TAENIACANTHODES DOJIRII N. SP. (COPEPODA: POECILOSTOMATOIDA: TAENIACANTHIDAE), FROM CORTEZ ELECTRIC RAYS (*NARCINE ENTEMEDOR*: TORPEDINIFORMES: NARCINIDAE) CAPTURED IN THE GULF OF CALIFORNIA, AND A PHYLOGENETIC ANALYSIS OF AND KEY TO SPECIES OF *TAENIACANTHODES*

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TAENIACANTHODES DOJIRII N. SP. (COPEPODA: POECILOSTOMATOIDA: TAENIACANTHIDAE), FROM CORTEZ ELECTRIC RAYS (*NARCINE ENTEMEDOR*: TORPEDINIFORMES: NARCINIDAE) CAPTURED IN THE GULF OF CALIFORNIA, AND A PHYLOGENETIC ANALYSIS OF AND KEY TO SPECIES OF *TAENIACANTHODES*

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ABSTRACT: *Taeniacanthodes dojirii* n. sp. (Copepoda: Poecilostomatoida: Taeniacanthidae) is described from adult female specimens collected from the body surface of Cortez electric rays *Narcine entemedor* (Torpediniformes, Narcinidae), captured at several locations in the Gulf of California. *Taeniacanthodes dojirii* is distinguished from its congeners, as well as from other members of Taeniacanthidae, by possessing unimerous fifth legs. A cladistic analysis of the 3 known species of *Taeniacanthodes* resulted in a single most parsimonious tree (tree length = 18 steps, consistency index = 1) demonstrating that *T. gracilis* and *T. haakeri*, both parasites of benthic teleosts, are more closely related to each other than to the new species.

Taeniacanthodes Wilson, 1935, contains 2 known species: *T. gracilis* Wilson, 1935, and *T. haakeri* Ho, 1972. These small poecilostomes (Poecilostomatoida: Copepoda) are mainly considered parasites of flatfishes belonging to Cynoglossidae, Paralichthyidae, and Pleuronectidae (Dojiri and Cressey, 1987), although they have occasionally been found on other teleosts as well (Dojiri, 1977). Recent examinations of Cortez electric rays *Narcine entemedor* captured in the Gulf of California have yielded a third *Taeniacanthodes* species that we describe herein. A phylogenetic analysis of and a dichotomous identification key to species of *Taeniacanthodes* are also presented.

MATERIALS AND METHODS

Copepods were collected from 13 Cortez electric rays as follows: 1 female ray with 6 copepods attached about its spiracle was caught off Bahia de Los Angeles, México, on 2 August 1993; 1 female ray with 5 copepods, 1 female ray with 4 copepods, and 1 female ray with 1 copepod were captured off Bahia de Los Angeles, México, on 3 August 1993; 1 female ray with 1 copepod was captured off Bahia de Los Angeles, México, on 4 August 1993; 2 female rays, each with 3 copepods on their dorsal and ventral body surfaces, were captured off Bahia de Los Angeles, México, on 6 August 1993; 1 male ray with 4 copepods on its ventral body surface was captured off Bahia de Los Angeles, México, on 31 May 1996; 2 female rays with 11 and 14 copepods, respectively, on their ventral body surfaces were captured off Bahia de Los Angeles, México, on 1 June 1996; 1 female ray with 10 copepods on its ventral body surface was captured off Bahia de Los Angeles, México, on 2 June 1996; 1 female ray with 3 copepods on its ventral body surface was captured off Santa Rosalía, México, on 14 June 1996; 1 female ray with 2 copepods on its ventral body surface was captured off Loreto, México, on 18 June 1996.

Hosts were examined in the field soon after capture, and copepods were fixed in 10% buffered formalin or 70 or 95% ethanol. In the laboratory, most copepods were studied using brightfield light microscopy. Prior to examination, specimens were cleared in lactic acid into which a pinch of lignin pink had been dissolved. Fine pins mounted in the tips of thin wooden dowels were used to dissect copepod body parts, and the wooden slide technique of Humes and Gooding (1964) facilitated the study of intact specimens and dissected appendages. Measurements were made using an ocular micrometer, and drawings were made with the aid of a camera lucida. Several specimens were studied using scanning electron microscopy. These specimens were prepared for gold–palladium sputter-coating by placing them in 100% ethanol (2 changes, 1 hr each) followed by immersion in a small volume of hexamethyldisilazane (15 min). Before mounting on metal stubs with 2-sided sticky tape, critical drying was achieved by placing specimens under a slight vacuum to remove the hexamethyldisilazane.

