

DESCRIPTION OF TWO NEW SPECIES OF *RIDGEWAYIA* (COPEPODA: CALANOIDA)  
FROM ANCHIALINE CAVES IN THE GALAPAGOS ARCHIPELAGO

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A B S T R A C T

Two new calanoid copepods, *Ridgewayia delfine* sp. nov. and *Ridgewayia tunela* sp. nov., are described from anchialine caves in the Galapagos Archipelago. Details of the female genital segment and the female and male fifth legs help distinguish these species from each other and from other members of the same genus. The two new species belong to the *Ridgewayia marki* species-group, which are found predominantly in the Caribbean with one member in the Mediterranean and one in the Indo-West Pacific. These are the first species of *Ridgewayia* described from the Eastern Pacific. The volcanic origin of the Galapagos necessitates the dispersal of these ridgewayiids to the islands from other regions. It is currently thought that *Ridgewayia* is a relict from the Tethyan Sea and that members of the *marki*-species group crossed from the Caribbean into the Pacific during the circumtropical existence of this sea. The possibility remains that this crossover and colonization of the Galapagos occurred more recently while the Panama seaway remained open. It is clear that the current knowledge of the ridgewayiids is insufficient for a definitive conclusion. Further exploration is necessary to generate an exhaustive list of species of Ridgewayiidae and their distribution.

KEY WORDS: anchialine caves, biogeography, Copepoda, East Pacific faunas, *Ridgewayia*

INTRODUCTION

The Galapagos are a cluster of volcanic islands located one-thousand kilometers off the coast of Ecuador. Because of their singular geographic setting, oceanographic conditions, and isolation from the continent for millions of years, a unique ecosystem has evolved in this region, with a rich flora and fauna not found anywhere else in the world. Since they are oceanic islands, the current biota of the Galapagos, including marine organisms, is composed of species whose ancestors must have originally dispersed to the islands from other regions (Jackson, 1993). This paper describes two new species of calanoid copepods belonging to the family Ridgewayiidae from marine caves in the Galapagos Islands. Ridgewayiidae is currently composed of nine genera, six of which are found only in marine caves: *Brattstromia*, *Exumellina*, *Normancavia*, *Robpalmeria*, *Stargatia*, and *Badijella* (Fosshagen and Iliffe, 1991; Fosshagen and Iliffe, 2003; Krsinic, 2005). The remaining three genera, *Placocalanus*, *Exumella*, and *Ridgewayia* are mainly hyper and/or epibenthic; but *Exumella* and *Ridgewayia* also have members that inhabit marine caves (Wilson, 1958; Fosshagen and Iliffe, 1998; Ohtsuka et al., 2000).

There are fourteen species and two subspecies belonging to the genus *Ridgewayia*, including the two new species described in this paper. Species of *Ridgewayia* have a disjunct distribution and have been found only in tropical and subtropical shallow waters of the Indo-West Pacific, the Caribbean, the Mediterranean (Barthelemy et al., 1998; Ohtsuka et al., 2000), and now in the Eastern Pacific. The two species of *Ridgewayia* from Galapagos were found inhabiting anchialine caves. Anchialine caves are defined as inland bodies of salt water with subterranean connections to the sea that have marine and terrestrial influences (Iliffe, 1991). The anchialine habitats in Galapagos and their fauna are described in detail by Iliffe (1991). Numerous species

new to science have been found in these habitats, and Iliffe (1991) mentions the presence of a specimen of *Ridgewayia* in one of his collections, but details are not given. It is possible that specimen belongs to one of the new species described in this article.

MATERIALS AND METHODS

Copepods were collected from many sites in various islands in the Galapagos Archipelago, Ecuador. Two of these sites contained undescribed species of Ridgewayiidae. The first site (00°45.426'S; 90°18.932'W) is located on the island of Santa Cruz, near the town of Puerto Ayora. This site is locally known as the Grietas, a Spanish word for fissure or crevasse, and it is a popular local swimming hole. It consists of two open pools about 300 m from shore, located on a tectonic fault line running along an east-west transect. The site is described in detail by Iliffe (1991), when it was known as Grietas Delfin, after the nearby, former Hotel Delfin. The first pool is about 5 m wide and 30 m long with a depth of about ten meters. The water can be reached after a fifteen meter descent into the tectonic fault. There are a series of fallen rocks that divide the second pool from the first, but a free flowing and direct connection persists under the surface. The second pool has dimensions similar to the first. These pools have a sub-surface connection with the sea and are influenced by tidal currents. The water has a salinity of about 17 to 19 pss throughout the first meter. A steep halocline follows, with salinities reaching 27 pss at depth. The water temperature is on average 24°C near the surface. The water in the Grietas is clear with visibility of about 10 m. The rock surfaces are covered with green algae, and the bottom is full of organic debris, a majority of which is composed of pieces from the local giant cactus, *Opuntia*. The larger fauna that inhabit the Grietas include several types of small fish, parrot fish, eels, small white-tip reef sharks, and small shrimp. Some of the smaller fauna include ostracodes, mysids, polychaetes, and a substantial array of copepods. Among the copepods there are several harpacticoid and cyclopoid species with a few calanoids, including the new species of *Ridgewayia* described in this study, two new species of *Pseudocyclops* (Figueroa, in litt.), and *Acartia levequei* Grice, 1964 that is endemic to near-shore waters throughout the Galapagos.

Samples were taken on 30 January, 6 February and 16 February 2005, by using two simple nets, one with 333 µm mesh and a mouth opening of 30 cm and one with 102 µm mesh and a mouth opening of 60 cm. These nets were towed at various depths by swimming with snorkeling equipment and/or by pulling a line from shore.

The second site (00°57.565'S; 90°59.417'W) is located on the southeastern side of the Island of Isabela, near the town of Puerto Villamil. This site was formerly known as Cueva de la Cadena, and it is described in detail by Peck and Peck (1986) and by Montoriol-Pous and Escola (1978). Today it is a visiting site along a Galapagos National Park nature trail, and it is called Tunel del Estero. It consists of a lava tunnel with an opening at about 40 m from shore. The tube extends into the sea where it plunges below the surface. Inside the lava tube, there is a shallow pool, of about 1 m depth that starts at the tube's opening on the shore and extends out to sea. It is directly influenced by the tide and its salinity (33 pss-35 pss) and temperature (25°C-27°C) are close to those of the sea. The bottom of the pool is very fine white sand and the walls are covered with green algae. The fauna found in Tunel del Estero is not as numerous or diverse as that of the Grietas. There are fiddler crabs along the intertidal section of the tunnel, while in the pool there are several small fish, a few species of cyclopoid and harpacticoid copepods, and a few calanoid copepods, including *A. levequei*, a species of *Bestiolina*, and the new species of *Ridgewayia* described in this study.

