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PHYLOGENETIC ANALYSIS OF THE EUDACTYLINIDAE (CRUSTACEA: COPEPODA: SIPHONOSTOMATOIDA), WITH DESCRIPTIONS OF TWO NEW GENERA

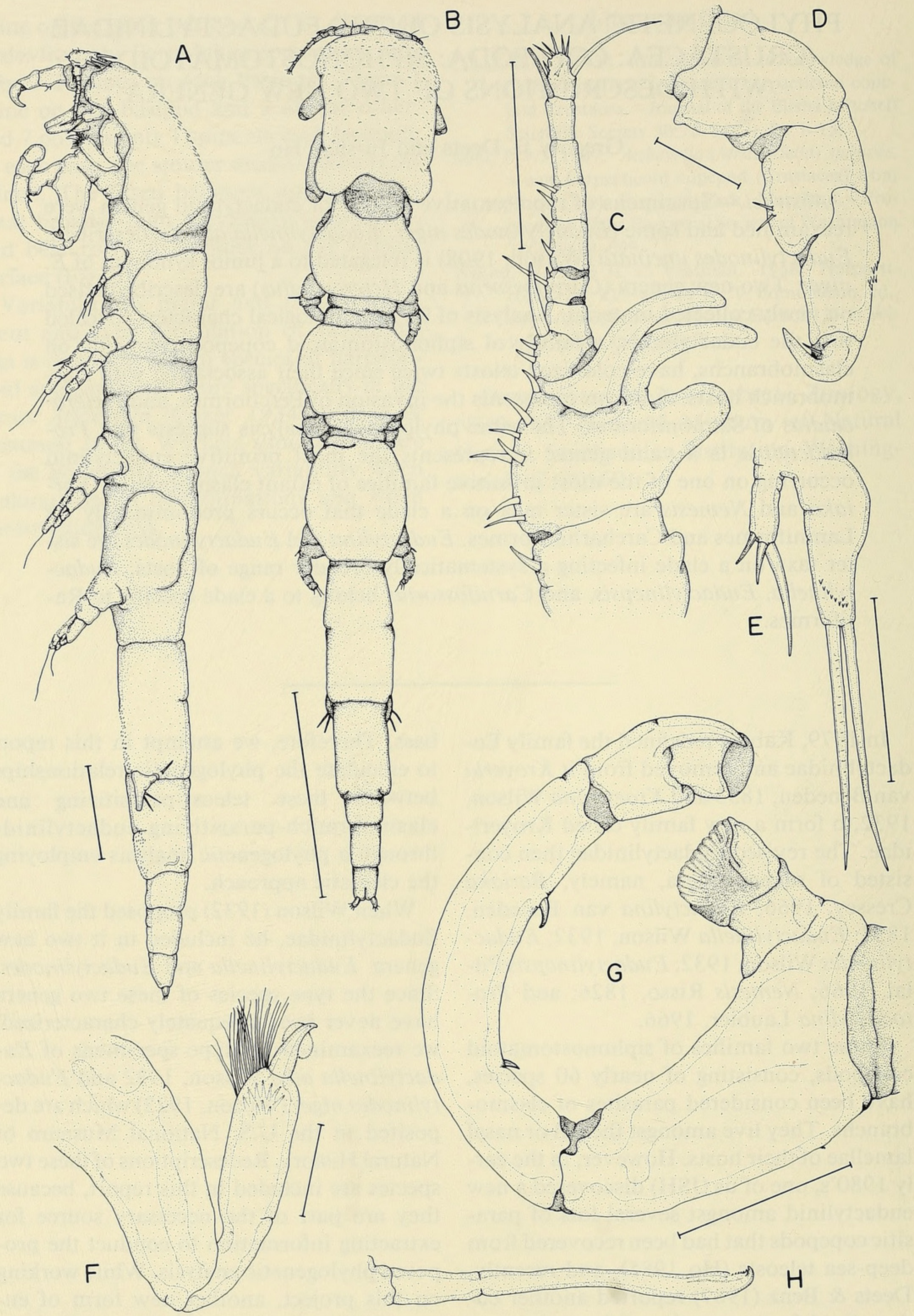
Gregory B. Deets and Ju-shey Ho

Abstract.—Specimens of representative species of eudactylinid genera were reexamined and some (*Eudactylinodes niger, Eudactylinella alba*) redescribed. *Eudactylinodes uncinata* (Wilson, 1908) is relegated to a junior synonym of *E. niger.* Two new genera (*Carnifossorius* and *Heterocladius*) are described based on newly collected material. Analysis of 90 morphological characters revealed that the eudactylinids, a family of siphonostomatoid copepods parasitic on elasmobranchs, have colonized telosts twice since their association with elasmobranch hosts. *Jusheyus* represents the invasion of Perciformes, and *Heterocladius* of Salmoniformes. The same phylogenetic analysis suggests that *Protodactylina* is a valid genus; it represents the most primitive eudactylinid occurring on one of the most primitive families of extant elasmobranch. *Bariaka* and *Nemesis* are sister taxa on a clade that occurs predominantly on Lamniformes and Carcharhiniformes. *Eudactylina* and *Eudactylinodes* are sister taxa on a clade infecting a systematically broader range of hosts. *Eudactylinella, Eudactylinopsis,* and *Carnifossorius* belong to a clade specific to Rajiformes.

In 1979, Kabata redefined the family Eudactylinidae and removed from it *Kroyeria* van Beneden, 1853 and *Kroeyerina* Wilson, 1932,to form a new family called Kroyeriidae. The revised Eudactylinidae then consisted of seven genera, namely, *Bariaka* Cressey, 1966; *Eudactylina* van Beneden, 1853; *Eudactylinella* Wilson, 1932; *Eudactylinodes* Wilson, 1932; *Eudactylinopsis* Pillai, 1966; *Nemesis* Risso, 1826; and *Protodactylina* Laubier, 1966.

These two families of siphonostomatoid copepods, consisting of nearly 60 species, have been considered parasites of elasmobranchs. They live amongst the gill or nasal lamellae of their hosts. However, in the early 1980's, one of us (JSH) discovered a new eudactylinid amongst several lots of parasitic copepods that had been recovered from deep-sea teleosts (Ho 1985), and recently, Deets & Benz (1987) reported another eudactylinid from a species of Australian sea bass. Therefore, we attempt in this report to elucidate the phylogenetic relationships between these teleost-parasitizing and elasmobranch-parasitizing eudactylinids through a phylogenetic analysis employing the cladistic approach.

When Wilson (1932) proposed the family Eudactylinidae, he included in it two new genera, *Eudactylinella* and *Eudactylinodes.* Since the type species of these two genera have never been adequately characterized, we reexamined the type specimens of *Eudactylinella alba* Wilson, 1932 and *Eudactylinodes niger* (Wilson, 1922) which are deposited in the U.S. National Museum of Natural History. Redescriptions of these two species are included in this report, because they are part of the necessary source for extracting information to conduct the proposed phylogenetic analysis. While working on this project, another new form of eudactylinid was discovered from a Siamese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rhinobatid in the collection of the California Academy of Science in San Francisco. The description of this new genus together with the one from a deep-sea teleost will be given in the following before discussing the phylogenetic analysis of the eudactylinid genera.

Eudactylinodes niger (Wilson, 1905)
Figs. 1–2

Material examined.—USNM 54071, containing 19 paratypes from gills of sand shark, *Eugomophodes littoralis,* collected at Woods Hole, Massachusetts, July, 1902.

Female.—Body (Figs. 1A, B) bearing denticles on dorsal surface of cephalothorax, anterior surface of legs 1–4, and ventral surface of 5th pediger. Cephalothorax distinctly longer than wide; carapace with emarginate posterior margin and lateral sides. First 3 free somites about as wide as cephalothorax, 5th pediger distinctly narrower and notched laterally. Genital complex longer than wide, with posterodorsally located oviducal openings. Abdomen 3-segmented, middle segment largest. Caudal ramus (Fig. 2B) small, bearing 5 elements: 1 setiform (inner subterminal) and 4 spiniform.

First antenna (Fig. 1C) 10-segmented, divisible into robust base (2 segments) and slender shaft (8 segments). First segment with 1 small seta on anterior margin and 1 thumb-like process on posterior surface. Second segment produced posteriorly into a large blunt process bearing 2 large, curved hooks on terminal surface and 7 small setae on anterior margin. Armature of 8-segmented shaft part: 2+1 spine, 0,2,2,2,0,1 aesthete, and 8. Second antenna (Fig. 1D) 3-segmented; first segment unarmed, second segment with 2 inner setae, third segment armed distally with large hook bearing 2 basal setae. Patch of denticles on mid-outer surface of third segment. Mandible (Fig. 1H) indistinctly 2-segmented, cutting blade armed with very fine teeth. First maxilla (Fig. 1E) biramous, with large endopod carrying 2 long setae and small exopod tipped by 1 long and 2 short setae. Second maxilla (Fig. 1F) 2-segmented; basal segment (lacertus) unarmed, but distal segment (branchium) armed terminally with subterminal cluster of long, thin bristles and another cluster of denticles; calamus a hook with lateral hyaline membranes. Maxilliped (Fig. 1G) 3-segmented, chelate, powerful (Fig. 1A). Basal segment small. Middle segment (corpus) with its myxa enlarged to form mitt-like receptacle. Terminal segment (subchela) long and arched, shaft bearing subterminal inner seta and claw with enlarged base carrying below hook a hollowed terminal piece.

Legs 1–4 biramous, with 3-segmented rami, their spines (Roman numerals) and setae (Arabic numerals) as follows:

Leg 1	Prp	0-0; 1-0	Exp	1-0; 1-0; 4
			Enp	0-I; 0-2; 5
Leg 2	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-I; 0-0; 4
Leg 3	Prp	0-0; 1-0	Exp	I-0; I-0; II,1
			Enp	0-I; 0-0; I,2
Leg 4	Prp	0-0; 1-0	Exp	I-0; I-0; II,1
			Enp	0-I; 0-0; I,2

Leg 1 exopod (Fig. 2A) smaller than endopod. Outer surface of leg 1 endopod bearing irregular protrusion near base. Outer distal corners of first 2 segments in leg 1 endopod produced into spiniform process. Similar spiniform process also developed in first segment of leg 2 endopod (Fig. 2C) and leg 3 endopod (Fig. 2D). Leg 4 similar to

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Fig. 1. *Eudactylinodes niger* Wilson, female: A, Habitus lateral; B, Habitus dorsal; C, First antenna; D, Second antenna; E, First maxilla; F, Second maxilla; G, Maxilliped; H, Mandible. Scales: 0.3 mm in A; 0 mm in B; 0.1 mm in C, G, H; 0.5 mm in D, E, F.