For the phylogenetic analysis, the most parsimonious cladogram was sought from all possible cladograms using the ''Exhaustive Search'' option of the software package PAUP* (Phylogenetic Analysis Using Parsimony [*and other methods]) (Swofford, 1999). A character matrix (Table I) was constructed using data in Dojiri and Cressey (1987) for *T. gracilis* and *T. haakeri* and data provided in this report for *T. dojirii* (Table II). In creating this matrix, an exhaustive search for basal synapomorphies for *Taeniacanthodes* was not undertaken. In the phylogenetic analysis, several multistate characters were released from possible transformation series bias by using the ''unordered'' analysis option of PAUP. To determine character state polarity, members of *Taeniacanthus* Sumpf, 1871, were used as the outgroup. Character states for *Taeniacanthus* spp. were determined using information in Dojiri and Cressey (1987). Host and other ecological information mapped onto the resultant cladogram were taken from Wilson (1935), Causey (1953, 1955), Ho (1969, 1972, 1975), Dojiri (1977), and Dojiri and Cressey (1987) or, in the case of *T. dojiri*, from information contained in this report. Information used to develop the dichotomous identification key to *Taeniacanthodes* spp. adult females was taken from Dojiri and Cressey (1987) or from this report.

Anatomical terminology conforms to that set forth by Kabata (1979) and Dojiri and Cressey (1987). Host nomenclature and systematics conform to Compagno (1999) for elasmobranchs and Eschmeyer (1998) for teleosts.

DESCRIPTION

Taeniacanthodes dojirii n. sp.

(Figs. 1–4)

Adult female: Body (Fig. 1) composed of cephalothorax, 4 free thoracic segments, genital complex, and 3-segmented abdomen. Mean total body length (not including setae of caudal rami) = 1.96 ± 0.14 mm (n = 10), body widest (mean = 0.67 ± 0.07 mm, n = 10) at level of second free thoracic segment. First pedigerous segment incorporated in suboval cephalothorax. Lateral margins of cephalothoracic shield wrapped ventrally, concealing portions of cephalothoracic appendages (Figs. 1B, 2B), posterolateral flaps issued ventrally from each side of cephalothorax (Figs. 1B, 2B, C). Rostrum with 1 stout ventromedial spine (Figs. 1B, 2B, D). Genital complex (Fig. 1) distinct, broadest at midregion, bearing sixth pair of legs. Embryos arranged multiseriately in allantoic egg sacs issued laterally from location just distal to midregion of genital complex, extending almost to tips of longest setae of caudal rami (Fig. 1). Abdomen (Fig. 1) (not including caudal rami) about 30% of total body length, first 2 segments approximately equal in size, third segment (not including caudal rami) longest. Caudal ramus

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TABLE I. Character states for 16 characters used in the phylogenetic analysis of *Taeniacanthodes* Wilson, 1935. Codes 0, 1, and 2 within data matrix identify particular character states for each character as described in Table II (note that 0 indicates a plesiomorphy rather than an absence).

	Character															
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. gracilis	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
T. haakeri	1	1	1	1	1	1	1	1	2	0	0	0	1	0	1	0
T. dojirii	1	1	1	1	1	1	1	2	1	0	0	0	0	1	0	0

(Fig. 3A, B) longer than wide, bearing 6 setae; 1 seta issued laterally about midway along length, 4 apical setae with inner 2 longest, 1 small seta issued dorsally, rank of spinules ventrally near apex (Fig. 3B); all setae bearing sparse, short pinnae.

First antenna (Fig. 3C) indistinctly 5-segmented, difficult to interpret, at least 17 setae on first segment, 7 setae on second segment, 5 on third segment, 2 setae and 1 aesthete on fourth segment, 7 setae and 1 aesthete on fifth segment. Most setae pinnate, some naked (Fig. 3C). Second antenna (Fig. 3D) 4 segments, first segment largest, third and fourth segments indistinctly separated. First segment bearing 1 long naked distolateral seta; second segment bearing 1 short naked distolateral seta; third segment bearing 2 short setae and several ranks of spinules; fourth segment small, apically issuing 7 naked setae and 1 stout clawlike element. Postantennal process absent. Labrum (Fig. 3E) with curved posterior margin fringed by rank of spinules. Mandible (Fig. 3F) with unequal blades, each with spinules along 1 border. Paragnath (Fig. 3G) pointed, labial area (Fig. 3G) bearing patches of spinules. First maxilla (Fig. 3H) with 1 long, 2 short, and 1 tiny setae and small anterior knob. Second maxilla (Fig. 3I) 2 segments; first segment unarmed; second segment with 2 thin, spinulated setae of unequal length and 1 stout spinulated process. Maxilliped (Fig. 3J) 3 segments; first segment small and unarmed; second segment (corpus) large and quadrate, with medial cuticular flap; third segment a stout complex claw with 1 small naked seta.

TABLE II. Descriptions of 16 characters and associated character states for phylogenetic analysis of *Taeniacanthodes* Wilson, 1935.

