-segmented eudactylinid antenna. Thus, the first segment is considered the coxa. If the above interpretation of segments is valid, the uniramous antenna of the eudactylinids and "caligiforms" can be traced back to *Archidactylina.* The antennae are biramous in the siphonostomatoids associated with invertebrates and in the lernaeopodids and sphyriids parasitic on fishes (Huys and Boxshall, 1991). This seems to suggest that the Siphonostomatoida is a polyphyletic copepod assemblage derived

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

from at least two different ancestral types, one with the biramous antennae and the other with uniramous antennae. The eudactylinid antenna is, however, distinct from that of *Archidactylina* in having armature, usually two setae, on the first endopodal segment without exception. This may indicate that *Archidactylina* is not the direct ancestral type for the eudactylinids.

The maxilliped of *Archidactylina* is primitive compared to that of eudactylinids. It is located on a discrete pedestal as in the "cyclopiform" siphonostomatoids, such as *Brychiopontius falcatus* Humes, 1974, and *Ecbathyrion prolixicauda* Humes (see Huys and Boxshall, 1991). The syncoxa is fused with the basis to form the corpus in *Archidactylina* as in the eudactylinids. It is free in the "cyclopiform" siphonostomatoids. The syncoxa has a setule as in the "cyclopiform" siphonostomatoids, while it is replaced by a myxal process in the eudactylinids as seen in *Protodactylina* and *Bariaka*. The size of the maxilliped of *Archidactylina* is relatively small compared with the other appendages, such as the antennule, antenna, and swimming legs. It has developed into the most powerful and largest appendage in the eudactylinids.

The swimming legs 1–4 are well developed in *Archidactylina,* retaining almost full setation of the ancestral siphonostomatoid presumed by Huys and Boxshall (1991), though lacking coxal setae. *Archidactylina* is one of a few siphonostomatoid genera in which the armature formula of III,I,5 for the third exopodal segment is retained on legs 2–4 in both sexes. Among the eudactylinids, the leg setation is modified variously, but a coxal seta is retained in *Protodactylina* on legs 2–4 of both sexes (Laubier, 1966; Schirl, 1978) and in *Bariaka* on legs 2–4 of the male (Cressey, 1966). In *Protodactylina,* which has the most armature elements on legs among the eudactylinids, the number of spines is reduced, having the formula of III,6 for the third exopodal segment on leg 2 and of II,6 on legs 3 and 4.

The host group of *Archidactylina,* Myxiniformes, has a long history. Possible agnathan remains first appear in the fossil record in the Late Cambrian and definite remains occur in the Middle Ordovician (Nelson, 1994). The jawless fishes have their greatest radiation in the Silurian and Lower Devonian. Stensio (1968) reported that hagfishes may be derivatives of the pteraspidomorphs and lampreys of the cephalaspidomorphs. Growing evidence suggests that hagfishes (Myxiniformes) are probably the most primitive agnathans and that lampreys (Petromyzontiformes) are more closely related to gnathostomes than to hagfishes (Nelson, 1994). The current view favors the hypothesis that the morphological and physiological similarities shared between lampreys and gnathostomes, but not hagfishes, are due to common ancestry and not convergent evolution (Nelson, 1994). Differences between the Archidactylinidae and Eudactylinidae are considered to be referable to the phylogenetic deviation between their hosts, agnathan Myxiniformes and gnathostome fishes, respectively.

ACKNOWLEDGEMENTS

I am indebted to Dr. J.-S. Ho, California State University, Dr. Z. Kabata, Pacific Biological Station, Nanaimo, Dr. G. A. Boxshall, British Museum (Natural History), and Dr. G. B. Deets, University of British Columbia, for their critical reading of and comments on the manuscript. Hearty thanks are also due to captains T. Jinno and I. Ishikura, and the crew of the training ship *Seisui-Maru* of Mie University for their cooperation in collecting host fishes.