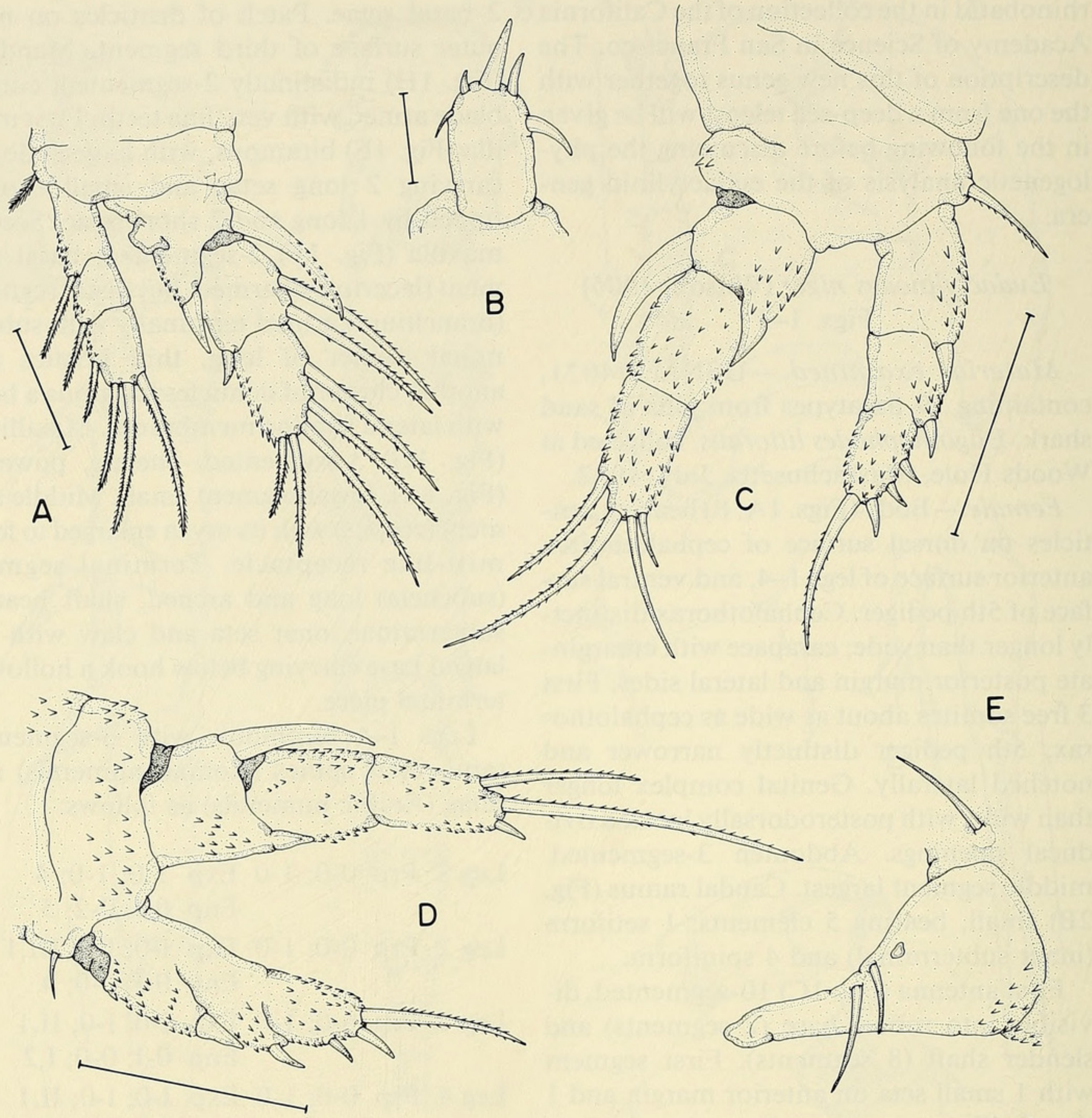

Fig. 2. *Eudactylinodes niger* Wilson, female: A, Leg 1; B, Caudal ramus; C, Leg 2; D, Leg 3; E, Leg 5. Scales: 0.05 mm in A; 0.02 mm in B; 0.1 mm in C, D, E.

leg 3, both with partly fused proximal segments in exopod (Fig. 2D). Free segments of leg 5 (Fig. 2E) carrying on dorsal surface 1 small spiniform process and 2 setae.

Male.—Not represented in USNM collection.

Remarks.—Since the gender of *Eudactylinodes* is masculine and *nigra* is feminine, it is mandatory to change the species name to the masculine, *niger.*

This species was first described by Wilson (1905) without illustrations. However, when it was redescribed with a set of illustrations (Wilson 1922), a pair of strange spines were shown coming off the posterior corners of the carapace. Curiously, this pair of spines were not mentioned in the text, neither in the original nor in the subsequent redescription. Nevertheless, in 1932, Wilson used this curious pair of spines as a major species distinction to separate the two species of his newly proposed genus, *Eudactylinodes.*

Through the assistance of Dr. Masahiro Dojiri we learned that the remaining specimens of *E. niger* deposited in the National Museum of Natural History (USNM 54070 and 54072) do not carry such spines either. Furthermore, reexamination of specimens in the type-lot of *E. uncinata* (Wilson, 1908) (USNM 38558: "from the gills of the soupfin shark, *Galeorhinus zyopterus* at La Jolla, California") revealed no significant morphological distinctions between it and *E. niger.* Therefore, we propose to relegate *E. uncinata* to a junior synonym of *E. niger.* Recently, Deets and Benz (1986a) described a new species of *Eudactylinodes, E. keratophagus,* from two species of horn sharks from off southern California and Baja California.

Eudactylinella alba Wilson, 1932
Figs. 3–6

Material examined.—USNM 5667, containing 3 females and one male taken from gills and nostrils of a sting ray, *Dasybatus marinus,* collected on Marthas Vineyard, Massachusetts, July, 1926.

Female.—Body (Fig. 3A) with distinct tagmosis. First pediger forming intersegmental area between cephalosome and second pediger, latter largest somite of body. Fifth pediger distinctly wider than long. Genital complex distinctly longer than wide, covered with spinules on ventral surface; genital opening on dorsolateral surface near anterior margin. Abdomen 2-segmented, both somites bearing spinules on ventral surface. Caudal ramus about 1.5 times longer than wide, bearing 6 elements as shown in Fig. 4E.

First antenna (Fig. 3C) 11-segmented, first and second segments partly fused. Armament of these segments: 1, 2, 2, 2, 1, 3, 1, 4, 1, 1 + 1 aesthete, and 10. Second antenna (Fig. 3B) 3-segmented; first segment unarmed second segment with 1 seta and anterodistal patch of denticles, third segment with anterobasal patch of denticles. Terminal claw with 2 basal setae. Mandible (Fig. 3G) bearing 8 teeth on cutting blade. First maxilla (Fig. 3F) biramous; endopod with denticles, tipped with 2 setae bearing spinules; exopod a long, bluntly pointed process carrying 2 short setae at about midlength. Second maxilla (Fig. 3D) 2-segmented; lacertus bearing small, proximal process and brachium, patch of denticles, tufts of bristles and terminal claw with two rows of fine denticles. Maxilliped 3-segmented (Fig. 3A), with huge basal segment. Corpus maxillipedis not swollen, its myxa bearing small spiniform process. Subchela an uncinate, single claw.

Legs 1–4 biramous, with 3-segmented rami, their spines (Roman numerals) and setae (Arabic numerals) as follows:

Leg 1	Prp	0-0; 1-I	Exp	I-0; I-0; IV
			Enp	0-0; 0-0; I
Leg 2	Prp	0-0; 0-0	Exp	I-0; I-0; III,I
			Enp	0-0; 0-0; 0
Leg 3	Prp	0-0; 0-0	Exp	I-0; I-0; III,I
			Enp	0-0; 0-0; I
Leg 4	Prp	0-0; 0-0	Exp	I-0; I-0; III,I
			Enp	0-0; 0-0; I

Outer-distal corners of endopodal segments in Leg 1 (Fig. 4A) protruded into small spiniform process. Third endopodal segment of leg 2 (Fig. 4B) a stout spiniform process with serrate outer edge; second segment of same ramus protruded distolaterally into large, bifid process. Leg 3 (Fig. 4C) and leg 4 (Fig. 4D) rather alike in segmentation and armature, both with first endopodal segment greatly protruded. Leg 5 (Fig. 4F) broad, sparsely covered with denticles and armed with 2 terminal setae and 1 subterminal seta.

Male.—Body (Fig. 5A) more slender than female; with much reduced fifth pediger. Genital somite wider anteriorly, with several rows of spinules on posterior part of ventral surface. Abdomen 4-segmented, each somite bearing spinules on ventral surface. Caudal ramus (Fig. 6G) about 2.4 times