No.	Character	State
1	Ventromedial rostral spine	Absent (0)
		Present (1)
2	Posterolateral flaps on cephalothorax	Absent (0)
		Present (1)
3	First antenna	6 or 7 segments (0)
		5 segments (1)
4	Postantennary process	Present (0)
		Absent (1)
5	Leg 3 endopod	3 segments (0)
		2 segments (1)
6	Leg 4 endopod	3 segments (0)
		2 segments (1)
7	Leg 3 endopod, terminal segment	Bearing 3 lateral spines (0)
		Bearing 1 lateral spine (1)
8	Leg 1 endopod, segment 3	Bearing 6 or 7 setae (0)
		Bearing 5 setae and tiny spiniform element (1)
		Bearing 5 setae (2)
9	Leg 2 endopod, segment 3 armature formula*	III, 3 (0)
		II, 4 (1)
		II, 1, I, 2 (2)
10	Leg 3 endopod, terminal segment, most medial armature element	Present (0)
		Absent (1)
11	First free thoracic segment	Wider than or about equal in width to second free thoracic segment (0)
		Narrower than second free thoracic segment, promoting a necklike appearance to cephalothorax–thorax region (1)
12	Leg 4 endopod, terminal segment, total no. of spines and setae	3 (0)
		2 (1)
13	Leg 5, total no. of spines and setae	5 (0)
		4 (1)
14	Leg 5	2 segments (0)
		1 segment (1)
15	Leg 4 exopod, segment 3, most medial seta	Present (0)
		Absent (1)
16	Leg 4 exopod, segment 3, seta next to most medial seta	Present (0)
		Absent (1)

* Spines indicated by roman numerals; setae indicated by arabic numerals.

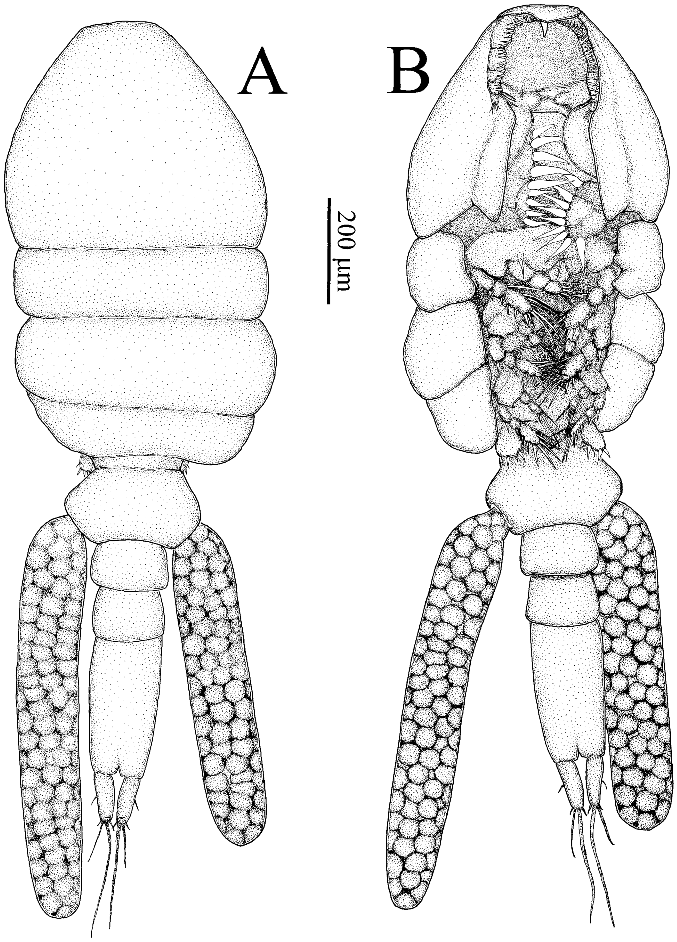

FIGURE 1. *Taeniacanthodes dojirii* n. sp., ovigerous female. (**A**) General habitus, dorsal view. (**B**) General habitus, ventral view.

