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A New Siphonostome Family (Copepoda) Associated with a Vestimentiferan in Deep Water off California[1]

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ABSTRACT: *Dirivultus dentaneus*, n. gen., n. sp. (Dirivultidae n. fam.) is characterized by a combination of several features: first antenna of the female 13-segmented and that of the male 12-segmented, second antenna with a 1-segmented exopod, mandible lacking a palp, second maxilla and maxilliped prehensile, leg 4 endopod with formula 0-0; I-1, and leg 5 in the female minute with 1 seta but in male larger with 3 setae, 2 setae on free segment and 1 adjacent seta. This is the first copepod to be described from Vestimentifera in the Pacific.

THE VESTIMENTIFERA Webb, 1969, a group originally ranked with the Pogonophora but more recently regarded as a class of the Annelida by van der Land and Nørrevang (1975, 1977), contains at present a small number of species of tubicolous worms living in deep water. Until now only 1 species of copepod has been described from Vestimentifera, the clausidiid *Tychidion guyanense* Humes, 1973, from *Lamellibrachia luymesi* van der Land and Nørrevang, 1975, in 500 m off Guyana. (This host was originally reported as *Lamellibrachia* sp.) Earlier Webb (1969:31), during his study of the type material of *Lamellibrachia barhami* Webb, 1969, noticed "as yet unidentified copepods which live in quite large numbers in interlamellar pockets in the tentacular crown." Through the kindness of Meredith L. Jones we have examined specimens of *Lamellibrachia barhami* collected by Eric Barham which, although not designated as paratypes, are from the same original lot as the type material described by Webb from the northeast Pacific. The purpose of this paper is to describe the copepods found on the tentacular crowns of these vestimentiferans.

MATERIALS AND METHODS

Two lots of copepods collected from 2 *Lamellibrachia barhami* Webb, containing 46 copepods (37 ♀♀, 8 ♂♂, and 1 copepodid), were sent to us for examination by Dr. Jones. In addition, we examined first hand 3 specimens of *Lamellibrachia barhami*. Not only did we collect 58 additional ♀♀ of *Dirivultus dentaneus* from 2 of these specimens, but we also had the opportunity to observe the attachment sites of the copepods on their host. The third specimen of *L. barhami* was infested but the copepods were not collected for fear of damaging the host.

All measurements were made from specimens in lactic acid. The figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The abbreviations used are A_1 = first antenna, A_2 = second antenna, MD = mandible, MX_1 = first maxilla, MX_2 = second maxilla, and MXPD = maxilliped.

DIRIVULTIDAE N. FAM.

Dirivultus n. gen.

DIAGNOSIS: Siphonostoma. Body unmodified. Urosome 5-segmented in female, 6-segmented in male. Caudal ramus with 6 setae. Rostrum weakly developed. First