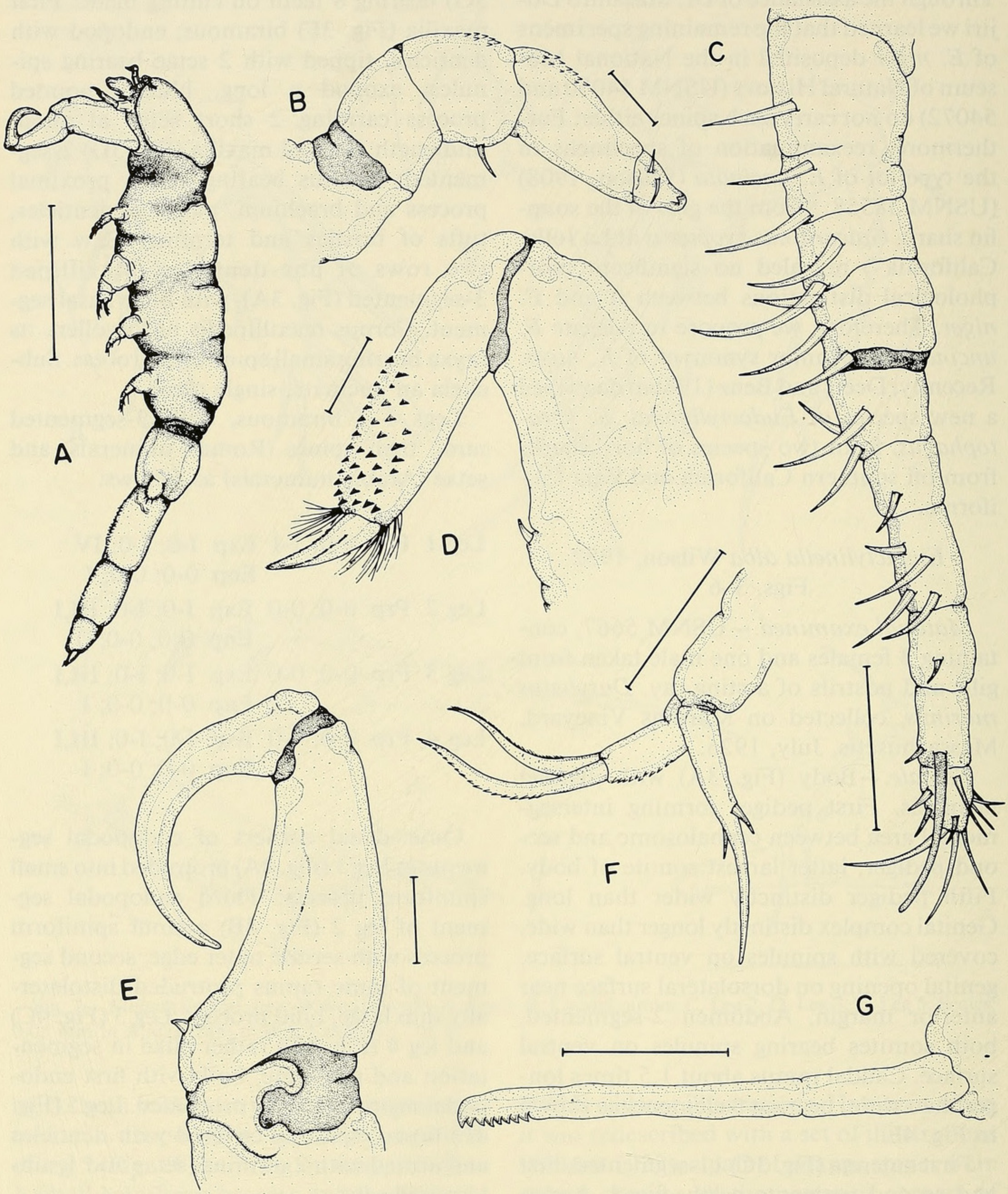

Fig. 3. *Eudactylinella alba* Wilson, female: A, Habitus lateral; B, Second antenna; C, First antenna; D, Second maxilla; E, Maxilliped; F, First maxilla; G, Mandible. Scales: 1 mm in A; 0.1 mm in E; 0.5 mm in B, C, D, F, G.

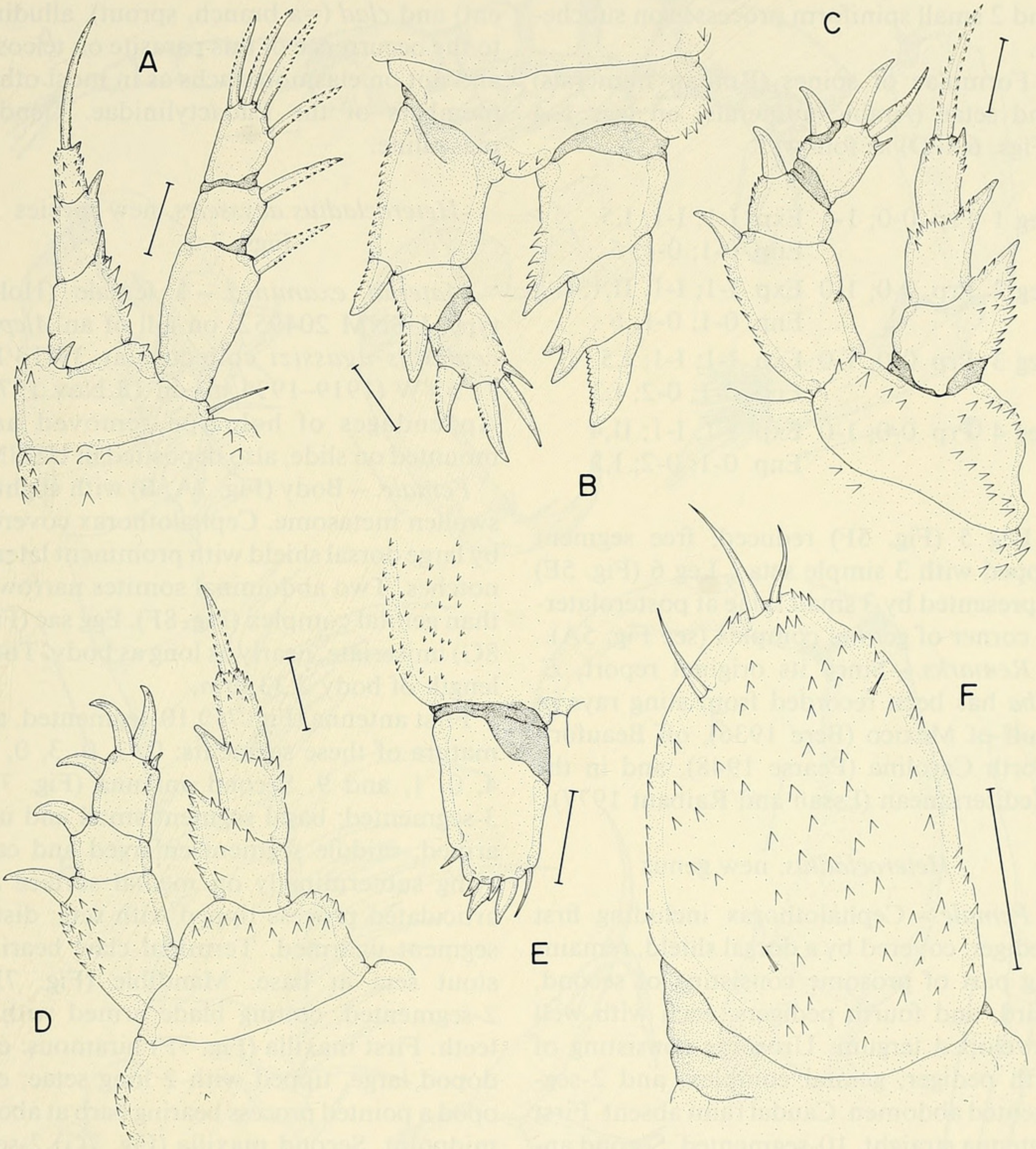

Fig. 4. *Eudactylinella alba* Wilson, female: A, Leg 1; B, Leg 2; C, Leg 3; D, Leg 4; E, Caudal ramus; F, Leg 5. Scales: 0.05 mm in A–F.

longer than wide, carrying 3 small, simple setae and 3 long plumose, terminal setae.

First antenna (Fig. 5B) geniculate, 15-segmented. Armature of these segments: 1, 2, 2, 5, 2, 1, 8, 1, 2, 2, 3, 3, 3, 1+1 aesthete, and 8. Second antenna (Fig. 5C) slender, 3-segmented; first and third segments unarmed but second segment bearing 2 setae on swollen inner surface; terminal claw with 2 basal setae. Mandible (Fig. 5G) as in female. First maxilla (Fig. 5E) resembling that in female, except for fine ornamentation on endopod. Second maxilla (Fig. 5D) different from female in lacking basal element on lacertus. Maxilliped (Fig. 5F) showing sexual dimorphism in ornamentation on corpus and 2 small spiniform processes on subchela.

Formulae of spines (Roman numerals) and setae (Arabic numerals) on legs 1–4 (Figs. 6A–D) as follows:

Leg 1	Prp 0-0; 1-1	Exp	I-1; I-1; I,5
		Enp	0-1; 0-1; 5
Leg 2	Prp 0-0; 1-0	Exp	I-1; I-1; II,1,4
		Enp	0-1; 0-1; 6
Leg 3	Prp 0-0; 1-0	Exp	I-1; I-1; I,5
		Enp	0-1; 0-2; I,3
Leg 4	Prp 0-0; 1-0	Exp	I-1; I-1; II,4
		Enp	0-1; 0-2; I,2

Leg 5 (Fig. 5F) reduced; free segment tipped with 3 simple setae. Leg 6 (Fig. 5E) represented by 3 small setae at posterolateral corner of genital complex (see Fig. 5A).

Remarks.—Since its original report, *E. alba* has been recorded from sting rays in Gulf of Mexico (Bere 1936), off Beaufort, North Carolina (Pearse 1948), and in the Mediterranean (Essafi and Raibaut 1977).

Heterocladius, new genus

Female.—Cephalothorax including first pediger, covered by a dorsal shield, remaining part of prosome consisting of second, third, and fourth pedigers, each with well developed tergum. Urosome consisting of fifth pediger, genital complex, and 2-segmented abdomen. Caudal rami absent. First antenna straight, 10-segmented. Second antenna 3-segmented, with uncinate terminal claw. Oral appendages generally as in *Eudactylina*. First 4 pairs of legs biramous, exopods distinctly shorter than endopods; rami 2- to 3-segmented. Fifth leg with one free segment.

Parasitic on gill of teleosts.

Male.—Unknown.

Type species.—*Heterocladius abyssetes*, n. sp.

Etymology.—The generic name is a combination of the Greek *heter* (=other, different) and *clad* (=a branch, sprout), alluding to the occurrence of this parasite on teleosts and not on elasmobranchs as in most other members of the Eudactylinidae. Gender masculine.

Heterocladius abyssetes, new species
Figs. 7–8

Material examined.—1 female (Holotype, USNM 204952) on gill of an *Alepocephalus agassizi* collected at 39°13′N, 71°53′W (1919–1974 m) on 18 Nov 1973. Appendages of holotype removed and mounted on slide, also deposited in USNM.

Female.—Body (Fig. 7A, B) with slightly swollen metasome. Cephalothorax covered by large dorsal shield with prominent lateral notches. Two abdominal somites narrower than genital complex (Fig. 8F). Egg sac (Fig. 8G) uniseriate, nearly as long as body. Total length of body 2.33 mm.

First antenna (Fig. 7C) 10-segmented, armature of these segments: 0, 3, 0, 3, 0, 1, 4, 0, 1, and 9. Second antenna (Fig. 7E) 3-segmented: basal segment small and unarmed; middle segment enlarged and carrying subterminally on medial surface an articulated process tipped with seta; distal segment unarmed. Terminal claw bearing stout seta at base. Mandible (Fig. 7D) 2-segmented, cutting blade armed with 8 teeth. First maxilla (Fig. 7F) biramous: endopod large, tipped with 2 long setae; exopod a pointed process bearing barb at about midpoint. Second maxilla (Fig. 7G) 2-segmented: lacertus large, but unarmed; brachium beaing subterminally a tuft of bristles. Terminal claw (Fig. 7H) armed with several rows of teeth. Maxilliped (Fig. 7I) subchelate and 3-segmented; basal segment large; corpus robust, myxa protruded into large stout spine, and bearing small, medial spiniform process; subchela armed with 3 spiniform processes on medial surface.