Leg 1 (Fig. 4A) biramous; coxa with 1 process bearing spinules and 1 naked projection; basis with distolateral plumose seta, short distal serrated seta, and tiny medial spine; interpodal bar with spinules along posterior margin. Endopod 3 segments; first and second segments each with spinules along lateral margin and 1 medial pinnate seta; third segment with spinules along lateral margin and 5 apical pinnate setae. Exopod 3 segments; first segment with setules along lateral margin and distolateral plumose seta; second segment with setules along lateral margin, distolateral plumose seta, and medial pinnate seta; third segment with 6 stout pinnate setae and 2 thinner plumose lateral setae. Leg 2 (Fig. 4B) biramous; coxa with distolateral patch of setules and robust medial pinnate seta; basis with arc of setules between exopod and endopod, and tiny distolateral spiniform seta; interpodal bar unarmed and unornamented. Endopod 3 segments; first segment with setules along lateral margin, small patch of distolateral spinules, and pinnate seta midway along medial margin; second segment with 2 pinnate medial setae, small patch of distolateral spinules, and setules along lateral margin; third segment with setules along apical to lateral margin, 4 pinnate setae followed by 1 small naked seta and 1 smaller spiniform seta on lateral margin. Exopod 3 segments; first segment with rank of spinules along lateral margin and stout distolateral seta with serrated margins; second segment with rank of spinules along lateral margin, stout distolateral seta with serrated margins, and long distomedial pinnate seta; third segment with 3 lateral regions of spinules, 3 stout lateral setae with serrated margins, 1 larger apical seta with 1 serrated lateral margin, and 5 longer and thinner pinnate setae located along apical to medial margin. Leg 3 (Fig. 4C) biramous, coxa with lateral rank of long spinules, basis with naked lateral seta, interpodal bar bearing 1 rank of posteriorly directed spinules. Endopod 2 segments; first segment with setules along lateral margin and distal rank of spinules; second segment with setules along medial margin, spinules along apical margin, 2 long apical pinnate setae, and 1 shorter distolateral seta with serrated margins. Exopod 3 segments; first segment with lateral rank of spinules and stout distolateral seta with serrated margins; second segment with lateral rank of spinules, stout distolateral seta with serrated margins, and medial pinnate seta; third segment with lateral border of spinules, 2 stout lateral setae each with serrated margins, 1 slightly longer distolateral seta with serrated margins, and 5 thinner and longer pinnate setae located along apical to medial margin. Leg 4 (Fig. 4D) biramous, coxa with lateral rank of long spinules, basis with naked lateral seta, interpodal bar with rank of posteriorly directed spinules. Endopod 2 segments; first segment unarmed and unornamented; second segment with spinules along lateral to apical margin, 1 short lateral serrated seta followed apically by 2 pinnate setae of unequal length. Exopod 3 segments; first segment with spinules along lateral margin, stout distolateral seta with serrated margins; second segment with spinules along lateral margin, stout distolateral seta with serrated margins, and longer naked distomedial seta; third segment with patches of spinules along lateral to apical margin, 1 lateral, 1 distolateral, and 1 apical setae each with serrated margins, and 4 thinner and longer, weakly pinnate setae located along apical to medial margin. Leg 5 (Figs. 2E, F, 4E) 1 segment; ventrally bearing 2 small pores; laterally issuing 1 thin naked seta; apically bearing 3 stout setae all with serrated margins, 1 thin naked seta, and several patches of spinules. Leg 6 (Figs. 2G, 4F) vestigial, located near point where egg sacs emerge from genital complex, represented by 2 short thin setae, each with sparse setules and 1 longer and stouter seta bearing spinules.

Male: Unknown.

Taxonomic summary

Type host: Narcine entemedor Jordan and Starks, 1895 (Torpediniformes: Narcinidae), English common name = Cortez electric ray, Spanish common name (according to McEachran and Notarbartolo di Sciara, 1995) = raya eléctrica gigante.

Infection site: Primarily on dorsal and ventral body surface (Fig. 2A).

Type locality: Gulf of California off Bahia de Los Angeles, Baja California Sur, México (28°55′N, 113°32′W). Other localities: off Santa Rosalía, Baja California Sur, México (27°19′N, 112°17′W), and Loreto, Baja California Sur, México (26°01′N, 111°21′W).

Material deposited: Holotype and 1 paratype (both females) deposited in the Colección Nacional de Crustáceos at the Instituto de Biologia, Universidad Nacional Autonoma de México, México City (CNCR 19129 and 19130); 5 paratypes (all females) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 1000138).

Etymology: The genus name established by Wilson (1935) denotes the likeness of *Taeniacanthodes* to *Taeniacanthus* Sumpf, 1871. The epithet of this new species binomen is coined in honor of our friend Dr. Masahiro Dojiri, a fine copepodologist who has significantly extended our understanding of taeniacanthids and other parasitic copepods.

Remarks

Taeniacanthodes dojirii is established within *Taeniacanthodes* Wilson, 1935, based on the presence of a cephalothorax with posterolateral