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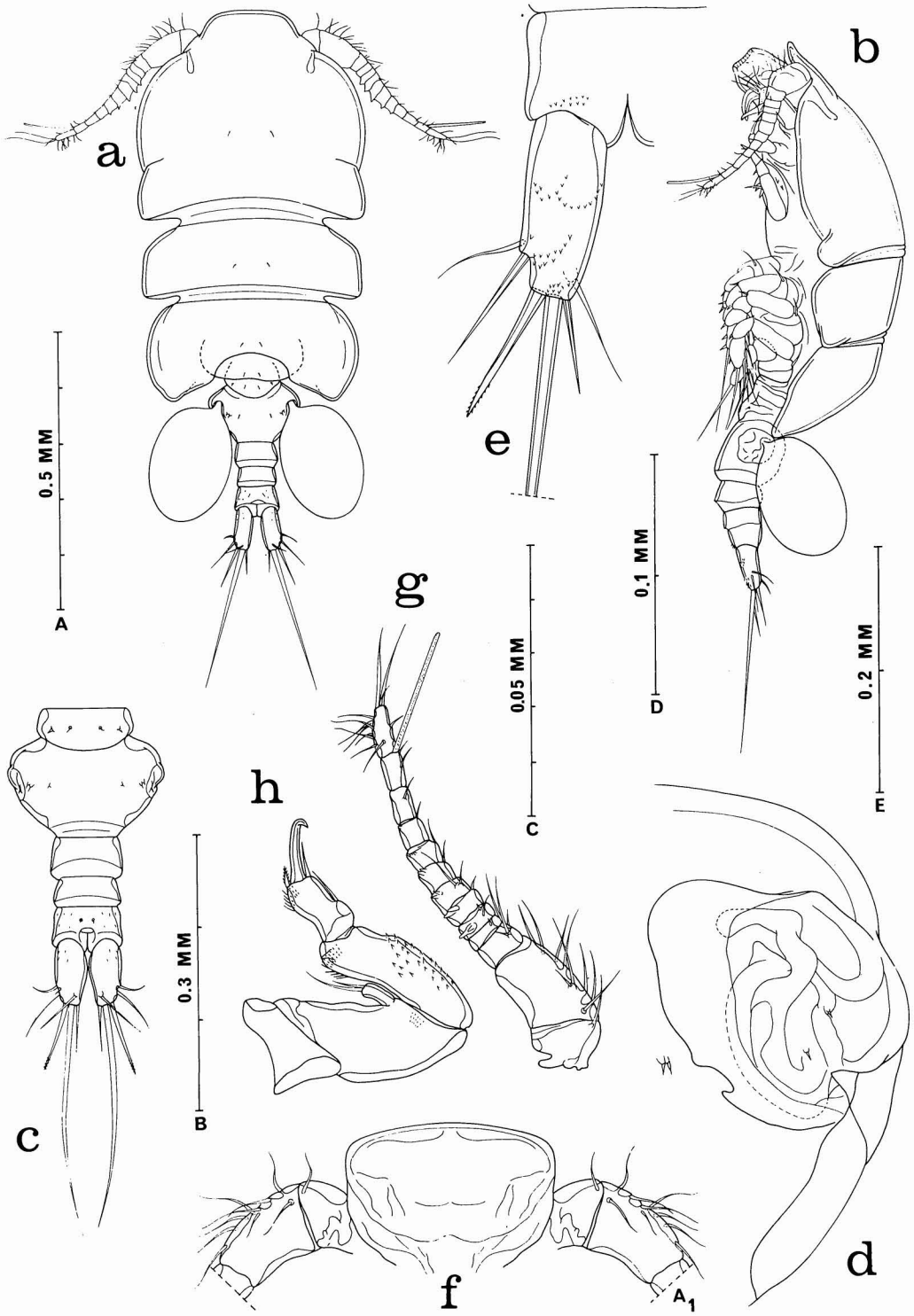


FIGURE 1. *Dirivultus dentaneus* n. gen., n. sp. Female: *a*, dorsal (A); *b*, lateral (A); *c*, urosome, dorsal (B); *d*, genital area, dorsolateral (C); *e*, caudal ramus, ventral (D); *f*, rostral area, ventral (E); *g*, first antenna, ventral (E); *h*, second antenna, posterior (D).

antenna of female 13-segmented with aesthete on segment 12; that of male 12-segmented, with aesthete on segment 11. Prehensile second antenna with 1-segmented exopod and 2-segmented endopod with 1 terminal claw.

Oral cone short. Mandible elongate, slender, with serrate tip, and lacking palp. First maxilla with outer lobe about two-thirds length of inner lobe. Second maxilla prehensile with terminal clawlike spine. Maxilliped prehensile and 4-segmented with terminal claw.

Legs 1–3 with 3-segmented rami. Leg 4 with 3-segmented exopod and 2-segmented endopod. Formula for endopod 0-0; I-1. Legs 1–4 alike in both sexes.

Leg 5 sexually dimorphic and placed ventrally, in female a minute free segment with 1 seta, in male a larger free segment with 2 setae and an adjacent seta. Leg 6 represented in female by 2 minute setae on genital area and in male by 2 setae on posteroventral flap on genital segment.

Other features as in species described below.

Associated with Vestimentifera.

Gender masculine.

TYPE SPECIES: *Dirivultus dentaneus* n. sp.

ETYMOLOGY: The generic name is a combination of Latin *dirus*, meaning fearful or horrible, and *vultus*, meaning countenance or aspect, alluding to the spines on the first antenna, on the base of the oral cone, and on the maxilliped.

Dirivultus dentaneus n. sp.