Samples from this site were taken on 23 March 2005 and 10 April 2005. A 333 µm simple net with a 30 cm mouth opening was used to collect the samples. The net was towed, with the aid of snorkeling equipment, through the pool, near the bottom, for a distance of about 25 m into the tunnel. The samples from both sites were immediately split and preserved after collection, one half placed in a 10% buffered formalin solution and the other half in a 97% ethanol solution.

#### SYSTEMATICS

Subclass Copepoda H. Milne Edwards, 1830

Order Calanoida G. O. Sars, 1903

Family Ridgewayiidae Wilson, 1958

Genus *Ridgewayia* Thompson and Scott, 1903

*Ridgewayia delfine*, n. sp.

(Figs. 1-4)

Material Collected.—34 specimens collected on 30 January 2005; 110 specimens collected on 6 February 2005 and 75 specimens collected on 16 February 2005 all from the same locality, the Grietas near the town of Puerto Ayora, on the Island of Santa Cruz, Galapagos, Ecuador. 25 ♀ and 25 ♂ were used for analysis, including dissection and measurements.

Body Length.—Female. Total length: range = 0.91-0.98 mm, (mean ± standard deviation = 0.95 ± 0.02 mm, n = 20); prosome length = 0.69-0.76 mm, (0.72 ± 0.02 mm, n = 20); urosome length = 0.22-0.26 mm, (0.23 ± 0.01 mm, n = 20). Male. Total length = 0.82-0.94 mm, (0.88 ± 0.03 mm, n = 21); prosome length = 0.61-0.68 mm, (0.64 ± 0.02 mm, n = 21); urosome length = 0.21-0.29 mm, (0.24 ± 0.02 mm, n = 21).

Types.—Deposited in the Smithsonian Museum of Natural History, Washington. Holotype: adult female, USNM 1098375; paratypes 7 adult females, USNM 1098376, and 7 adult males, USNM 1098377. All collected on 30 January 2005 (00°45.426'S; 90°18.932'W).

Description.—Female (holotype). Body (Fig. 1A, B), bright red in life, slender, prosome 6-segmented. Cephalosome clearly separate from first pedigerous somite. Posteriolateral angles of prosome rounded and extending a third of length along genital double somite. Large eye present in anterior section of cephalosome, red pigmented in fresh specimens. Rostrum a simple process produced ventrally with rounded tip; pair of secretory gland openings present near tip. Urosome (Fig. 1C) four segmented. Genital double somite symmetrical; and genital operculum somewhat offset to

right of midventrum. Seminal receptacle present on left side only. All urosomal segments, except for anal segment, have row of denticles along posterior borders. In genital double somite, row of denticles has a gap (Figs. 1C and 4A) along border directly behind genital operculum. Surface of all segments, except for area around genital opening, entirely covered with small spinules (Fig. 4A and 4C). Caudal rami symmetrical with their surfaces covered with minute setules, and bearing six setae (Figs. 1C and 4C). Small, blade-like seta sited on outer distal corner, followed medially by longer naked seta striated with helical lines, then two long, plumose median setae jointed basally. Small plumose seta extends dorsally, followed by longer plumose seta on distal inner margin. Distal third of inner margin bearing row of long setules.

Antennule (Fig. 1D, E) barely reaches the tip of caudal ramus. Variation in length among individuals, with few specimens with antennules extending slightly beyond caudal ramus. 26-segmented, segments 13 to 22 each with distal transverse row of spinules. Fusion pattern and armature as follows: I-1 (setae) + ae (aesthetasc), II-III-3 + ae, IV-2, V-1 + ae, VI-1 + ae, VII-2 + ae, VIII-1 + ae, IX-2 + ae, X-1 + ae, XI-2 + ae, XII-2, XIII-1 + ae, XIV-2 + ae, XV-1 + ae, XVI-2 + ae, XVII-2 + ae, XVIII-2 + ae, XIX-2, XX-2, XXI-2 + ae, XXII-1, XXIII-1, XXIV-2, XXV-1 + ae, XXVI-2, XXVII-XXVIII-5 + ae.

Antenna (Fig. 2A) with plumose seta on coxa adjacent to patch of setules. Basis with two setae of unequal length. Exopod indistinctly 8-segmented, with setal formula 1, 1, 1, 1, 1, 1, 4. Endopod 2-segmented with first bearing two subterminal setae. Second segment bilobed; subterminal lobe has nine setae, terminal lobe with seven. Two rows of spinules/setules along inner margin of second segment.

Mandible (Figs. 2B and 4D) with gnathobase bearing nine teeth. With row of ten smaller teeth at distal inner edge of mandible blade forming a saw-like element. Tuft of fine setules present on gnathobase, near attachment of palp; basis with four setae along inner margin (one large, two medium and one small). Exopod indistinctly 4-segmented with setal formula 1, 1, 1, 3; endopod 2-segmented; first segment bearing four setae, second segment bearing eleven.

Maxillule (Fig. 2D) well developed; precoxal arthrite bearing six spiniform and three spinulose distal setae and one anterior and four slender posterior setae. With tuft of fine setules present along insertion of posterior seta. Coxa has nine setae on epipodite and five setae on endite. Basis with one seta on exite, four setae on first endite and five setae on second endite. Exopod as one segment, with 3 + 8 setae. Endopod 2-segmented with setal formula 4 + 4, 7.

Maxilla (Fig. 2C) with first precoxal endite bearing one proximally directed seta at base and five long distal setae. Second precoxal endite and first and second coxal endites with three setae each. Basis with one sclerotized seta and three long setae. Endopod is 4-segmented with the distal 3 segments partly fused, bearing 3, 2, 2, 3 setae. With tuft of fine setules present around distal edge of first and second precoxal endites and first and second coxal endites.