Legs 1–4 (Figs. 8A–D) biramous, their spines (Roman numerals) and setae (Arabic numerals) as follows:

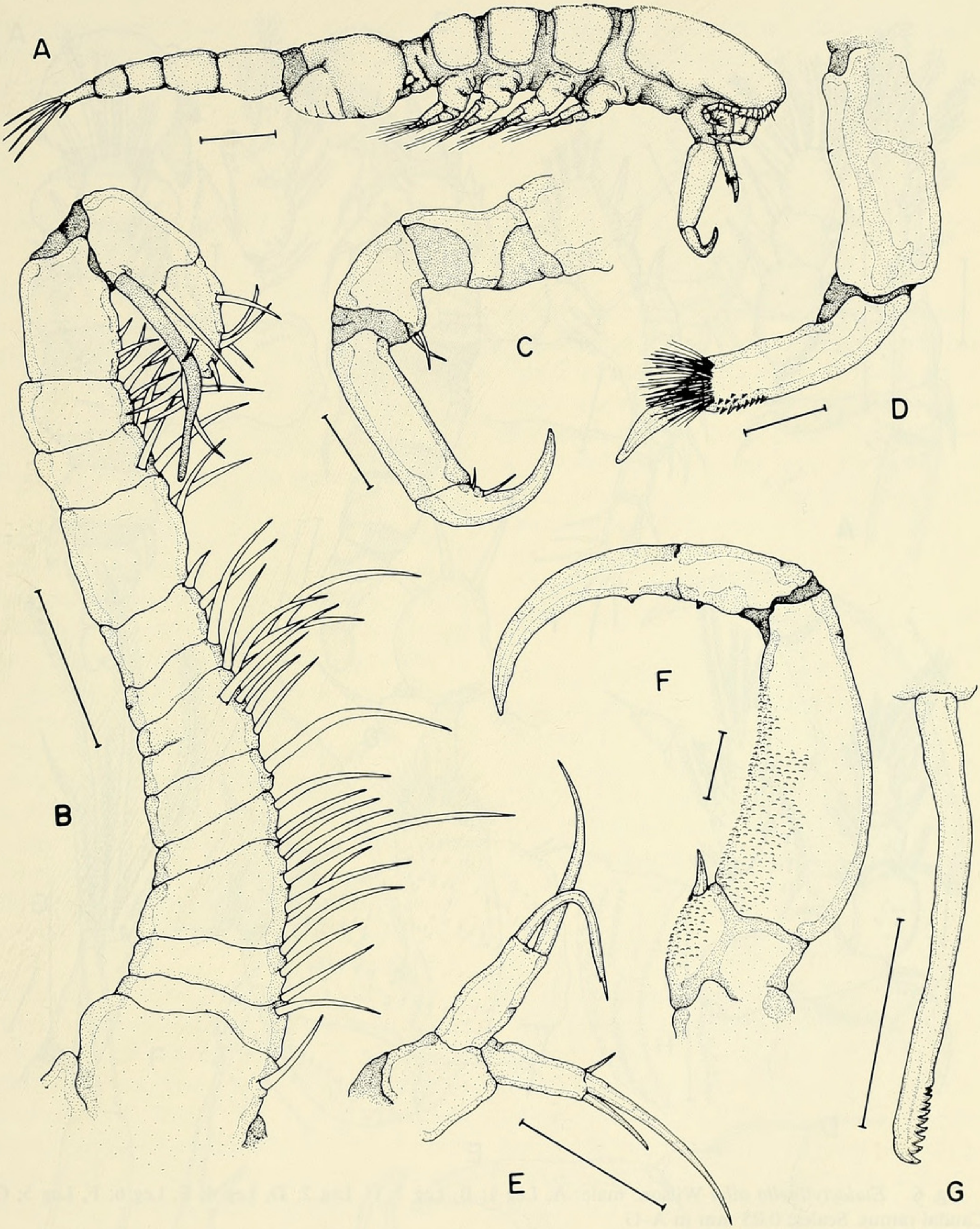

Fig. 5. *Eudactylinella alba* Wilson, male: A, Habitus lateral; B, First antenna; C, Second antenna; D, Second maxilla; E, First maxilla; F, Maxilliped; G, Mandible. Scales: 0.2 mm in A; 0.05 mm in B–G.

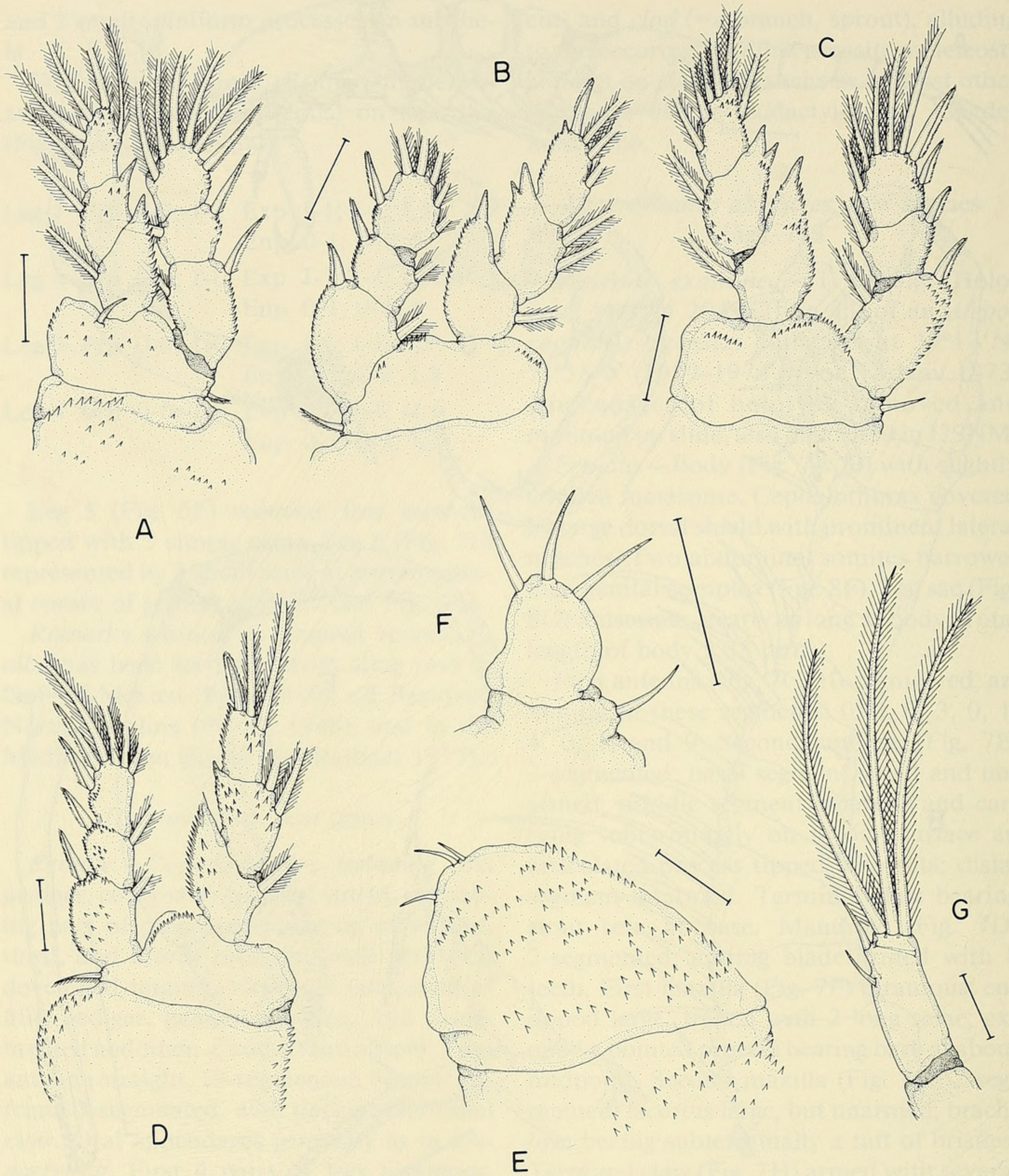

Fig. 6. *Eudactylinella alba* Wilson, male: A, Leg 1; B, Leg 3; C, Leg 2; D, Leg 4; E, Leg 6; F, Leg 5; G, Caudal ramus. Scales: 0.05 mm in A–G.

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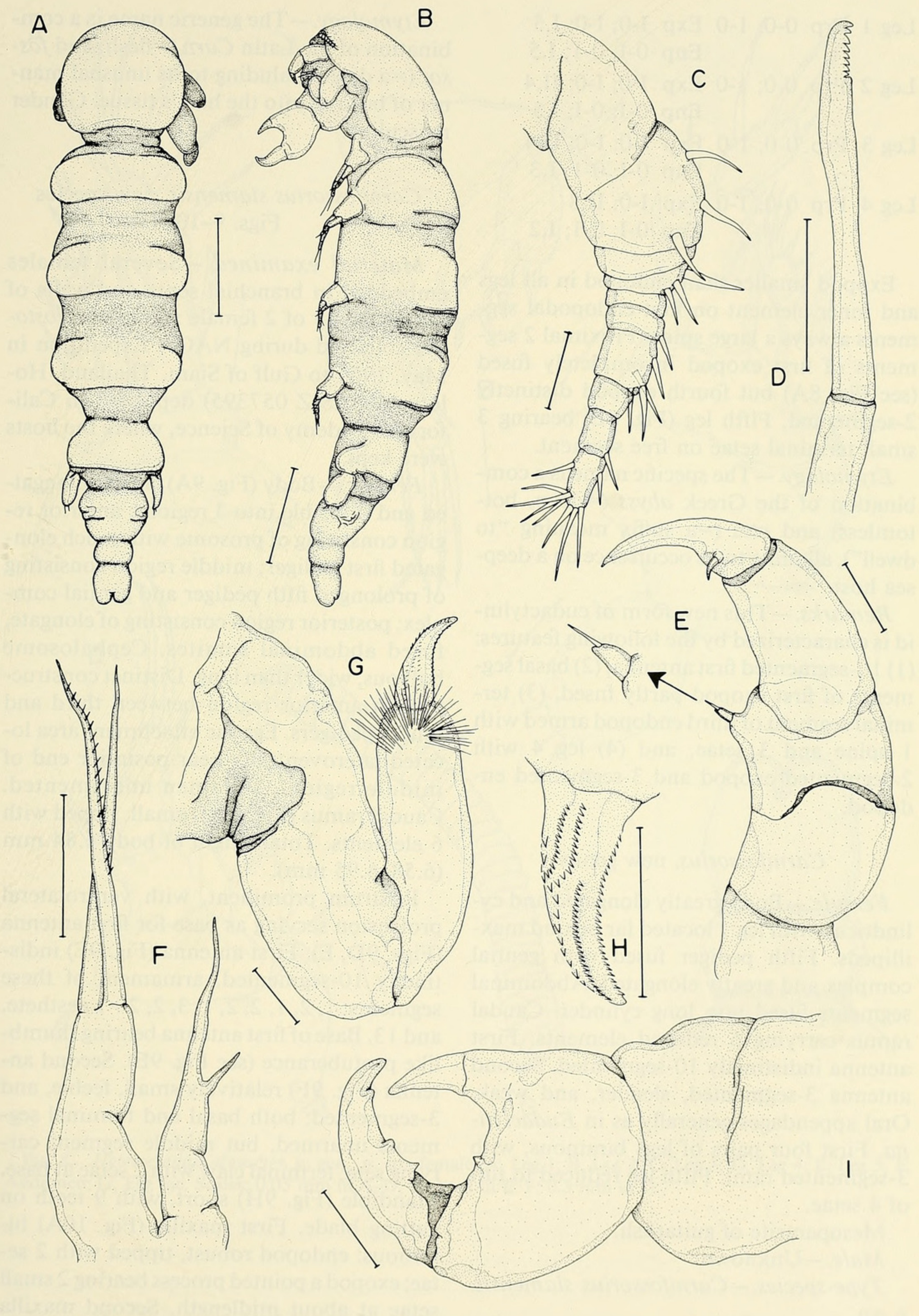
Fig. 7. *Heterocladius abyssetes,* n. gen., n. sp., female: A, Habitus dorsal; B, Habitus lateral; C, First antenna; D, Mandible; E, Second antenna; F, First maxilla; G, Second maxilla; H, Tip of second maxilla; I, Maxilliped. Scales: 0.5 mm in A, B; 0.1 mm in C, I; 0.05 mm in D–H.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Leg 1	Prp 0-0; 1-0	Exp	I-0; I-0; I,5
		Enp	0-I; 0-1; I,5
Leg 2	Prp 0-0; 1-0	Exp	I-0; I-0; II,4
		Enp	0-I; 0-I; I,5
Leg 3	Prp 0-0; 1-0	Exp	I-0; I-0; II,4
		Enp	0-I; 0-1; I,3
Leg 4	Prp 0-0; 1-0	Exp	I-0; II,3
		Enp	0-I; 0-1; I,2