Figures 1*a–h*, 2*a–h*, 3*a–j*

TYPE MATERIAL: 95 ♀♀, 8 ♂♂, and 1 copepodid from the tentacular crown of four vestimentiferans, *Lamellibrachia barhami* Webb, in 1125 m, off southern California, 32°19.6′ N, 117°19.08′ W, 17 December 1966. These vestimentiferans collected by Eric Barham, and, although not designated as paratypes, from the same original lot as the type material described by Webb (1969). Holotype ♀ (USNM 172622), allotype (USNM 172623), 94 paratypes (89 ♀♀, 4 ♂♂, and the copepodid) (USNM 172624) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; the remaining paratypes (dissected) in the collection of the first author.

FEMALE: Body (Figure 1*a*, *b*) moderately elongate, with prosome flattened dorsoventrally. Length (not including setae on caudal rami) 0.90 mm (0.89–0.93 mm) and greatest width 0.39 mm (0.37–0.40 mm), based on 10 specimens in lactic acid. Segment of leg 1 incompletely separated from cephalosome. Segments of legs 1–3 and cephalosome of nearly equal width, but segment of leg 4 small and partly covered in dorsal view by tergum of segment of leg 3. Ratio of length to width of prosome 1.63:1. Ratio of length of prosome to that of urosome 1.89:1.

Segment of leg 5 (Figure 1*c*) 43 × 97 μm. Genital segment 108 × 162 μm, broadest in its anterior third. Genital areas located dorsolaterally near middle of segment. Each area (Figure 1*d*) with 2 minute setae 4 μm long. Three postgenital segments from anterior to posterior 49 × 81, 32 × 70, and 49 × 76 μm. Anal segment with posteroventral patch of small spines on each side (Figure 1*e*).

Caudal ramus (Figure 1*e*) moderately elongate, 76 × 32 μm, ratio of length to width 2.38:1. Outer lateral seta 32 μm, dorsal seta 49 μm, outermost terminal seta 59 μm, and innermost terminal seta 38 μm, all smooth. Two median terminal setae unequal, outer seta 65 μm with slightly blunt and minutely barbed tip, inner seta 275 μm with finely attenuate tip and smooth. Ventral surface of ramus with small spines as illustrated.

Body surface with few small hairs (sensilla) as shown in Figure 1*a*.

Egg sac (Figure 1*a*) containing a single oval egg of variable size, 184 × 115 μm to 207 × 138 μm.

Rostral area (Figure 1*f*) projecting anteriorly and lacking well-defined posteroventral border.

First antenna (Figure 1*g*) 334 μm long and 13-segmented. Lengths of segments (measured along their anterior setiferous margins): 41 (24 μm along posterior margin), 84 (70 μm along posterior margin), 23, 10, 13, 13, 17,