Maxilliped (Fig. 2E) with syncoxal endites bearing 1, 2, 4, and 3 setae, respectively. Several setules on each of first three endites, and large patch of fine setules present on

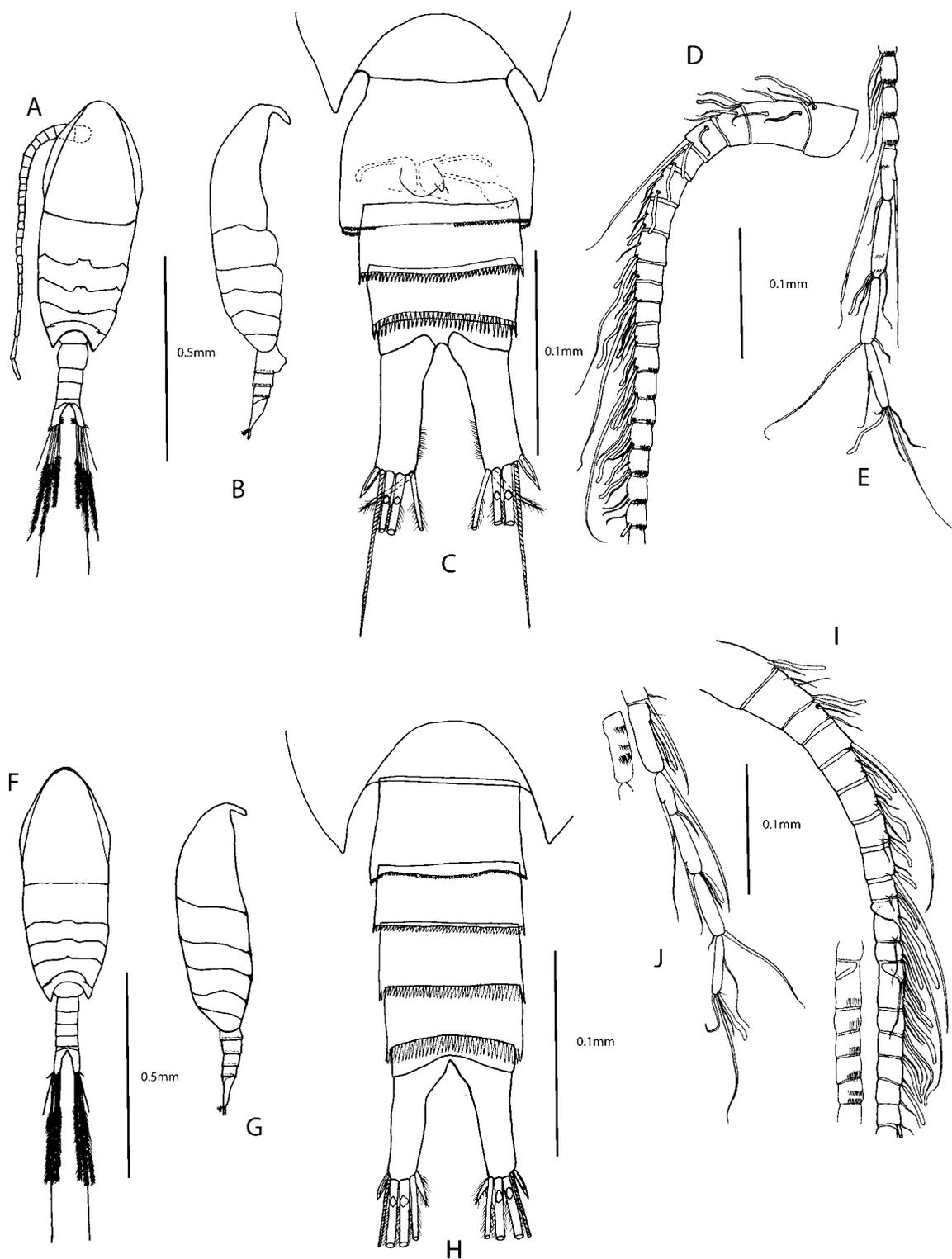


Fig. 1. *Ridgewayia delfine* sp. nov., A-E, female; A, dorsal habitus; B, lateral habitus; C, ventral urosome; D, antennule, segments 1-19 (I-XX); E, antennule, segments 20-26 (XXI-XXVIII). F-J, male; F, dorsal habitus; G, lateral habitus; H, ventral urosome; I, antennule, segments 1-19 (I-XX) with reverse detail of segments 14-18 (XV-XIX); J, antennule, segments 20-24 (XXI-XXVIII) with reverse detail of segment 20 (XXI-XXIII).

fourth endite. Basis bears 3 setae, with patch of long setules along inner margin. Endopod 6-segmented, with setal formula 2, 4, 4, 3, 3 (inner) + 1 (outer), 4. First endopod segment distinctly separate from basis.

Legs 1-4, have 3-segmented rami (Fig. 3A-D). Seta and spine formulae given in Table 1. Inner coxal setae present on legs 1-4. Coxae of all legs have several patches of fine setules. Surface of coxae, bases, exopods and endopods,