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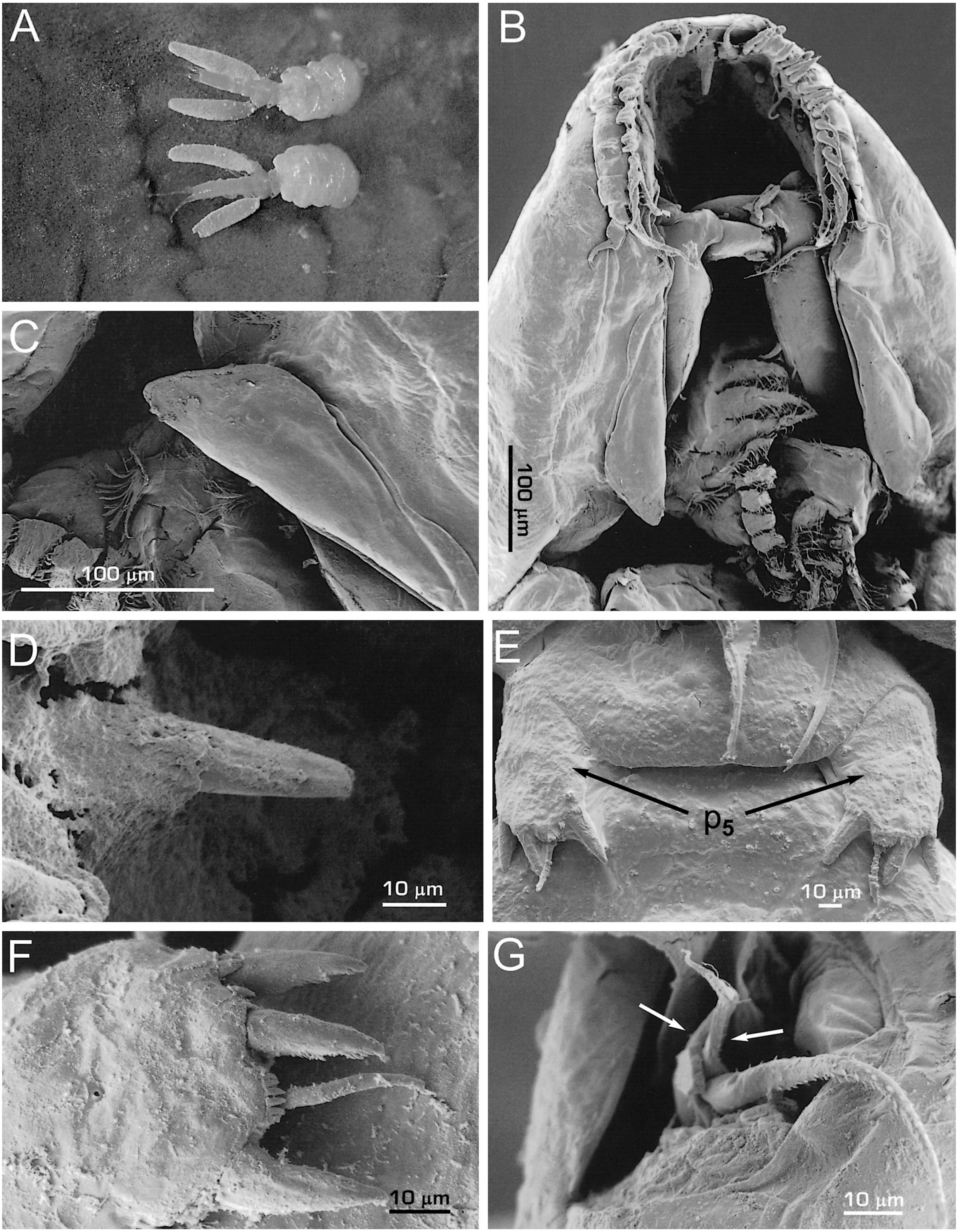
FIGURE 2. *Taeniacanthodes dojirii* n. sp., ovigerous females. (**A**) Two ovigerous females in situ. (**B**–**G**) Scanning electron microscope micrographs. (**B**) Anterior of body, ventral view. (**C**) Posterolateral flap of cephalothorax. (**D**) Rostral spine. (**E**) Fourth free thoracic segment, ventral view; p_5 = fifth legs. (**F**) Leg 5, ventral view. Note that most lateral seta is not visible. (**G**) Leg 6, arrows denote locations of 2 closely applied setae.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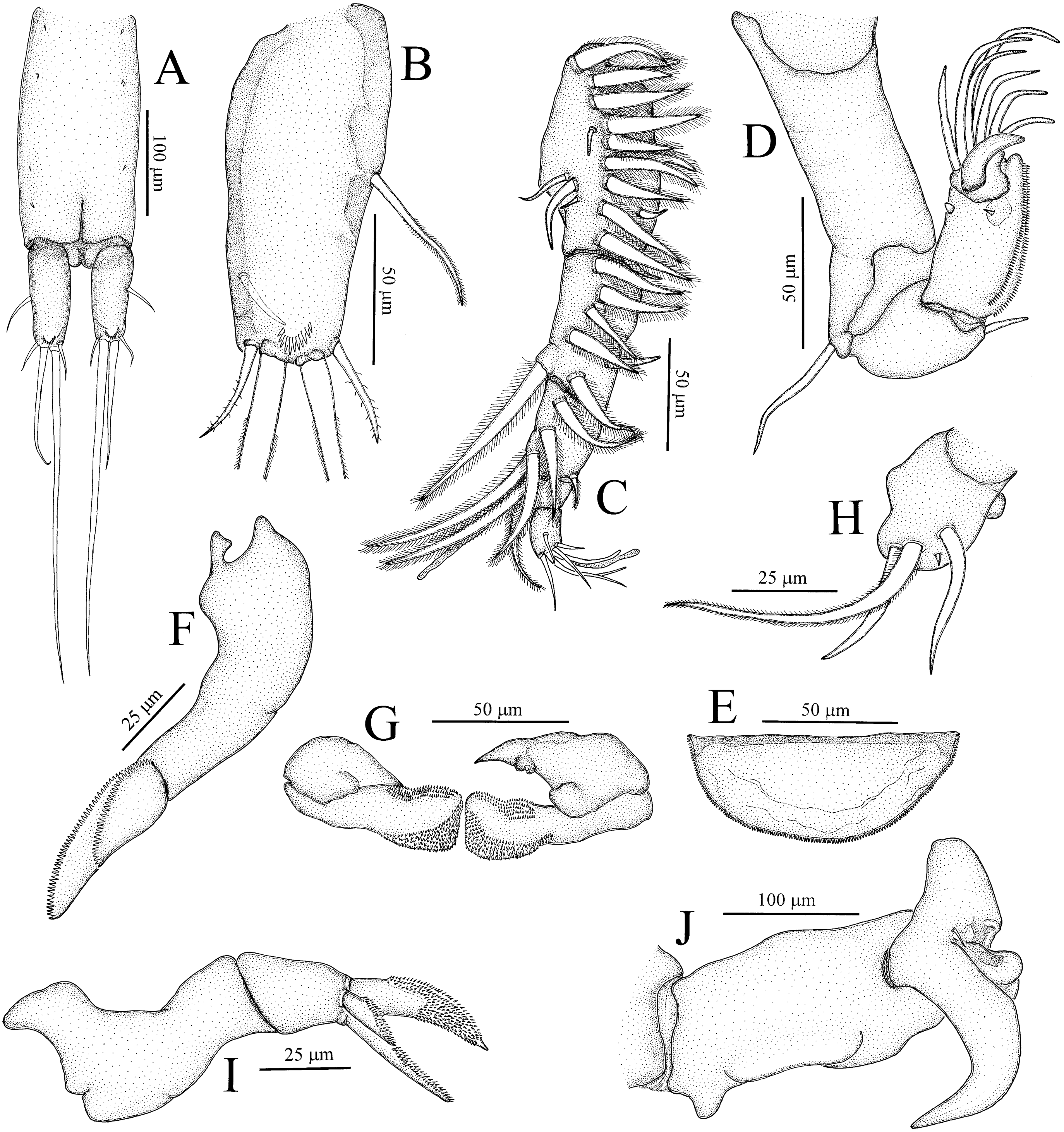