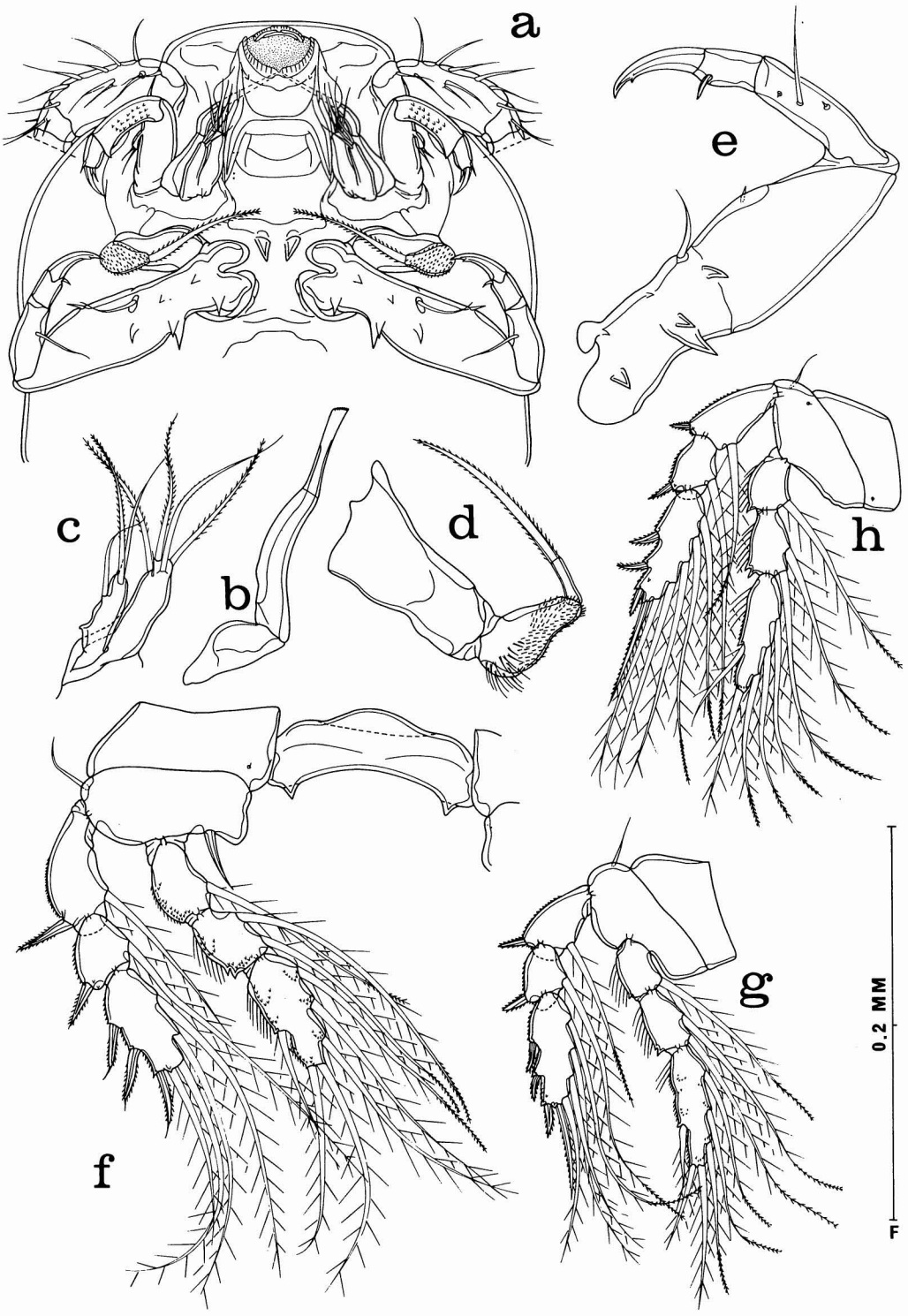


FIGURE 2. *Dirivultus dentaneus* n. gen., n. sp. Female: *a*, cephalosome, ventral (E); *b*, mandible, posterior (D); *c*, first maxilla, posterolateral (D); *d*, second maxilla, anterior (D); *e*, maxilliped, posterior (F); *f*, leg 1 and intercoxal plate, anterior (F); *g*, leg 2, anterior (E); *h*, leg 3, anterior (E).

18, 20, 22, 25, 29, and 37 μm respectively. Formula for armature: 1, 9, 4, 1, 2 + bifid spine, 1 + bifid spine, 2 + bifid spine, 1 + bifid spine, 1 + bifid spine, 1 + spine, 1, 2 + 1 aesthete, and 12. Series of 5 bifid spines prominent in dorsal view (Figure 1*a*) and decreasing in size distally.

Second antenna (Figure 1*h*) 198 μm long including claw and 4-segmented, consisting of a 2-segmented protopod, first segment unarmed, second segment bearing few distal spinules on anterior surface, and 1-segmented exopod with 2 naked terminal setae, and 2-segmented endopod bearing claw. First endopod segment with posteroventral spines, anterodorsal spinules, and a small distal mammillate process. Second endopod segment (fourth second antennal segment) with 1 smooth lateral seta, 1 terminal claw 34 μm flanked by 2 setae, 1 smooth and 1 delicately barbed, and ornamented with distal outer row of spinules.

Oral cone (Figure 2*a*) projecting in lateral view (Figure 1*b*). Labrum forming anterior surface of oral cone. At posterolateral areas of origin of oral cone a pair of large prominent posteriorly directed dentiform spines, conspicuous both in ventral view (Figure 2*a*) and laterally (Figure 1*b*).

Mandible (Figure 2*b*) long slender weakly bipartite sclerotized blade 99 μm long with finely serrate tip. No trace of paragnaths found. First maxilla (Figure 2*c*) with outer lobe about two-thirds length of inner lobe. Outer lobe with 3 setae, 1 of them barbed, and proximal outer thornlike process. Inner lobe with 5 setae, 4 long and barbed and 1 very short and naked. Second maxilla (Figure 2*d*) with first segment 70 μm long and unornamented. Second segment 50 μm long and 25 μm wide proximally, heavily ornamented with spinules. Terminal clawlike spine 95 μm, finely barbed distal to proximal subdivision. Maxilliped (Figure 2*e*) with first 2 segments indistinctly separated, first segment with 1 seta and 6 spines, second segment with 1 seta. Combined length of these 2 segments 200 μm. Third and fourth segments slender, third 78 μm with 1 seta and 2 small spinules, fourth 34 μm with 1 seta and 1 terminal claw 54 μm having small tooth on distal concave margin. Between insertions of second maxillae and maxillipeds a pair of medial stout spines (Figure 2*a*).