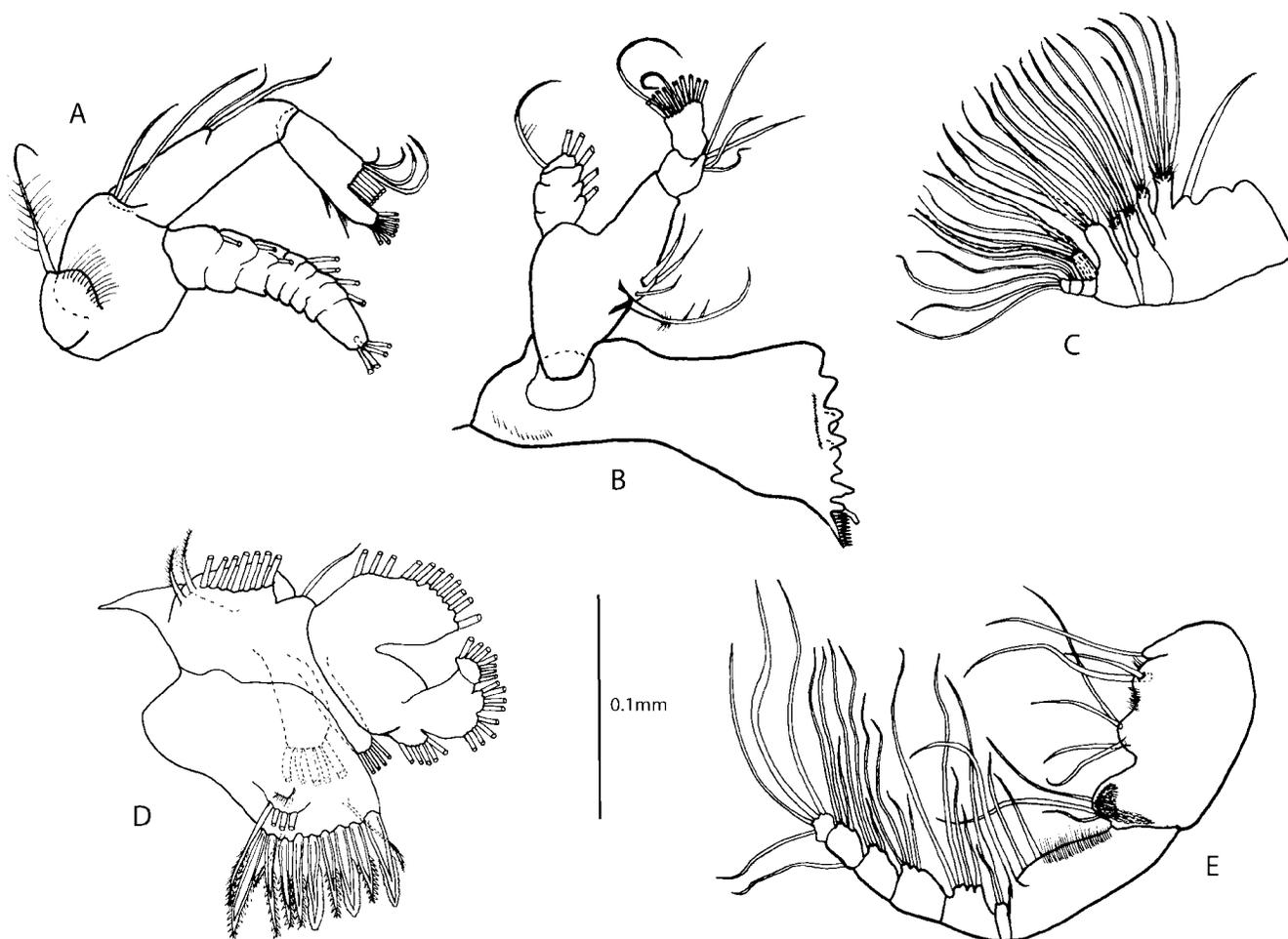


Fig. 2. *Ridgewayia delfine* sp. nov., female mouthparts. A, antenna; B, mandible; C, maxilla; D, maxillule; E, maxilliped.

covered with patches of minute setules and/or denticles (Fig. 4B). Leg 1 (Fig. 3A) with von Vaupel Klein organ, for grooming (Barthelemy et al., 1998), consisting of curved inner basal setae and a distally serrated process originating anteriorly from first endopod segment and extending halfway along second segment. With tuft of setules present on surface of this process. With row of fine setules present on distal edge of first exopod segment. Segment two, with lamellate, serrated process at distal margin, between outer setae and insertion point of third segment. With seta-like process in between outer setae and this lamellate process. Legs 2, 3, and 4, (Fig. 3B-D) with serrated distal margins on first and second endopod segments; with hairy protuberances on center distal margin of second exopod segment. Leg 5 (Fig. 3E) with 3-segmented exopod and a 2-segmented endopod. Inner coxal seta absent, basal seta present. Surface of leg covered with minute setules and/or denticles.

Male (paratype). Body (Fig. 1F, G) as in female. Urosome (Fig. 1H) 5-segmented. Caudal rami similar to those of female, except lacking row of setules on distal inner margins. Left antennule as in female.

Right antennule (Fig. 1J, I) 24-segmented, weakly geniculate with four segments beyond geniculation. Fusion

pattern and armature as follows; I-1 + ae, II-III-3 + ae, IV-2, V-1 + ae, VI-1 + ae, VII-2 + ae, VIII-2 + ae, IX-2 + ae, X-2 + ae, XI-1 + ae, XII-1 + ae, XIII-1 + ae, XIV-2 + ae, XV-2 + ae, XVI-2 + ae, XVII-1 + ae, XVIII-1 + ae, XIX-1, XX-2, XXI-XXIII-4 + ae, XXIV-2, XXV-2 + ae, XXVI-2, XXVII-XXVIII-5 + ae. Rows of spinules present on segments XV, XVI, XVII, XVIII, XIX, and XXI-XXIII. Segments XI and XIV constricted.

Legs 1-4 as in female. Leg 5 (Fig. 3F, G) biramous, asymmetrical, and strongly modified. Coxa without setae. Basis of right leg bears single seta on posteriolateral surface, near distal outer margin. Distal half of inner margin serrated and covered with minute setules. Right leg (Fig. 3F) with 2-segmented exopod and 1-segmented, elongate, endopod. Exopod segments without setae. First exopod segment with outer spine reaching base of first outer spine on second exopod segment. Second exopod segment with two outer spines. Distal end of this segment modified, with two processes on anterior surface (Fig. 4E). First process, next to base of second spine, consisting of curved flange with brush-like elements on outer surface. Second process, just distal to first, protruding anteriorly and covered with brush-like elements. Exopod ends with terminal projection, outer surface of which covered with brush-like elements.