LITERATURE CITED

Boxshall, G. A. 1990. The skeletomusculature of siphonostomatoid copepods, with an analysis of adaptive radiation in structure of the oral cone.—Philosophical Transactions of the Royal Society of London, B, 328: 167–212.

———, and R. Huys. 1994. *Asterocheres reginae,* a new species of parasitic copepod (Siphonostomatoida: Asterocheridae) from a sponge in Brazil.—Systematic Parasitology 27: 19–33.

Cressey, R. F. 1966. *Bariaka alopiae* n. gen., n. sp. (Copepoda: Caligoida), a parasite on the gills of a thresher shark.—Bulletin of Marine Science 16: 324–329.

———. 1977. *Boylea longispica* n. g., n. sp. and other parasitic copepods from Pacific fishes.—Transactions of the American Microscopical Society 96: 467–476.

———, and G. Boxshall. 1989. *Kabatarina pattersoni,* a fossil parasitic copepod (Dichelesthiidae) from a lower Cretaceous fish.—Micropaleontology 35: 150–167.

Deets, G. B., and G. W. Benz. 1986. *Eudactylinodes keratophagus* sp. nov., the first record of Eudactylinidae Kabata, 1979 (Copepoda: Siphonostomatoida) from horn sharks (*Heterodontus francisci* (Girard, 1854), and *H. mexicanus* Taylor and Castro-Aguirre, 1972).—Canadian Journal of Zoology 64: 2499–2502.

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022

———, and ———. 1987. *Jusheyus shogunus* gen. et sp. nov. (Siphonostomatoida: Eudactylinidae), a gill parasite of the bass *Polyprion oxygeneios* (Percichthyidae) from Coffs Harbour, Australia.—Canadian Journal of Zoology 65: 940–945.

———, and J.-S. Ho. 1988. Phylogenetic analysis of the Eudactylinidae (Crustacea: Copepoda: Siphonostomatoida), with descriptions of two new genera.—Proceedings of the Biological Society of Washington 101: 317–339.

Humes, A. G. 1974. New cyclopoid copepods associated with an abyssal holothurian in the eastern North Atlantic.—Journal of Natural History 8: 101–117.

Huys, R., and G. A. Boxshall. 1991. Copepod evolution.—The Ray Society, London, England. Pp. 1–468.

Izawa, K. 1991. Evolutionary reduction of body segments in the poecilostome Cyclopoida (Crustacea: Copepoda).—Bulletin of Plankton Society of Japan, Special Volume: 71–86.

Kabata, Z. 1970. Copepoda parasitic on Australian fishes X. Families Eudactylinidae and Pseudocycnidae.—Journal of Natural History 4: 159–173.

———. 1979. Parasitic Copepoda of British fishes.—The Ray Society, London, England. Pp. 1–468.

Laubier, L. 1966. Crustacea Copepoda. *In:* L. Laubier, C. Maillard, and G. Oliver. 1966. Contribution à l'étude des parasites du "griset": *Hexanchus griseus* (Bonnaterre, 1788).—Vie et Milieu, Sér. A, 17: 1197–1233.

Nelson, J. S. 1994. Fishes of the world, third edition.—John Wiley & Sons, Inc. New York, New York. Pp. 1–600.

Schirl, K. 1978. Description of the male and a female variation of *Protodactylina pamelae* Laubier, 1966 (Copepoda, Caligoida, Eudactylinidae).—Annalen der naturhistorisch Museum der Wien 81: 597–606.

Stensio, E. 1968. The cyclostomes with special reference to the diphyletic origin of the Petromyzontida and Myxinoidea.—*In:* T. Orvig, ed., Current problems of lower vertebrate phylogeny.—Pp. 13–71. Wiley-Interscience, New York, New York.

RECEIVED: 5 September 1995.
ACCEPTED: 10 November 1995.

Address: Faculty of Bioresources, Mie University, 1515 Kamihama, Tsu, Mie 514, Japan.

Downloaded from https://academic.oup.com/jcb/article/16/2/406/2418824 by guest on 02 March 2022