Ventral area between maxillipeds and leg 1 weakly sclerotized.

Legs 1–4 (Figures 2*f–h*, 3*a*) biramous, with all rami 3-segmented except for 2-segmented endopod of leg 4. Formula for armature as follows (roman numerals indicating spines, arabic numerals representing setae):

P_1 coxa 0-0 basis 1-I	exp I-1; I-1; III, 4
	enp 0-1; 0-2; 1, 2, 3
P_2 coxa 0-0 basis 1-0	exp I-1; I-1; III, I, 4
	enp 0-1; 0-2; 1, 2, 3
P_3 coxa 0-0 basis 1-0	exp I-1; I-1; III, I, 5
	enp 0-1; 0-2; 1, 1, 3
P_4 coxa 0-0 basis 1-0	exp I-1; I-1; II, I, 4
	enp 0-0; I-1

Leg 1 (Figure 2*f*) with intercoxal plate having pair of pointed processes on ventral margin. Basis with smooth inner spine 30 μm long. Spines on exopod flagellate, those on third segment 21, 23, and 23 μm and segment itself 55 μm. Segments of endopod ornamented on anterior surface with small spines. Proximal 4 inner setae on endopod with short closely spaced spinules near tips. Leg 2 (Figure 2*g*) with third segment only of endopod ornamented with spines on anterior surface. Several setae on both rami with short spinules near tips. Leg 3 (Figure 2*h*) lacking surficial spines on endopod and several setae with short distal spinules as in leg 2. Leg 4 (Figure 3*a*) with exopod 211 μm, its outer spines very short, 8.5, 8.5, 8.5, and 9.6 μm from proximal to distal. Endopod with unarmed first segment 27 × 23 μm. Second segment 88 × 23 μm, with terminal barbed spine 97 μm and inner seta 112 μm; segment with spinules on inner margin proximal to seta.

Leg 5 (Figure 3*b*) consisting of minute ventrally placed free segment bearing one seta 3.6 μm.

Leg 6 probably represented by 2 minute setae on genital area (Figure 1*d*).

Color unknown.

MALE: Body (Figure 3*c*) with general form resembling that of female. Length (excluding setae on caudal rami) 1.01 mm (0.96–1.09 mm) and greatest width 0.42 mm (0.40–0.44 mm), based on 8 specimens in lactic acid. Ratio of length to width of prosome 1.54:1.