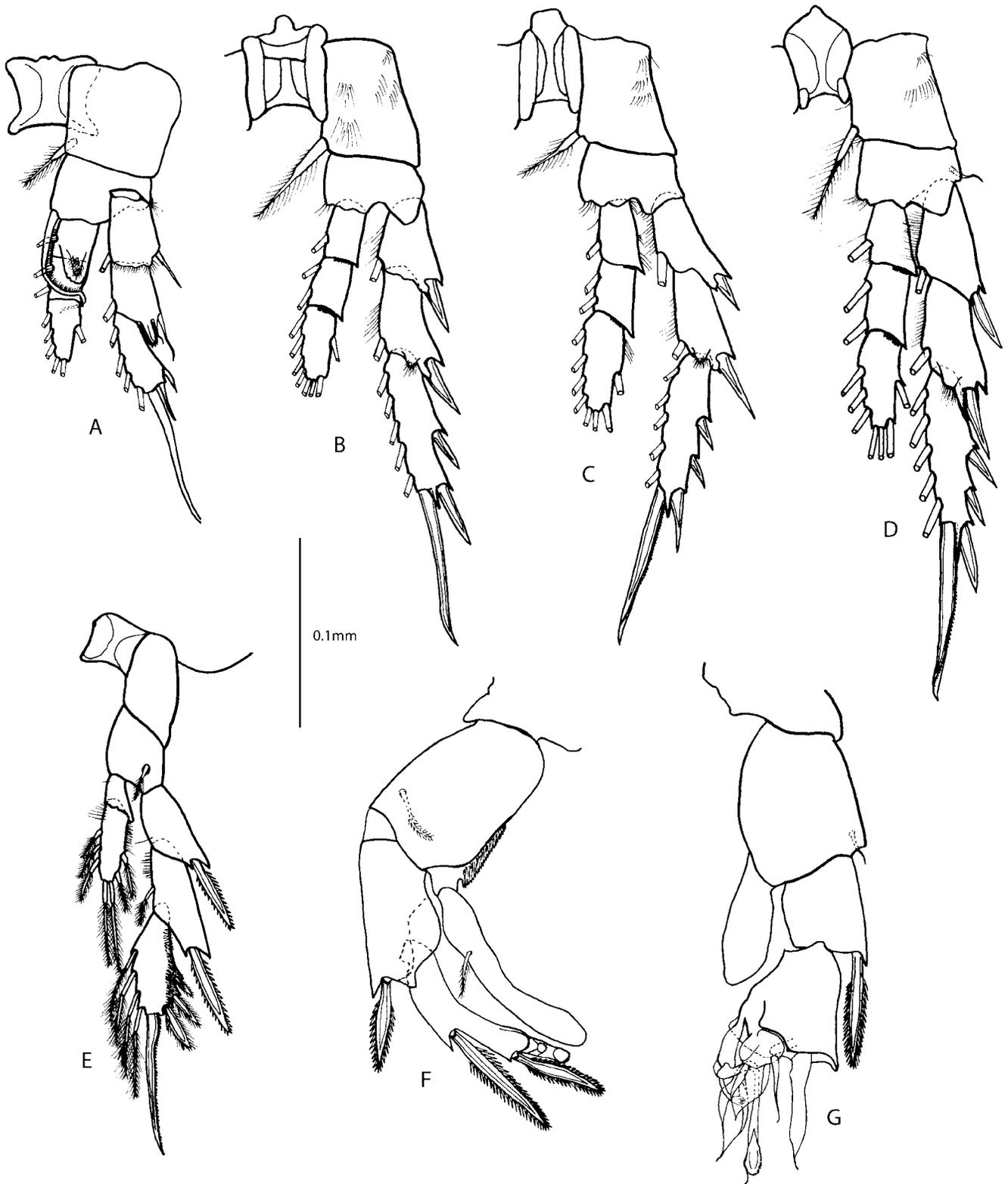


Fig. 3. *Ridgewayia delfine* sp. nov. A-E, female; A, anterior leg 1; B, anterior leg 2; C, anterior leg 3; D, anterior leg 4; E, anterior leg 5. F-G, male; F, anterior right leg 5; G, anterior left leg 5.

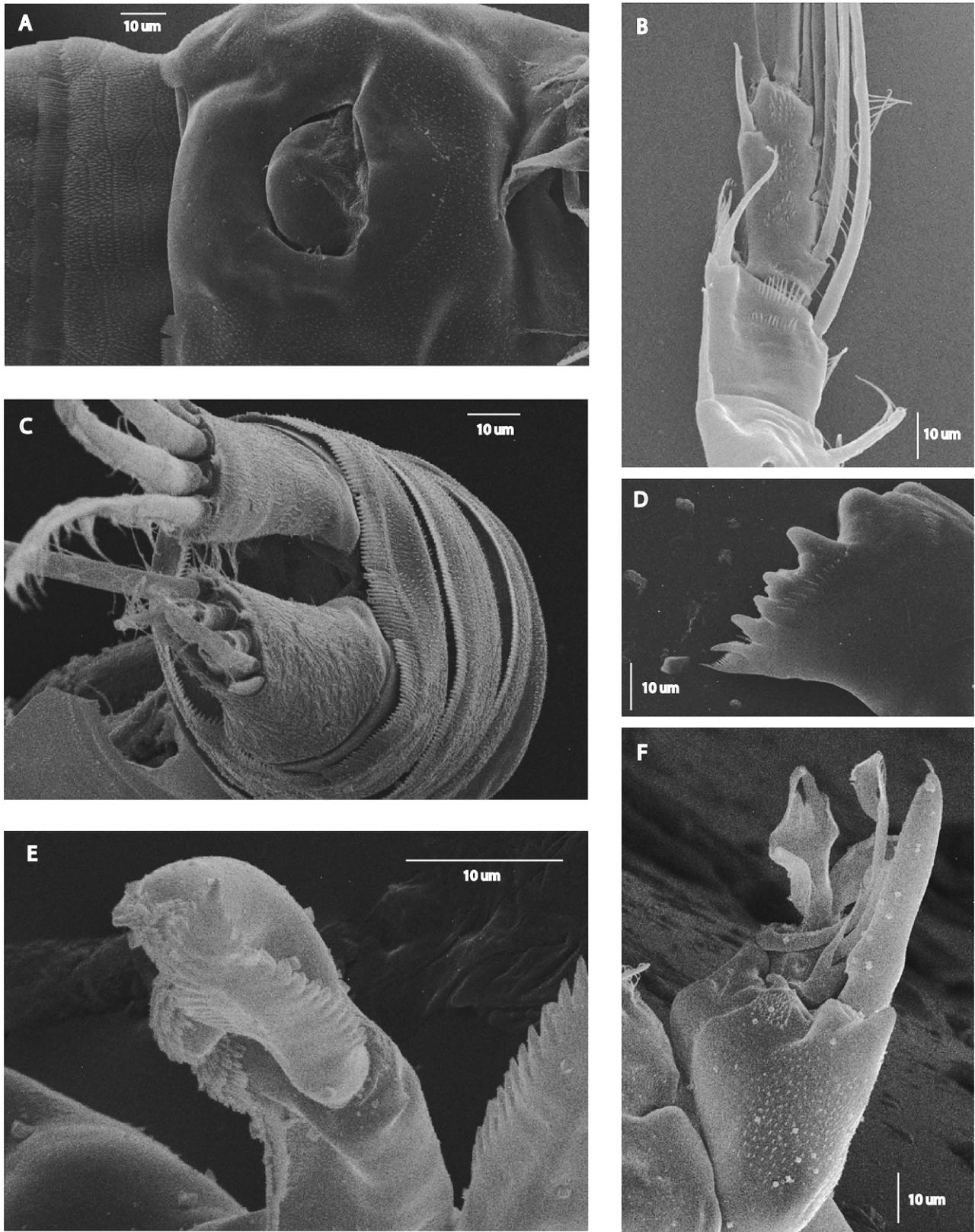


Fig. 4. *Ridgewayia delfine* sp. nov., Scanning Electron Microscope Images. A-D, female; A, ventral genital double somite; B, leg 1 exopod posterior; C, posterior-dorsal caudal rami; D, anterior mandible. E-F, male; E, right leg 5 tip of second exopod segment; F, left leg 5 posterior.

Endopod elongate, reaching tip of exopod. Seta present on anterodistal margin, before mid-length of segment; otherwise unarmed. Left leg (Fig. 3G) with single seta on anterolateral surface of basis, near distal outer margin. Exopod 3-segmented. First segment with outer spine reaching distal edge of second segment. Second segment with small acute process on distal outer margin. Outer spine on second segment long and straight, rather conical in shape, with thick base tapering slightly distally. Tip of spine very thin and curved inward. Brush-like setules along posterior and anterior inner margins of spine. Third segment complex and strongly modified (Fig. 4F), with five discernable elements. In order from anterior to posterior: first element as thin naked seta near outer margin; second element leaf-like, with anteriorly directed marginal folds; third element slender, lamellate and protruding from middle of second element, with several thin, finger-like extensions at tip; fourth element consists of two segments, first thick and rectangular along inner edge, second stems from strong distal joint, slender and curved towards outer spine and then projects distally and inwards with forked tip and small, petal-like process; fifth element as another leaf-like process with anteriorly directed marginal folds, and tapering distally into very thin tip.