FIGURE 3. *Taeniacanthodes dojirii* n. sp., adult female. (**A**) Posterior of abdomen, ventral view. (**B**) Caudal ramus. (**C**) First antenna. (**D**) Second antenna. (**E**) Labrum. (**F**) Mandible. (**G**) Paragnaths and labial area. (**H**) First maxilla. (**I**) Second maxilla. (**J**) Maxilliped.

flaps, a rostrum bearing 1 ventromedial spine, and endopods of legs 3 and 4 each with 2 segments. However, as originally diagnosed by Wilson (1935) and later reiterated by Dojiri and Cressey (1987), members of *Taeniacanthodes* possess fifth legs with 2 segments. The legs of *T. dojirii* are clearly 1-segmented, and as far as we are aware, this is unique within Taeniacanthidae (Dojiri and Cressey, 1987). Consideration of the armature elements of leg 5 of *T. dojirii* leads us to believe that this unimerous condition evolved via the coalescence of a 2-segmented condition as seen in other taeniacanthids rather than via the loss of a particular leg segment. For example, in *Taeniacanthus* spp., leg 5 typically possesses a smaller first segment with 1 distolateral seta and a longer second segment with 4 distal armature elements (Dojiri and Cressey, 1987). In *T. gracilis* and *T. haakeri*, the first segment of leg 5 is like that of *Taeniacanthus* spp.; however, the second segment bears only 3 distal elements (Dojiri and Cressey, 1987). In *T. dojirii*, it appears as if the 2 segments seen in the *Taeniacanthus* spp. condition merged and