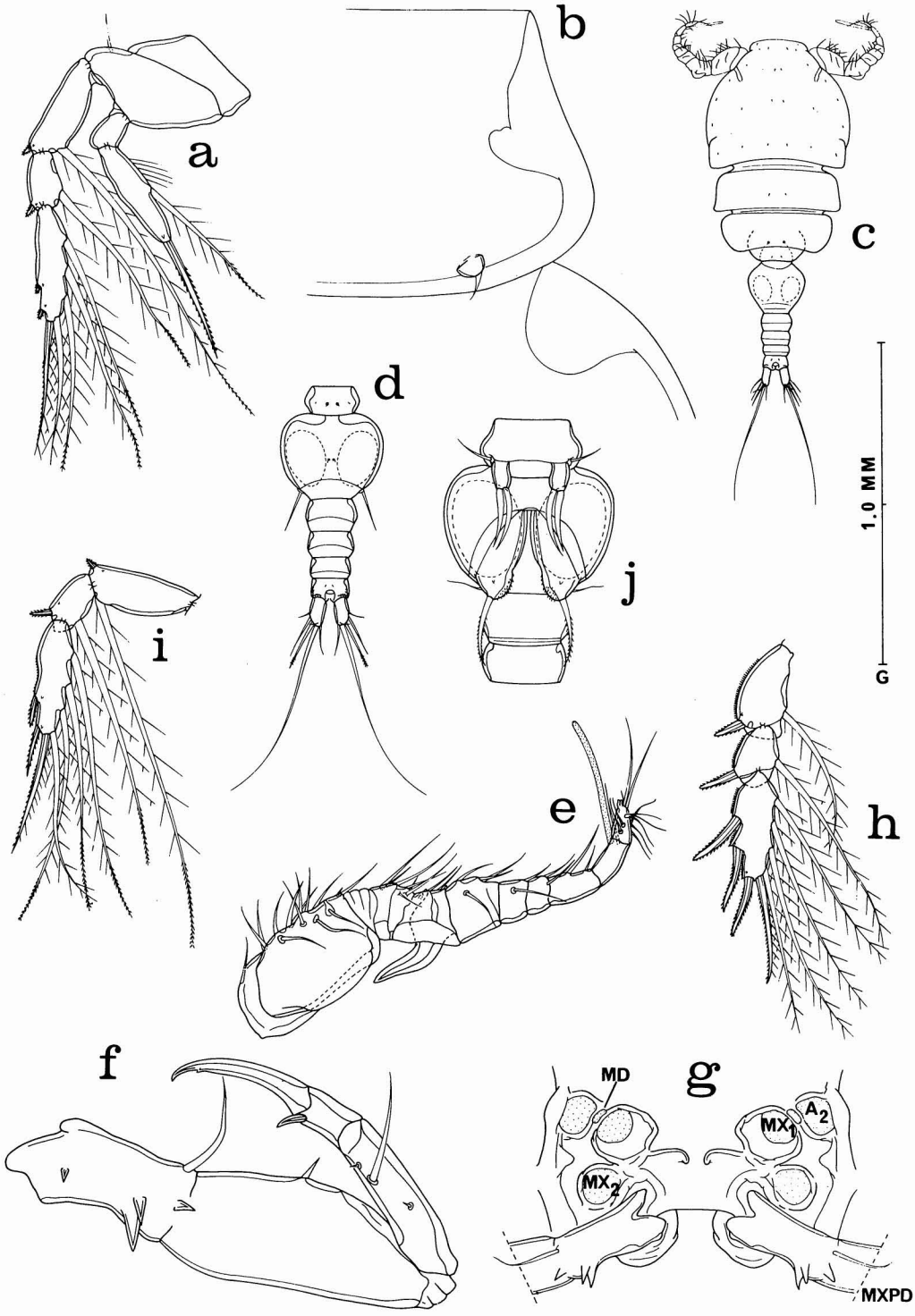


FIGURE 3. *Dirivultus dentaneus* n. gen., n. sp. Female: *a*, leg 4, anterior (E); *b*, leg 5, ventral (C). Male: *c*, dorsal (G); *d*, urosome, dorsal (A); *e*, first antenna, dorsal (E); *f*, maxilliped, posterior (F); *g*, area of mouthparts, ventral (E); *h*, exopod of leg 2, anterior (E); *i*, exopod of leg 4, anterior (E); *j*, anterior part of urosome showing leg 5 and leg 6, ventral (B).

Ratio of length of prosome to that of urosome 1.54:1.

Segment of leg 5 (Figure 3*d*) 38 × 97 μm. Genital segment 146 × 178 μm, a little longer than wide. Four postgenital segments from anterior to posterior 54 × 89, 46 × 78, 30 × 70, and 43 × 65 μm.

Caudal ramus resembling that of female but smaller, 54 × 27 μm, ratio 2:1.

Body surface and rostral area as in female.

First antenna (Figure 3*e*) 360 μm long and 12-segmented. Lengths of segments (measured along their anterior setiferous margins): 38 (14 μm along posterior margin), 103 (100 μm along posterior margin), 23, 13, 13, 14, 41, 23, 18, 25, 35, and 32 μm respectively. Armature: 1, 14, 3, 4, 1 + 2 knobs, 1 + 1 knob and large recurved spine directed posteromedially, 4, 2, 2, 2, 1 + 1 aesthete, and 11 + bifid knob.

Second antenna, oral cone, mandible, first maxilla, and second maxilla as in female. Maxilliped (Figure 3*f*) resembling that of female but first segment with only 4 spines and claw 68 μm long. Area between insertions of first maxillae with pair of recurved sclerotizations (Figure 3*g*); pair of stout spines located more posteriorly in female here absent.