Exopod smaller than endopod in all legs and inner element on first endopodal segments always a large spine. Proximal 2 segments of first exopod incompletely fused (see Fig. 8A) but fourth exopod distinctly 2-segmented. Fifth leg (Fig. 8E) bearing 3 small terminal setae on free segment.

Etymology.—The specific name is a combination of the Greek *abyss* (=deep, bottomless) and *etes* (=a suffix meaning "to dwell"), alluding to its occurrence on a deep-sea host.

Remarks.—This new form of eudactylinid is characterized by the following features: (1) 10-segmented first antenna, (2) basal segments of first exopod partly fused, (3) terminal segment of third endopod armed with 1 spine and 3 setae, and (4) leg 4 with 2-segmented exopod and 3-segmented endopod.

Carnifossorius, new genus

Female.—Body greatly elongated and cylindrical, with leg 1 located far behind maxillipeds. Fifth pediger fused with genital complex and greatly elongated. Abdominal segments fused into long cylinder. Caudal ramus carrying 6 reduced elements. First antenna indistinctly 10-segmented. Second antenna 3-segmented, slender, and weak. Oral appendages generally as in *Eudactylina.* First four pairs of legs biramous, with 3-segmented rami. Fifth leg reduced to tuft of 4 setae.

Mesoparasite of guitarfish.

Male.—Unknown.

Type-species.—*Carnifossorius siamensis,* n. sp.

Etymology.—The generic name is a combination of the Latin *Carn* (=flesh) and *fossor* (=a digger), aluding to its unusual manner of borirng into the host's tissue. Gender masculine.

Carnifossorius siamensis, new species
Figs. 9–10

Material examined.—Several females embedded in branchial septa and walls of buccal cavity of 2 female *Rhina ancylostoma* collected during NAGA Expedition in May, 1961 to Gulf of Siam, Thailand. Holotype (CASIZ 057395) deposited in California Academy of Science, where the hosts were kept.

Female.—Body (Fig. 9A) greatly elongated and divisible into 3 regions: anterior region consisting of prosome with much elongated first pediger; middle region consisting of prolonged fifth pediger and gential complex; posterior region consisting of elongate, fused abdominal somites. Cephalosome bulbous, wider than long. Distinct construction in anterior region between third and fourth pedigers. Egg sac attachment area located lateroventrally near posterior end of middle region. Abdomen unsegmented. Caudal ramus (Fig. 10G) small, tipped with 6 elements. Total length of body 6.84 mm (6.58–6.95 mm).

Rostrum prominent, with ventrolateral protrusion serving as base for first antenna (Figs. 9D, E). First antenna (Fig. 9E) indistinctly 10-segmented, armament of these segments: 1, 2, 1, 2, 2, 1, 3, 2, 2+1 aesthete, and 13. Base of first antenna bearing thumb-like protuberance (see Fig. 9E). Second antenna (Fig. 9F) relatively small, feeble, and 3-segmented; both basal and terminal segments unarmed, but middle segment carrying seta; terminal claw with 2 setae at base. Mandible (Fig. 9H) short, with 9 teeth on cutting blade. First maxilla (Fig. 10A) biramous: endopod robust, tipped with 2 setae; exopod a pointed process bearing 2 small setae at about midlength. Second maxilla

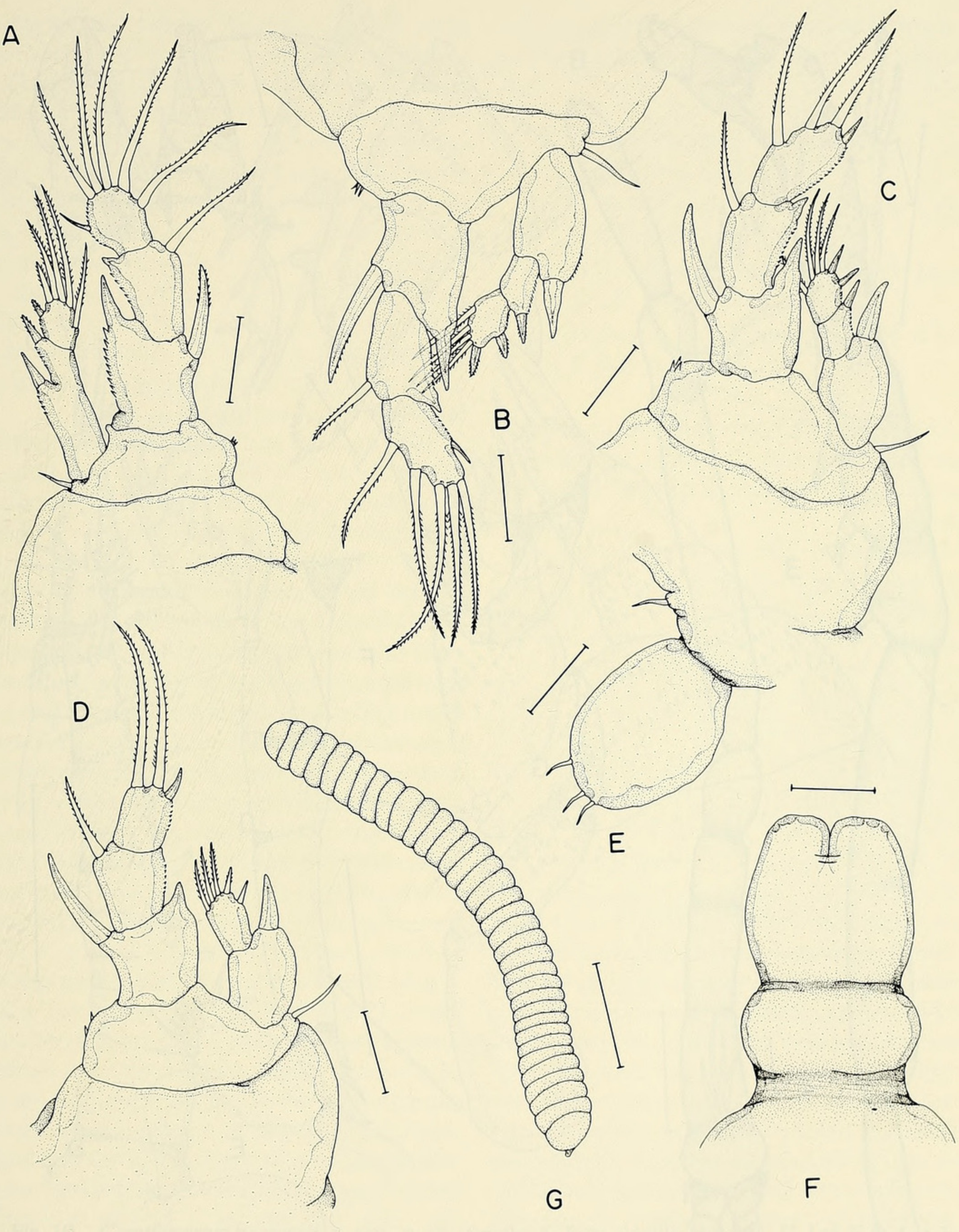

Fig. 8. *Heterocladius abyssetes*, n. gen., n. sp., female: A, Leg 1; B, Leg 2; C, Leg 3; D, Leg 4; E, Leg 5; F, Abdomen; G, Egg sac. Scales: 0.05 mm in A–D; 0.1 mm in E, F; 0.5 mm in G.