**Etymology.**—The species name *delfine* refers to the former name, Grietas Delfin, of the anchialine pool that is the type locality.

***Ridgewayia tunela* n. sp.**  
(Figs. 4-5)

**Material Collected.**—3 specimens collected on 23 March 2005 and 47 specimens collected on 10 April 2005 all from the same locality, Tunel del Estero on the Island of Isabela, Galapagos, Ecuador (00°57.565'S; 90°59.417'W). 25 ♀ and 3 ♂ were used for analysis, including dissection and measurements.

**Body Length.**—Female. Total length: range = 0.78-0.87 mm, (mean ± standard deviation = 0.83 ± 0.02 mm, n = 20); prosome length = 0.61 - 0.67 mm (0.63 ± 0.01 mm, n = 20), urosome length = 0.18-0.22 mm (0.20 ± 0.01 mm, n = 20). Male. Total length = 0.71-0.75 mm (0.73 ± 0.02 mm, n = 3), prosome length = 0.53-0.56 mm (0.54 ± 0.02 mm, n = 3), urosome length = 0.18-0.20 mm (0.19 ± 0.02 mm, n = 3).

**Types.**—Deposited in the Smithsonian Museum of Natural History, Washington. Holotype: adult female, USNM 1098378; paratypes 7 adult females, USNM 1098379, and 2 adult males, USNM 1098380. All collected on 10 April 2005 (00°57.565'S; 90°59.417'W).

**Description.**—Female (holotype). Body (Figure 5A, B) slender and 6-segmented. Other than for its smaller size, habitus indistinguishable from *Ridgewayia delfine*. Eye and rostrum as in *R. delfine*. Urosome 4-segmented. Genital double somite symmetrical and genital operculum mid-ventral, not offset to right as in *R. delfine* (Fig. 5C). Seminal receptacle present on left side only. Tuft of long setules present on right ventrolateral side of genital double somite. As in *R. delfine*, small spinules cover surface of all prosome

Table 1. Seta and spine formulae for legs 1-5 of female *Ridgewayia delfine*.

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

and urosome segments, and all urosomal segments, except for anal segment, bear rows of denticles along posterior borders, with gap along border directly behind genital operculum. Caudal ramus as in *R. delfine*. Antennules 26-segmented and extending beyond caudal ramus by 1½ segments. Antennule length varies among individuals, but in all specimens tips of antennules reach beyond caudal rami by ½ to 1½ segments. Fusion pattern and armature as in *R. delfine*.

No noticeable differences between mandibles, maxillules, maxillae, and maxillipeds of *R. delfine* and *R. tunela*. Legs 1-4 as *R. delfine*. Leg 5 similar to *R. delfine*; but outer spines on first and second exopod segments considerably longer in *R. tunela* (Fig. 5D). Surfaces of legs also covered with minute setules and/or denticles.

**Male (paratype).** Body as in female (Fig. 5E, F). Urosome and caudal ramus as in *R. delfine*. Antennules as in *R. delfine*, except for their length. Antennules extending beyond caudal rami by 1½ segments. Legs 1-4 as in the female. Leg 5 (Fig. 5G, H) similar to *R. delfine* with following exceptions: endopod on right leg shorter, only reaching ¾ along length of third exopod segment; outer spine on first exopod segment of right leg longer, reaching halfway along outer spine on second exopod segment; with row of fine setules present along proximal inner margin of second exopod segment on right leg; spine on first exopod segment of left leg longer, reaching well beyond distal edge of second exopod segment; finally tuft of long setules present along proximal inner margin of second exopod segment of left leg.

**Etymology.**—The species name *tunela* refers to the site where this ridgewayiid was collected, a submerged lava tunnel.

#### DISCUSSION

Barthelemy et al. (1998) divided the members of the genus *Ridgewayia* into three species-groups: 1) *marki* species-group; 2) *gracilis* species-group; and 3) *typica* species-group. The two new species from the Galapagos belong to the *marki* species-group. Members of this group are characterized by Ohtsuka et al. (2000) as having an inner coxal seta on leg 1, two outer spines on the second exopod segment of the male right fifth leg, and a simple and unarmed endopod on the male left fifth leg. Both *R. delfine* and *R. tunela* meet these characteristics. Therefore, the *marki* species-group is now comprised of eight members: *R. marki marki* Wilson, 1958; *R. shoemakeri* Wilson, 1958; *R. fosshageni* Humes and Smith, 1974; *R. klausruetzleri* Ferrari, 1995; *R. marki minorcaensis* Razouls and Carola,