Legs 1–4 segmented and armed as in female. Outer spines on exopods longer than in female. Leg 1 with 3 outer spines on third segment of exopod 41, 35, and 39 μm from proximal to distal; segment 55 μm. These spines on exopod of leg 2 (Figure 3*h*) distinctly longer than in female. Leg 4 with spines on exopod (Figure 3*i*) 10, 19, 34, 46, and 103 μm from proximal to distal.

Leg 5 (Figure 3*j*) placed ventrally. Free segment 31 × 22 μm, with 2 broad terminal setae 68 μm and 70 μm. Seta near insertion of free segment (dorsal seta) 35 μm. All setae naked.

Leg 6 (Figure 3*j*) a posteroventral flap on genital segment bearing 2 setae, slender smooth seta 38 μm and stouter barbed seta 68 μm. Patch of minute spines on ventroinner surface of flap near larger seta.

Spermatophore not seen.

Color unknown.

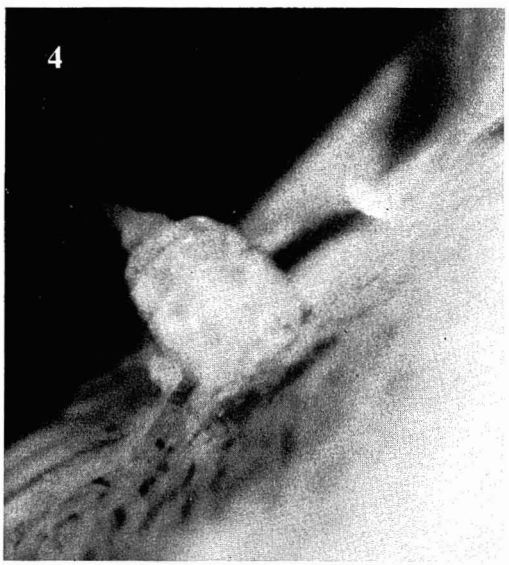
ETYMOLOGY: The specific name *dentaneus*, Latin meaning showing the teeth or threatening, refers to the pair of large dentiform spines on the base of the oral cone.

DISCUSSION

The copepods were attached to the filaments (Figure 4), usually occurring between the outer fused tentacular lamellae and the inner tentacular lamellae or what Webb (1969) called the "interlamellar pockets in the tentacular crown." Although Webb stated that the copepods "do not appear to damage the tissue" of the host, indentations on the lamellar tissues where the copepods were attached were observed (Figure 5).

The habits of the copepods were not observed since no living specimens were available. It is possible that the copepods feed on the tentacular lamellae or associated mucus of their host. However, even if the copepods do not feed directly on the host tissue, the prehensile organs of the copepods may cause damage to the filaments. In addition, as reported for other parasitic copepods (Kabata 1970), the mere presence of these copepods occupying space may cause pressure atrophy to the host tissue. The deep indentations (Figure 5) at the site of the copepods suggest a harmful effect on the host, particularly since the copepods occur in relatively large numbers on each host. On the other hand, it must be mentioned that these indentations may be artifacts, caused after the fixation of the hosts and the copepods. In any case, a possible deleterious effect on the host cannot be excluded.

In comparing the new family with other families of siphonostomes (excluding families parasitic on fishes which were so distinctly different that they were not considered), 17 families were reviewed (Table 1). Of these 17 families, 9 can be distinguished from the Dirivultidae by the modified nature of the body in these families. They are Calvocheridae, Cancerillidae, Entomolepidae, Nanaspididae, Nicothoidae, Saccopsidae, Spongiocnizontidae, Stellicomitidae, and Ventriculinidae. The nonprehensile nature of the second antenna of the Artotrogidae, Asterocheridae, Dyspontiidae, Megapontiidae, and Myzopontiidae excludes *Dirivultus* from



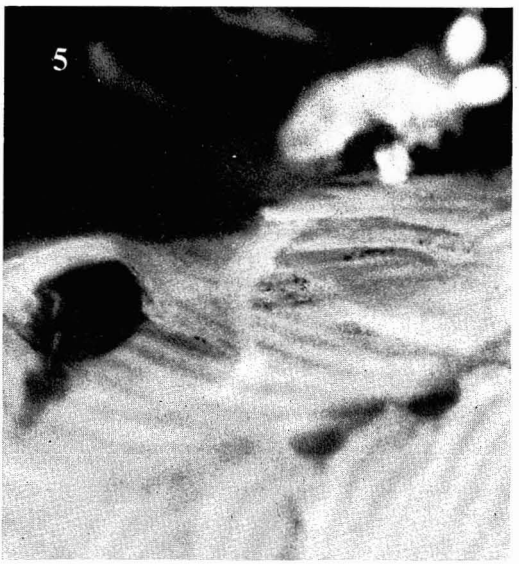


FIGURE 4. *Dirivultus dentaneus* n. gen., n. sp. with the anterior portion of its head imbedded into the lamellar tissues of the host.