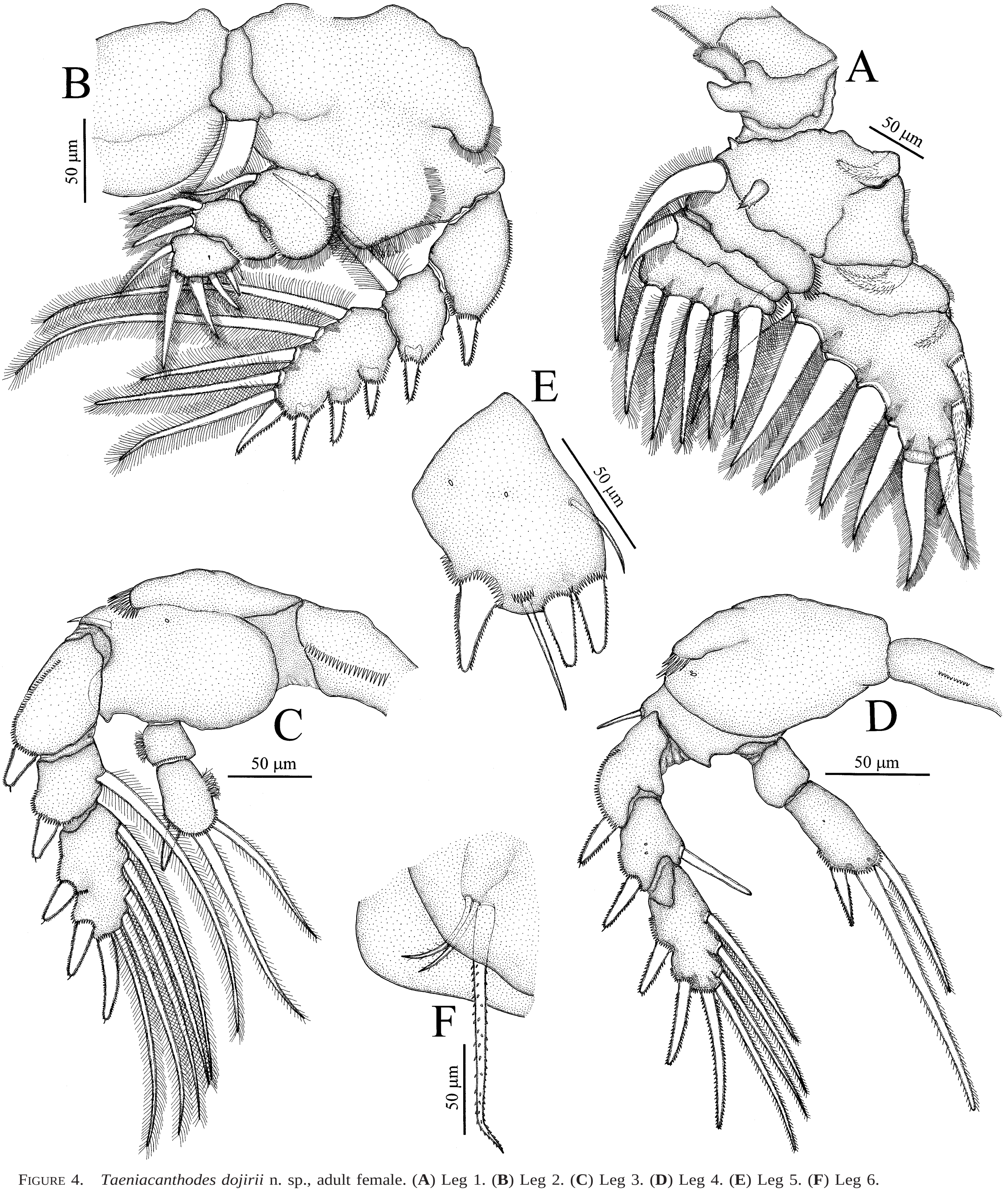

FIGURE 4. *Taeniacanthodes dojirii* n. sp., adult female. (**A**) Leg 1. (**B**) Leg 2. (**C**) Leg 3. (**D**) Leg 4. (**E**) Leg 5. (**F**) Leg 6.