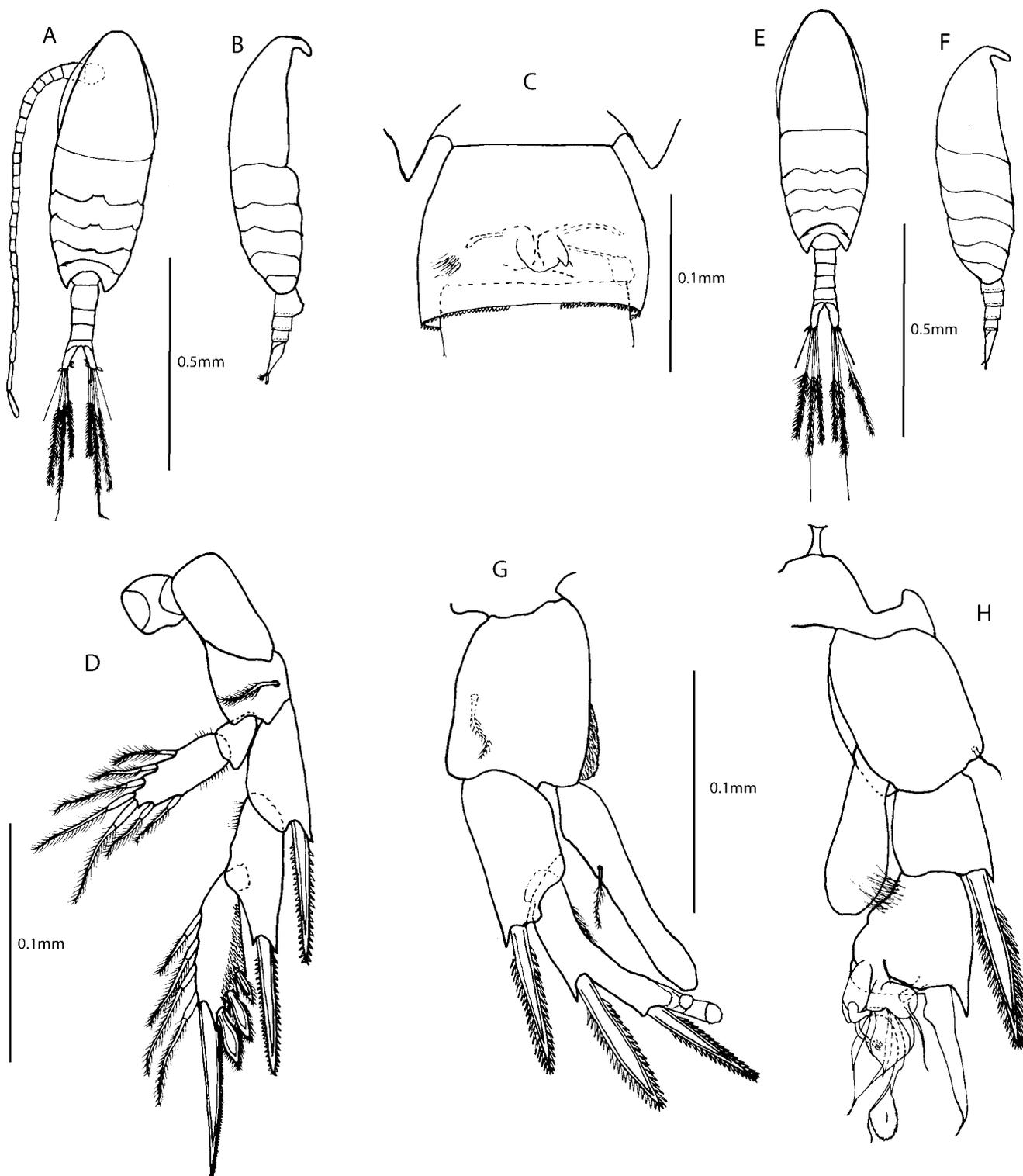


Fig. 5. *Ridgewayia tunela* sp. nov. A-D, female, A, dorsal habitus; B, lateral habitus; C, genital double somite, ventral; D, leg 5, anterior. E-H, male; E, dorsal habitus; F, lateral habitus; G, right leg 5 anterior; H, left leg 5 anterior.

1996; *R. stygia* Ohtsuka et al., 2000; and *R. delfine* and *R. tunela* from the present study.

There are several characters that can help distinguish *R. delfine* and *R. tunela* from other members of the *marki*

species-group (Tables 2 and 3). Both *R. delfine* and *R. tunela* have minute spinules/denticles covering the surface of their legs, urosome, and caudal ramus, as in *R. stygia* and *R. fosshageni*, while other members of this group lack this

Table 2. Distinguishing characters among female *ridgewayiids* of the *marki* species-group. Characters for *R. delphine* and *R. tunela* were obtained from original descriptions.

	<i>R. marki marki</i>	<i>R. marki minorcaensis</i>	<i>R. klausruetzleri</i>	<i>R. shoemakeri</i>	<i>R. fosshageni</i>	<i>R. stygia</i>	<i>R. delphine</i>	<i>R. tunela</i>
Total length (mm)	1.00	1.00	0.87	0.68	0.75	0.98	0.95	0.83
Number of setae on basipod of mandible	3 short	?	3 short 1 long	3 short	2 short 1 long	3 short 1 long	3 short 1 long	3 short 1 long
Ventrolateral setules on genital double somite	yes on right	?	yes on left	no	no	no	no	yes on right
Seminal receptacles	no	?	?	?	yes 1 on left	yes 1 on left	yes 1 on left	yes 1 on left
Caudal rami w/spinules	no	no	no	no	yes	yes	yes	yes
Antennules beyond caudal rami	yes	yes	yes	no	yes	yes	most no	yes
Median setae on caudal rami	not jointed	?	?	not jointed	jointed	?	jointed	jointed
Genital opening	center	offset right	center	?	center	offset left	offset right	center
Genital operculum near distal margin	yes	yes	no, mid-ventral	yes overlaps	no, mid-ventral	yes overlaps	no, mid-ventral	no, mid-ventral
P5, number of seta/spines on 2 <sup>nd</sup> exopod seg.	7	7	7	7	6	7	7	7
P5, outer spine on 1 <sup>st</sup> exopod seg. long	no	yes, beyond 2 <sup>nd</sup> seg.	no	no	no	no	no	yes, beyond 2 <sup>nd</sup> seg.
P5, outer spine on 2 <sup>nd</sup> exopod seg. reaching beyond tip of spine on 3 <sup>rd</sup> exopod seg.	no (barely reaches tip)	yes	no (only to tip of 2 <sup>nd</sup> spine)	no (only to tip of 2 <sup>nd</sup> spine)	yes	no (only to tip of 2 <sup>nd</sup> spine)	no (barely reaches tip)	yes

characteristic. *Ridgewayia delphine* and *R. tunela* have a long and straight outer spine on the second *exopod segment* of the male left fifth leg. This spine is also long in *R. shoemakeri*, *R. fosshageni*, and *R. stygia*, but the shape of the spine varies: in *R. shoemakeri* it curves inward; in *R. fosshageni* it is irregular, with the outer edge concave medially; and in *R. stygia* it is also irregular and sinusoidal in shape. The

other members of this group, *R. marki marki*, *R. marki minorcaensis*, and *R. klausruetzleri* have a short, stout, spine. The two long median setae on the caudal rami are jointed in *R. delphine* and *R. tunela*, a character shared with *R. fosshageni* but not present in *R. shoemakeri* or *R. marki marki*. The genital operculum in *R. marki marki*, *R. marki minorcaensis*, *R. shoemakeri*, and *R. stygia* is located

Table 3. Distinguishing fifth leg characters among male *ridgewayiids* of the *marki* species-group. Characters for *R. delphine* and *R. tunela* were obtained from original descriptions.

	<i>R. marki marki</i>	<i>R. marki minorcaensis</i>	<i>R. klausruetzleri</i>	<i>R. shoemakeri</i>	<i>R. fosshageni</i>	<i>R. stygia</i>	<i>R. delphine</i>	<i>R. tunela</i>
Left P5, outer spine on 2 <sup>nd</sup> exopod seg.	short	short	short	long/irregular	long/irregular	long/irregular	long/irregular	long/irregular
Left P5, outer spine on 2 <sup>nd</sup> exopod seg. longer than seg.	no, shorter, about 1/3 of segment	no, shorter, about 1/3 of segment	no, shorter, about 1/3 of segment	yes, almost 2 times as long	yes, 1.4 times as long	yes, almost 2 times as long	no, same size as segment	yes, 1.2 times as long
Left P5, Spine on 1 <sup>st</sup> exopod seg. reaching beyond distal edge of seg. 2	yes	yes	yes	yes	yes	yes	no, barely reaches edge	yes
Left P5, tuft of hairs present along proximal inner margin of 2 <sup>nd</sup> exopod seg.	no	no	no	no	no	no	no	yes
Right P5 with medial expansion on 1 <sup>st</sup> exopod seg.	no	no	no	yes	no	no	no	no
Right P5, endopod reaching to base of 2 <sup>nd</sup> spine on 2 <sup>nd</sup> exopod seg.	yes	just short of base	yes	yes	yes	yes	no, beyond base and near distal edge	no, beyond base not near distal edge
Right P5 spine on 1 <sup>st</sup> exopod seg. reaching beyond midlength of spine on 2 <sup>nd</sup> exopod seg.	no, only 1/3 of spine	yes	no, only 1/3 of spine	no, only 1/4 of spine	yes	no, only 1/3 of spine	no, barely reaches base of spine	yes
Right P5 with row of hairs along inner margin of 2 <sup>nd</sup> exopod seg.	no	no	no	no	no	no	no	yes