FIGURE 5. Indentation (cavity) left after removal of *Dirivultus dentaneus* n. gen., n. sp. from the lamellar tissues of the host. Note that the dark cavity on the left assumes the outline of the copepod.

TABLE 1

COMPARISON OF THE DIRIVULTIDAE N. FAM. WITH OTHER FAMILIES OF SIPHONOSTOMES (EXCLUDING SIPHONOSTOMES PARASITIC ON FISHES)

FAMILIES	A_1	A_2	Md	Mx_2	P_1–P_3	P_4	EGG SACS
Artotrogidae Brady, 1880		×		×		×	×
Asterocheridae Giesbrecht, 1899	×	×	×	×		×	
Brychiopontiidae Humes, 1974	×	×		×		×	×
Calvocheridae Stock, 1968		×	×	×	×		
Cancerillidae Giesbrecht, 1897	×			×	×	×	
Dinopontiidae Murnane, 1967	×	×	×			×	
Dyspontiidae G. O. Sars, 1915	×	×	×	×		×	×
Entomolepidae Brady, 1899	×	×	×	×		×	
Megapontiidae Heptner, 1968		×	×			×	
Micropontiidae Gooding, 1957		×	×	×	×	×	
Myzopontiidae G. O. Sars, 1915		×		×			×
Nanaspididae Humes & Cressey, 1959	×	×	×		×	×	×
Nicothoidae Dana, 1852	×		×	×		×	×
Saccopsidae Lützen, 1964	×	×	×	×	×	×	×
Spongiocnizontidae Stock & Kleeton, 1964	×	×			×	×	
Stellicomitidae Humes & Cressey, 1958	×	×	×	×	×	×	
Ventriculinidae Leigh-Sharpe, 1934	×	×			×		×

NOTE: × = striking difference; blanks = similarity or unknown from literature.

these 5 families. The segmentation of the first antenna of the female in the Dinopontiidae (5–9 segments) and Brychiopontiidae (18 segments) prevents the inclusion of the new genus in either of these families. Finally, based on the presence of a palp on the mandible and the absence of an exopod on the second antenna in members of the Micropontiidae, *Dirivultus* cannot be placed in this family.

Other differences than those just mentioned exist between the Dirivultidae and the other families of siphonostomes (Table 1). There are fundamental differences in the segmentation of the first antenna, the nature of the second antenna, the structure of the mandible and second maxilla, and the egg sacs (many having multiseriate arrangements). Based on this comparison there is little doubt that *Dirivultus* represents a new family of siphonostome copepods.

One of the most distinctive features of *Dirivultus dentaneus*, besides the structure of the mouth appendages and the endopod of leg 4, is the presence of a pair of fanglike dentiform spines at the base of the oral cone (siphon). These "fangs," along with the spines on the second antenna, the spines medial to the second maxilla, and the spines at the bases of the maxilliped may act as a functional complex preventing slippage on the host. These spines structurally resemble the sternal furca seen in many members of the Caligidae, a copepod family predominantly parasitic on fishes. The function of the sternal furca is not yet known but, as suggested by Gnanamuthu (1948), Kabata and Hewitt (1971), Wilson (1905), and others, the sternal furca may act to prevent the parasitic copepod from slipping backward on the host.

Although the dentiform spines are structurally and presumably functionally similar to the sternal furca, these 2 structures are not homologous. The location of the sternal furca in the caligids is immediately posteromedial to the bases of the maxillipeds, a location removed from that of the fanglike structures of *Dirivultus dentaneus*. Both these features probably represent elaborations of a cuticular structure.

Since members of the recently discovered group known as the Vestimentifera live in deep water, a habitat where copepods associated with invertebrates have been very little investigated, it is perhaps not surprising to find a representative of a new family of copepods associated with these worms. We have found other copepods associated with large vestimentiferans recently collected in the Galapagos Rift area and the East Pacific Rise. The study of these copepods is underway, with the results to be published in a subsequent paper.

ACKNOWLEDGMENTS

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