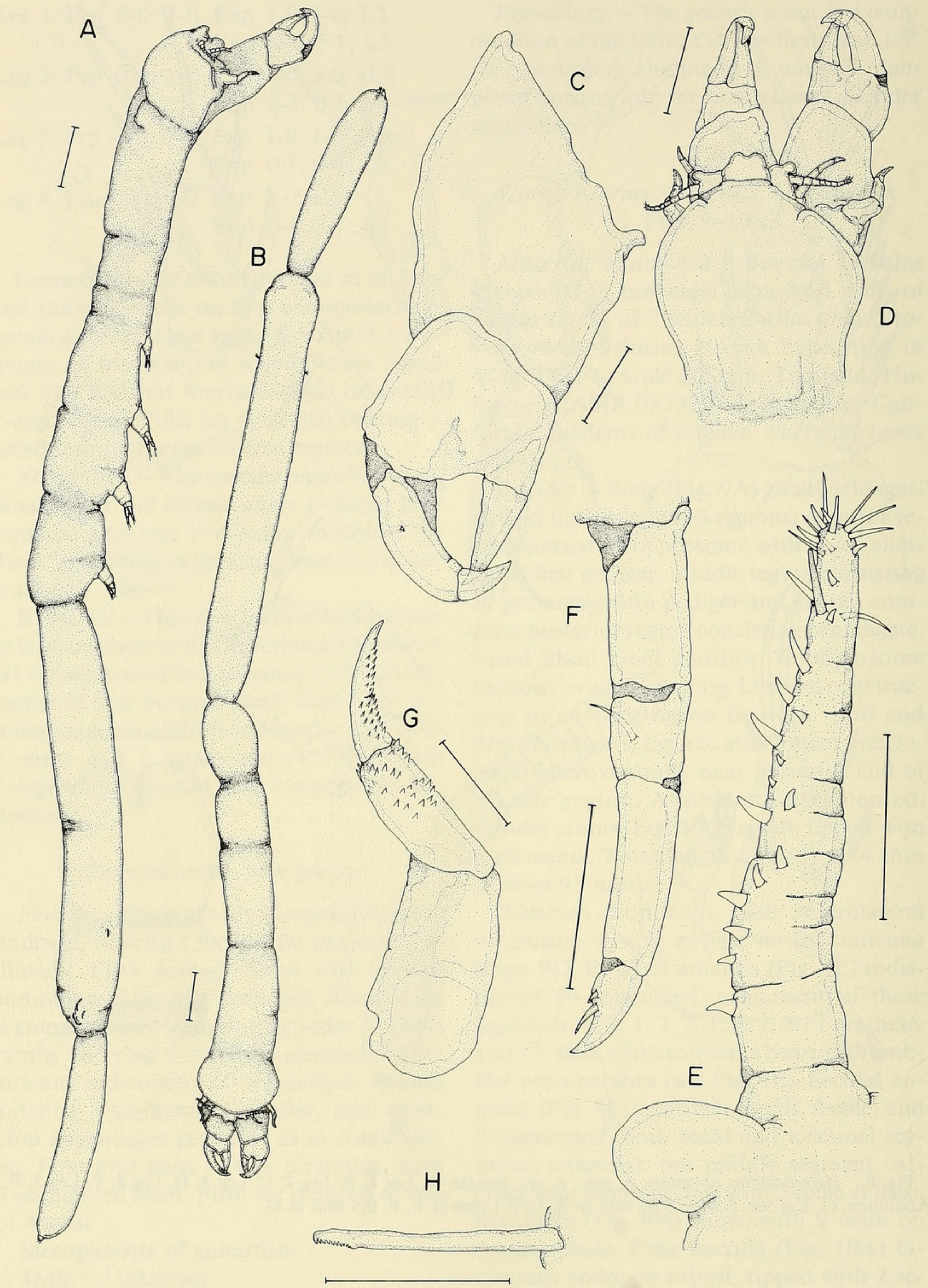

Fig. 9. *Carnifossorius siamensis,* n. gen., n. sp., female: A, Habitus lateral; B, Habitus dorsal; C, Maxilliped; D, Cephalothorax dorsal; E, First antenna; F, Second antenna; G, Second maxilla; H, Mandible. Scale: 0.1 mm in A–C; 0.2 mm in D; 0.05 mm in E–H.

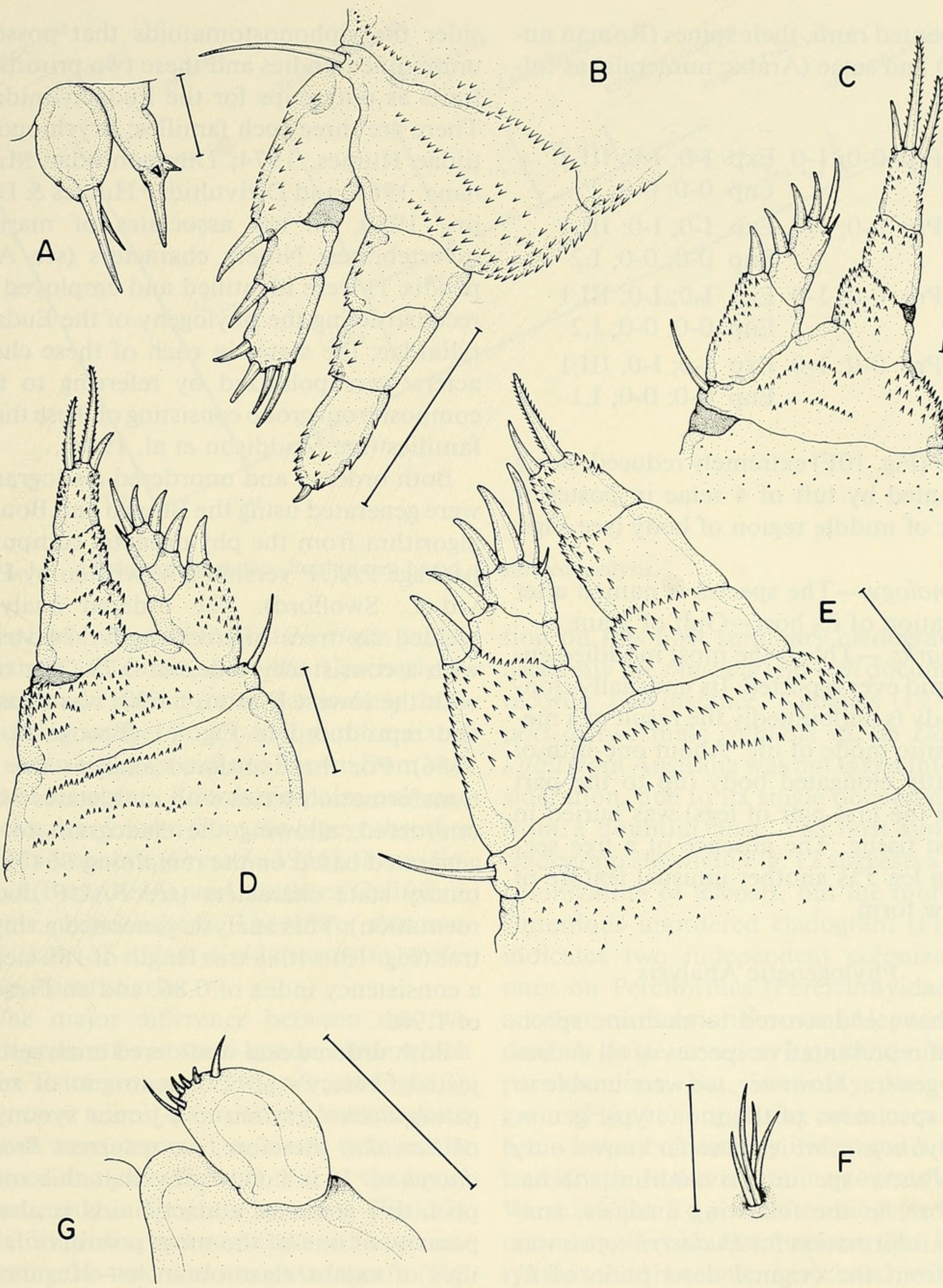

Fig. 10. *Carnifossorius siamensis*, n. gen., n. sp., female: A, First maxilla; B, Leg 1; C, Leg 2; D, Leg 3; E, Leg 4; F, Leg 5; G, Caudal ramus. Scales: 0.02 mm in A; 0.1 mm in C; 0.03 mm in F; 0.05 mm in B, D, E, G.

(Fig. 9G) 2-segmented: lacertus largest but unarmed, and brachium carrying denticles; terminal claw armed with scattered denticles. Maxilliped (Fig. 9C) subchelate and 3-segmented: basal segment large; corpus short and broad, with myxa protruded into large spine; subchela short and unarmed, terminal claw with pocket for receiving tip of myxa.

Legs 1–4 (Figs. 10B–E) biramous with

3-segmented rami, their spines (Roman numerals) and setae (Arabic numerals) as follows:

Leg 1	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; 1
Leg 2	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; I,2
Leg 3	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; I,2
Leg 4	Prp	0-0; 1-0	Exp	I-0; I-0; III,1
			Enp	0-0; 0-0; I,1

Leg 5 (Fig. 10F) extremely reduced, being represented by tuft of 4 setae in posterior quarter of middle region of body (see Figs. 9A, B).

Etymology.—The species is named after the location of its host—Gulf of Siam.

Remarks.—This is the most modified eudactylinid ever reported. Its unusually elongate body is undoubtedly the result of a mesoparasitic mode of life. About one-fifth of its greatly elongated body (up to the part bearing the first pair of legs) was buried in the host tissue. The absence of a free segment in leg 5 is another unusual feature of this new form.

Phylogenetic Analysis

We have endeavored to examine specimens of representative species of all eudactylinid genera. However, we were unable to obtain specimens of the monotypic genus, *Eudactylinopsis,* which is so far known only from *Pristis* sp. in Trivandrum, India. Therefore, in the following analysis, anatomical information for *Eudactylinopsis* was taken from the original description of *E. curvatus* given by Pillai (1968). Inasmuch as three eudactylinid genera are known only from females, the analysis below is based solely on the female characters.

Several families of siphonostomatoids are remarkable in bearing certain primitive traits, like having an exopod in the second antenna, or a palp in the mandible. We consider the siphonostomatoids that possess unmodified bodies and these two primitive traits as outgroups for the Eudactylinidae. There are three such families: Brychiopontiidae Humes, 1974; Dinopontiidae Murnane, 1967; and Dirivultidae Humes & Dojiri, 1980; all are associates of marine invertebrates. Ninety characters (see Appendix 1) were identified and employed in reconstructing the phylogeny of the Eudactylinidae; the states in each of these characters were polarized by referring to the composite out group consisting of these three families (see Maddison et al. 1984).

Both ordered and unordered cladograms were generated using the Branch and Bound algorithm from the phylogenetic computer package PAUP version 2.4 (written by David L. Swofford). The ordered analysis yielded six trees of tree length 174 steps, with a consistency index of 0.79. The tree with the lowest F-ratio, 5.650, was chosen and reproduced in Fig. 11 (Brooks et al. 1986). For the unordered analysis the 24 transformation series with multistates were unordered, allowing the cladogram to be generated based on the remaining 66 (73%) binary state characters (see PAUP documentation). This analysis generated a single tree (Fig. 13) with a tree length of 159 steps, a consistency index of 0.86, and an F-ratio of 1.98.

Both ordered and unordered analyses rejected Cressey's (1977) treatment of relegating *Protodactylina* to a junior synonym of *Bariaka,* therefore, we resurrect *Protodactylina.* It is noteworthy that this most primitive genus of eudactylinids is also a parasite of one of the most primitive families of extant elasmobranchs—Hexanchidae. Only one species is known in *Protodactylina* but it has a fairly wide distribution, occurring in the Mediterranean (Laubier et al. 1966; Schirl 1978) and off northern California (Cressey 1977).