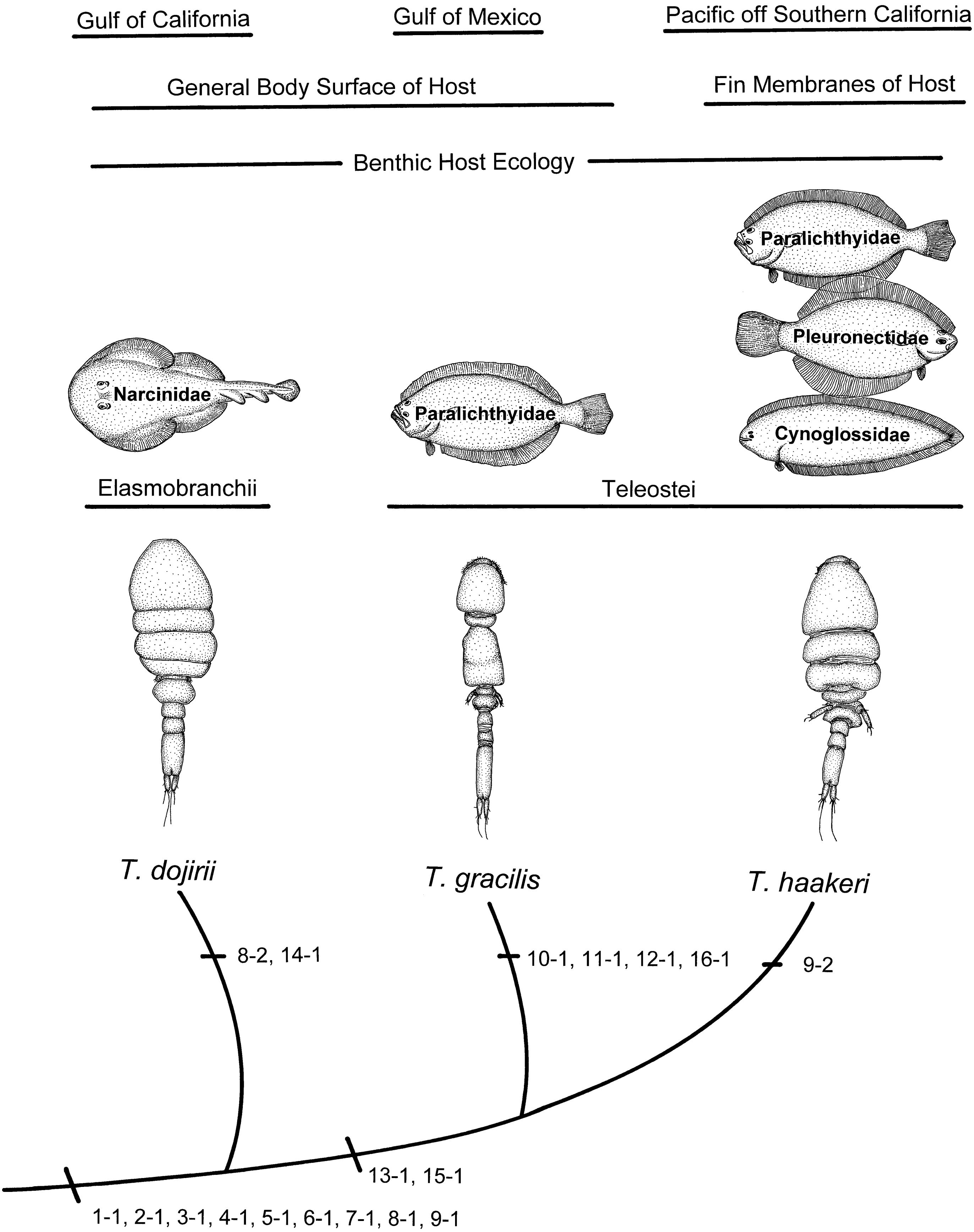

FIGURE 5. Cladogram (tree length = 18 steps, consistency index = 1) of *Taeniacanthodes* species. Numbers on tree correspond to apomorphies defined in Table II. Host taxa, host ecology, parasite attachment site, and parasite geographic distribution summaries are mapped above each taxon.

became altered to form a squat leg with all of the armature elements formerly possessed by the 2-segmented condition. Hence, relative to members of other taeniacanthid genera, the fifth leg of *T. dojirii* possesses underived (total number of armature elements) as well as derived (number of leg segments) characteristics. In light of the foregoing, it is recommended that the sentence detailing leg 5 in the genus diagnosis for *Taeniacanthodes* Wilson, 1935, provided by Dojiri and Cressey (1987) be replaced by the following: Leg 5 composed of 1 or 2 segments.

Phylogenetic analysis of *Taeniacanthodes*

A single most parsimonious tree (tree length = 18 steps, consistency index = 1) resulted from the cladistic analysis of *Taeniacanthodes* species, with *T. gracilis* and *T. haakeri* residing as sister taxa within the 3-taxon topology (Fig. 5). Because taeniacanthids that appear closely allied to *Taeniacanthodes* spp. infect both elasmobranchs and teleosts (Dojiri and Cressey, 1987), the cladogram must be considered inconclusive regarding whether elasmobranchs or teleosts were colonized by *Taeniacanthodes* species. However, the utilization of hosts with tight benthic ecologies (rays and flatfishes) appears to be a conservative trait of all *Taeniacanthodes* species (Fig. 5). Preliminary indications suggest that the attachment location of *T. haakeri* on the fin membranes of its hosts represents a derived attachment mode within *Taeniacanthodes* (Fig. 5). Because of the wide geographic distributions of members of the host genera known to be infected by *Taeniacanthodes* species, the current geographic distribution data for species of *Taeniacanthodes* should be recognized as indications of sampling deficiencies rather than as patterns of vicariance.

Key to *Taeniacanthodes* spp. adult females

1Total number of spines and setae on terminal endopod segment of legs 3 and 4 = 2; first free thoracic segment narrower than second, providing a necklike appearance to the cephalothorax–thorax junction.T. gracilisTotal number of spines and setae on terminal endopod segment of legs 3 and 4 = 3; first free thoracic segment wider than second.22Leg 5 composed of 2 segments; total number of armature elements (spines and setae) on leg 4 exopod segment 3 = 6.T. haakeriLeg 5 composed of 1 segment; total number of armature elements on leg 4 exopod segment 3 = 7.T. dojirii

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