The sister group between *Bariaka* and *Nemesis* is strongly suggested in our phylogenetic analysis. Many species of sharks

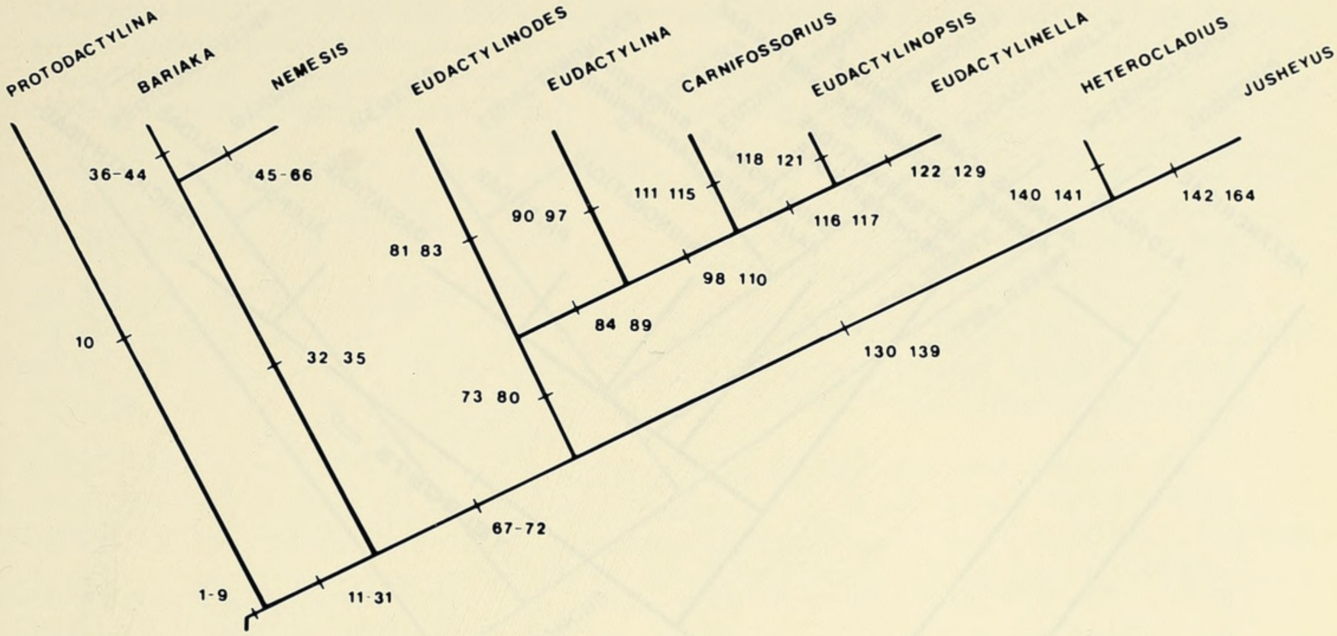

Fig. 11. Cladogram of eudactylinid genera based on ordered analysis.

have been reported to host *Nemesis,* but so far they are confined to the Carcharhiniformes and Laminiformes, particularly those occurring in the North Atlantic, for six of the seven valid species are known from that part of the ocean. *Bariaka* contains only one species; it is known from the bigeye thresher off Madagascar (Cressey 1966), New England (Benz 1986), and southern California (Deets, unpublished). Therefore, this second clade of eudactylinids seems to prefer laminiform sharks.

The major difference between the two cladograms lies in the 6-genera clade which is the sister group of *Jusheyus* (see Fig. 13). The two teleost-parasitizing eudactylinid genera were depicted as sister taxa in the ordered analysis (Fig. 11), but in the unordered analysis they are not (see Fig. 13). This difference is more apparent upon inspecting the host summary cladogram (Fig. 12).

The cladogram in Fig. 12 represents the phylogenetic relationships of the eudactylinids' hosts based on the phylogeny of the parasites obtained from the ordered analysis. It was produced by replacing the parasite genera in Fig. 11 with their respective host families or orders. To place information on this host summary cladogram, we used only the *multiple* and *well* documented records. For instance, Kabata's (1970) report of two male *Nemesis* sp. on *Dasyatis kuhli* from Australia was not taken into consideration, due to its single documentation from a doubtful host. The host summary cladogram shown in Fig. 12 suggests a single colonization of teleosts, but the more parsimonious unordered cladogram (Fig. 13) indicates two independent colonizations, once on Perciformes (Percichthyidae) and another on Salmoniformes (Alepocephalidae). A single invasion hypothesis is more parsimonious, but, ironically, the cladogram (Fig. 11) suggesting such occurrence has a lower consistency index and a longer tree length. Is this a genuine contradiction? We think not. To postulate a single invasion one must invoke assumptions that eudactylinids had become associated with the ancestor of Euteleostei and subsequently dissociated (secondarily lost) from Ostariophysi, Stenopterygii, Scopleomorpha, and Paracanthopterygii; whereas to accept two independent invasions, no multiple assumptions of subsequent dissociation are necessary. Therefore, the host-parasite associations do not contradict the phyloge-

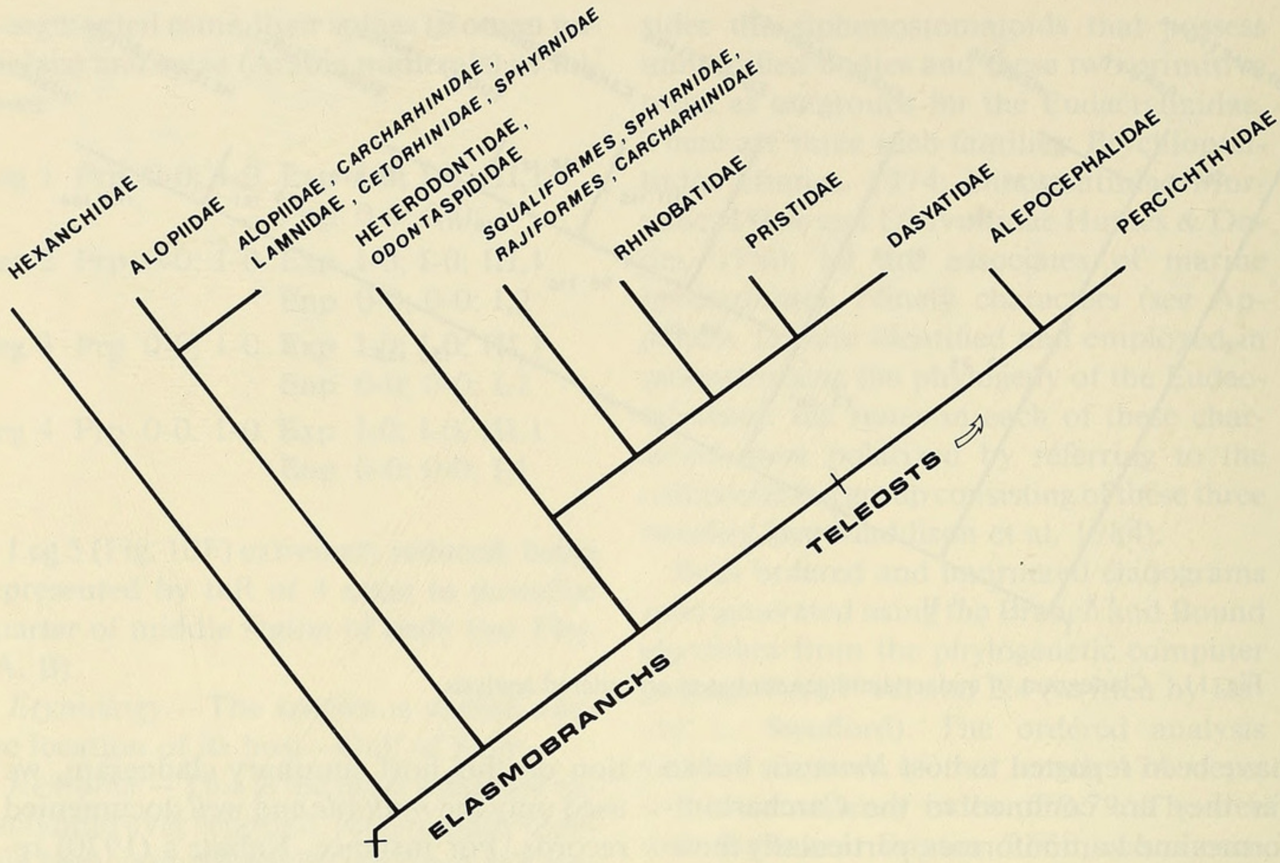

Fig. 12. Host summary cladogram. A parasite cladogram from ordered analysis with host Family or Order superimposed. Showing one host shift from elasmobranchs to teleosts.

netic hypothesis resulting from the unordered analysis.

Eudactylina is by far the largest genus of the eudactylinids, consisting of 26 species. The genus has a systematically broader host association; it is found on Carcharhiniformes, Squaliformes, and Rajiformes. It is interesting to note that 73% (19 species) of *Eudactylina* occur in the North Atlantic (including the Mediterranean) and only five species (19%) are reported from the entire Pacific Ocean (Ho & McKinney 1981). Does this mean the North Atlantic was the cradle of *Eudactylina*? A phylogenetic analysis of the genus is necessary to provide an answer. The sister group of this genus, *Eudactylinodes,* is a much smaller genus, with only two species occurring in North American waters off both east and west coasts.

The remaining three genera, *Eudactylinella, Eudactylinopsis,* and *Carnifossorius,* are monophyletic in both ordered and unordered cladograms. This monophyletic hypothesis is also supported by their host-parasite association, for they are so far known only from the rajiform elasmobranchs. Also, from the standpoint of historical biogeography, the unordered cladogram (Fig. 13) is to be selected, because it indicates that cladogenesis in this part of the eudactylinid phylogeny was caused by a vicariant event—the collision of the Africa-Arabia land mass with Eurasia.

We speculate that the ancestor of these rajiform-parasitizing eudactylinids lived in the Tethys Sea between Laurasia and Gondwana before the time of the Oligocene–Miocene transition, when (about 35 million years ago) the African continent came into contact with Eurasia. After the Tethys Sea was cut into two parts, the eudactylinids in the eastern Tethys (Indian Ocean) gave rise to

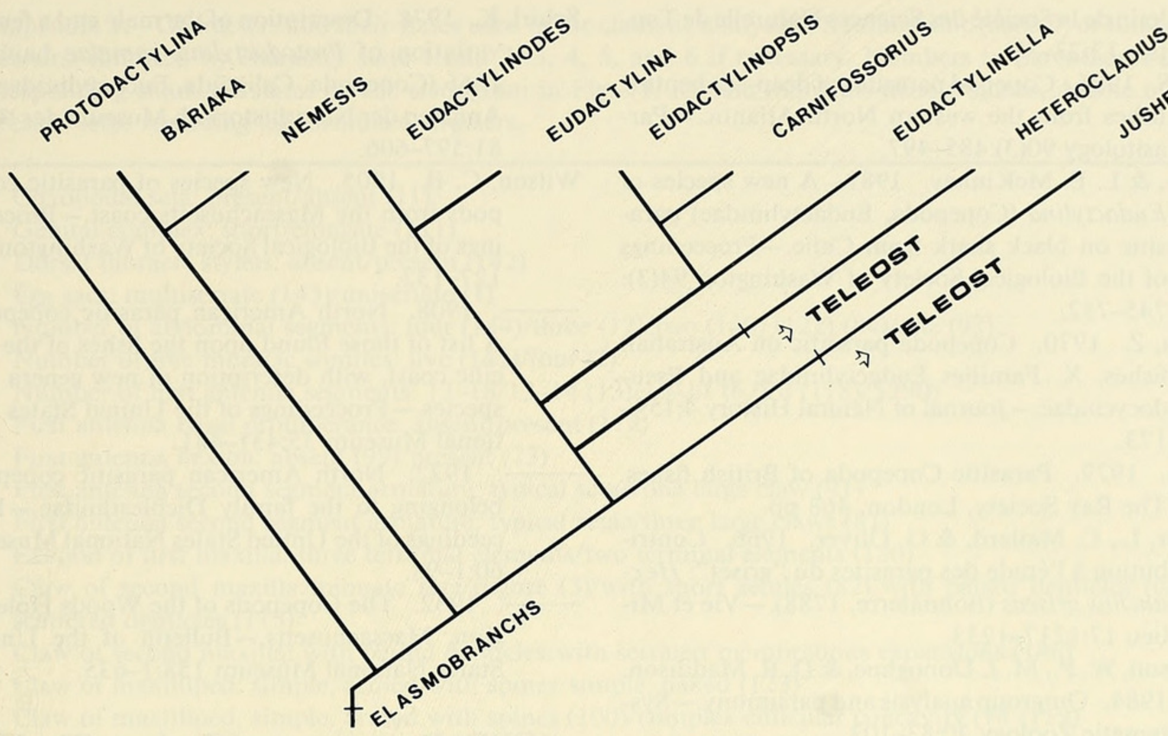

Fig. 13. Cladogram of eudactylinid genera based on unordered analysis. Host-parasite associations same as in Fig. 12. Showing two independent colonizations of teleosts.

Eudactylinopsis and *Carnifossorius* and those in the western Tethys (Atlantic Ocean, including the Mediterranean) evolved into *Eudactylinella.* Current distribution of these three genera supports this hypothesis: *Eudactylinopsis* is found in the Arabian Sea (Pillai 1968), *Carnifossorius,* in the Gulf of Siam (present report), and *Eudactylinella,* in the western North Atlantic (Wilson 1932; Pearse 1948), Gulf of Mexico (Bere 1936), and the Mediterranean Sea (Essafi & Raibaut 1977).

In conclusion, based on the 90 selected morphological characters, the cladogram reproduced in Fig. 13 is the best representation of the eudactylinid phylogeny.

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Appendix 1.—Characters and their states used in the cladistic analysis. Plesiomorphic (code 0) or linkage state given first followed by character state 1 and 2, 3, 4, 5, and 6 if necessary. Numbers in parentheses identify corresponding character states on the cladogram in Fig. 11. Roman numerals denote spines, Arabic numerals represent setae regarding leg formula characters.

1. Coxopodal seta: present/absent (11)
2. Genital complex: short/elongate (111)
3. Dorsal thoracic stylets: absent/present (142)
4. Egg sacs: multiseriate (143)/uniseriate (1)
5. Number of abdominal segments: four (144)/three (12)/two (140) (122) (84)/one (98)
6. Number of free thoracic somites: five (145)/four (2)
7. Number of first antenna segments: 17–18/13–14 (13)/10–11 (67)/8 (118)/5 (90)
8. First antenna basal protuberance: absent/present (112)
9. First antenna flexion: absent (99)/present (73)
10. First antenna second segment armature: typical setae/one large claw (91)
11. First antenna second segment armature: typical setae/three large claws (81)
12. Exopod of first maxilla: three terminal elements/two terminal elements (130)
13. Claw of second maxilla: pinnate seta/rugose (3)/with short setules (82)/with paired denticles (68)/with scattered denticles (113)
14. Claw of second maxilla: with paired denticles/with serrated membranous expansions (146)
15. Claw of maxilliped: simple, armed with spines/simple, naked (123)
16. Claw of maxilliped: simple, armed with spines (100)/complex cuticular concavity (74 (119)
17. Claw of maxilliped: simple, armed with spines/with pocket (114)
18. Myxa of maxilliped: absent/slight, with spine (4) (124) (147)/large, forming chela (69) (101)/membrane (75)
19. Myxa of maxilliped: absent/with dual tines (36) (10)
20. First exopod segment number: three/three, partially fused (131)/two (148)
21. First exopod segment number: three/two, modified (45)
22. First exopod distal segment formula: III,5/II,5 (5)/II,4 (14)/V (120)/IV (85)/III (92)
23. First exopod distal segment formula: II,4/VI (32)/IV (46)
24. First exopod distal segment formula: II,4/4 (83)
25. First exopod second segment formula: I,1/I,0 (70)
26. First exopod proximal segment formula: I,1 (47)/I,0 (15)
27. First exopod proximal segment formula: I,1/modified (48)
28. First endopod segment number: three/two (149)
29. First endopod segment number: three/two, modified (49)
30. First endopod distal segment formula: 6 (132)/(16) (125)/III (102)/I (115)
31. First endopod distal segment formula: 6/I,5 (133)/I,4 (150)
32. First endopod distal segment formula: 5/2 (93)/1 (126)
33. First endopod distal segment formula: 5/modified III (50)
34. First endopod distal segment formula: 5/modified II (37)
35. First endopod proximal segment formula: 0,1/modified (51)
36. First endopod proximal segment formula: 0,1/0,0 (38) (76)
37. Second exopod segment number: three/two (151)
38. Second exopod segment number: three/modified two (52)
39. Second exopod distal segment formula: 9/III,6 (6)/III,1 (77)/IV (103)
40. Second exopod distal segment formula: III,6/VIII (33)
41. Second exopod distal segment formula: III,6/II,4 (134)/II,3 (152)
42. Second exopod distal segment formula: III,1/III (94)
43. Second exopod middle segment formula: I,1/I,0 (17)
44. Second exopod proximal segment formula: I,1 (53)/I,0 (18)
45. Second exopod proximal segment formula: I,1/modified I,I (54)
46. Second endopod segment number: three/two (153)
47. Second endopod segment number: three/modified two (55)
48. Second endopod distal segment formula: 6/I,5 (19)/II,2 (78)/IV (121)/III (104)/modified 0 (127)
49. Second endopod distal segment formula: I,5/I,3 (154)
50. Second endopod distal segment formula: I,5/VI (56)

Appendix 1.—Continued.

51. Second endopod distal segment formula: I,5/modified II (39)
52. Second endopod distal segment formula: II,2/2 (95)
53. Second endopod middle segment formula: 0,2/0,1 (135)/0,0 (20)
54. Second endopod proximal segment formula: 0,1 (86) (155)/0, I (21)
55. Second endopod proximal segment formula: 0,1/0,0 (87)
56. Third exopod segment number: three/two (156)
57. Third exopod segment number: three/modified two (57)
58. Third exopod distal segment formula: 9/II,6 (7)/II,4 (22) (105)/II,1 (79)
59. Third exopod distal segment formula: II,6/VII (34)/VI (40)
60. Third exopod distal segment formula: II,4/II,3 (157)
61. Third exopod distal segment formula: II,4/IV (106)
62. Third exopod middle segment formula: I,1/I,0 (23)
63. Third exopod proximal segment formula: I,1 (58)/I,0 (24)/0,0 (158)
64. Third exopod proximal segment formula: I,1/modified I,I (59)
65. Third endopod segment number: three/two (159)
66. Third endopod segment number: three/modified two (60)
67. Third endopod distal segment formula: 5/I,4 (25)/I,3 (141)/I,2 (71)/III (107)/I (116)/I, toothed (128)
68. Third endopod distal segment formula: I,4/I (41)
69. Third endopod distal segment formula: I,4/V (61)
70. Third endopod distal segment formula: I,2/2 (96)
71. Third endopod middle segment formula: 0,2/0.1 (136)/0,0 (26)
72. Third endopod proximal segment formula: 0,1/0,I (88) (42)
73. Fourth exopod segment number: three/two (160)
74. Fourth exopod segment number: three/modified two (62)
75. Fourth exopod distal segment formula: 9/II,6 (8)/II,3 (72)/IV (108)
76. Fourth exopod distal segment formula: II,3/I,4 (161)
77. Fourth exopod distal segment formula: II,6/IV (35)
78. Fourth exopod distal segment formula: II,3/II,1 (80)
79. Fourth exopod middle segment formula: I,1/I,0 (27)/0,0 (137)
80. Fourth exopod proximal segment formula: I,1/I,0 (28)/0,0 (162)
81. Fourth endopod segment number: three/two (163)
82. Fourth endopod segment number: three/modified two (63)
83. Fourth endopod distal segment formula: 5 (64)/I,2 (9)/I,1 (110)/I (117)/I, toothed (129)
84. Fourth endopod distal segment formula: I,2/modified I (43)
85. Fourth endopod distal segment formula: I,2/2 (97)
86. Fourth endopod distal segment formula: 5/V (65)
87. Fourth endopod middle segment formula: 0,2/0,1 (138)/0,0 (29)
88. Fourth endopod proximal segment formula: 0,1/0,I (30)/0,0 (44) (89)
89. Fourth endopod proximal segment formula: 0,I/I,I (66)
90. Caudal ramus elements: pinnate (139)/naked (31)

Appendix 2.—Character data matrix for the Eudactylinidae. Codes 0 through 6 identify particular characters (note that code 0 does not necessarily indicate an absence). Determination of the plesiomorphic state of the 90 transformtion series was obtained by reference to the composite outgroup referred to in text. Code 9 refers to missing data.

000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000	Outgroup
000101000000100001100100000000000000000100000000000000000010000000001000000010000000100000000	*Protodactylina*
100111100000100001100210010001000101001100110001001021000120011000110021001010110011002201	*Bariaka*
1001112010102001030002011100010000010020001100020000210003000110003000200020011100100002101	*Eudactylinodes*
100131000093001020003001100020000010030001100030000201002100111000500021003000110030002201	*Eudactylinopsis*
100121200000301001000400110001020001003000110005000020100200111000600210030001100400002201	*Eudactylinella*
110131210000400012000400110003000001003000110004000020100200111000400021003000110020002201	*Carnifossorius*
100121200001300002010200110000100000001010110001000011000200011000200010102000910010001109	*Heterocladius*
100121401100300103000500110001010001002001110002000120100300011000300121002001110010102201	*Eudactylina*
10011110000001000010012209010110010100111119010110100910011110090101101090011010910100019111	*Nemesis*
101000100001310001020200910100200000101020910101100090010201092010300090002100221010009000	*Jusheyus*