near the distal margin of the genital double somite (the operculum actually seems to overlap the distal edge in *R. shoemakeri*, and *R. stygia*); while in *R. delfine*, *R. tunela*, *R. fosshageni* and *R. klausruetzleri* there is considerably more space between the distal margin of the genital double somite and the operculum. Both *R. delfine* and *R. tunela* have 7 setae on the second endopod segment of the female fifth leg, a character shared by all members of this group except for *R. fosshageni*, which has only 6.

There are also several differences between *R. delfine* and *R. tunela* (Table 2). *Ridgewayia delfine* is significantly larger than *R. tunela*. *Ridgewayia delfine*'s antennules are shorter, only reaching the end of the caudal ramus (a few specimens have antennules slightly longer than the caudal ramus); in *R. tunela* all specimens have antennules reaching beyond the caudal ramus. The genital opening in *R. delfine* is midventral, but offset to the right; while in *R. tunela* it is well centered. *Ridgewayia tunela* has a patch of setules on the right ventrolateral side of the female genital double somite, similar to those found in *R. marki marki*, and *R. klausruetzleri* (although in *R. klausruetzleri* they are on the left side). *Ridgewayia delfine* lacks these setules. The outer spine on the first exopod segment of the female fifth leg is long in *R. tunela*; it reaches beyond the distal edge of the second exopod segment, similarly to that of *R. marki minorcaensis*. All other members of this group, including *R. delfine*, have a shorter spine. The outer spine on the second exopod segment of the female fifth leg is also longer in *R. tunela*; reaching beyond the tip of the third outer spine of the third exopod segment (it barely reaches the tip of the third spine in *R. delfine*). In *R. delfine*, the endopod of the male right fifth leg is long, almost reaching the distal edge of the second exopod segment; in *R. tunela*, it only extends to the base of the second outer spine of the second exopod segment. The outer spine on the first exopod segment of the male fifth leg is long in *R. tunela*, reaching beyond the midlength of the first outer spine on the second exopod segment; while in *R. delfine* it only reaches the base of the first outer spine. In *R. tunela*, there is a row of fine setules along the proximal inner margin of the second exopod segment of the male right fifth leg, that is not present in *R. delfine*. In *R. tunela*, the outer spine on the first exopod segment of the male left fifth leg reaches well beyond the distal edge of the second exopod segment. This character is shared by all the members of the *marki* species-group except for *R. delfine*, where the spine barely reaches the distal edge of the second segment. Finally, in *R. tunela*, there is a tuft of long setules present along the proximal inner margin of the second exopod segment of the male left fifth leg. All other members of this group including *R. delfine* lack this character.

It is presently thought that *Ridgewayia* is a Tethyan relict (Ohtsuka et al. 2000). Most members of the *marki* species-group are found in the Caribbean and they include: *R. marki marki* (Bermuda), *R. shoemakeri* (Dry Tortugas, Florida), *R. fosshageni* (Bahamas and Panama), and *R. klausruetzleri* (Belize). There is one member from the Mediterranean, *R. marki minorcaensis* (Minorca) and one from the Indo-West Pacific, *R. stygia* (Palau). Ohtsuka (2000) points out the faunistic link between the Western Central Pacific and

Caribbean, and suggests that the ancestor of *R. stygia* migrated from the Caribbean into the Western Central Pacific during the Miocene when the Tethys Sea was circumtropical. This is a feasible theory, and the discovery of *R. delfine* and *R. tunela* in the Eastern Pacific can be viewed as further evidence of a westward dispersal of these *marki* species-group ridgewayiids. The present Galapagos Islands are geologically young, the oldest Islands have been dated to be 4-5 million years old (Hall, 1983); but there is evidence that sea mounts and/or islands have been emerging from the Galapagos hot spot as far back as 75-95 million years ago, Hoernle et al. (2002) show that the entire Caribbean plate originated from the Galapagos hotspot during the Cretaceous period. This places the emergence of oceanic islands around the Galapagos hot spot well within the time frame needed for a Tethyan dispersal of the ancestors of *R. stygia*, *R. delfin*, and *R. tunela* from the Caribbean into the Pacific. Although this Tethyan hypothesis is one of the favored explanations for the present distribution of anchialine fauna, it does not exclude the possibility that some of the inhabitants of anchialine systems have colonized these habitats more recently (Boxshall and Jaume, 1999).

The Tethys Sea remained open and circumtropical until about 20 million years ago (Hrbek and Meyer, 2003), but the dispersal of the *marki* species-group from the Caribbean into the Pacific could have taken place after this period before the closing of the Panama seaway 3.5 million years ago (Nesbitt and Young, 1997). Thus, the colonization of Galapagos by the members of the *marki* species-group could have come directly from the Caribbean to the present day islands. Both dispersal scenarios call for the colonization of the *marki* species-group from the Caribbean into the Pacific, but the possibility remains that members of this group present in the Western Pacific subsequently migrated into the Caribbean. A major argument against a modern day dispersal of ridgewayiids is the 5000 km expanse of deep water separating the Central Pacific and the Eastern Pacific. This marine barrier was first mentioned by Darwin (1859) in *The Origin of Species*, and it is now referred to as the Eastern Pacific Barrier (EPB). Since there are no islands present across this vast stretch of deep ocean, the EPB acts as a barrier to dispersal of shallow water species. The effectiveness of this barrier has been demonstrated by the large number of shallow species that are not shared by these two regions, in contrast to the very few species that are found on both sides (Lessios et al., 1998; Lessios and Robertson, 2006).

There is a debate about the few transpacific species, whether they are the remnants of a previously continuous Tethyan distribution that have not evolved morphological differences since the emergence of the EPB, or whether there is dispersal across the EPB that maintains sufficient gene flow to prevent speciation (Lessios et al., 1998; Lessios and Robertson, 2006). Lessios et al. (1998) showed that for the sea urchin *Echinothrix diadema* (present in the Central and Eastern Pacific) the latter is the case, since substantial gene flow was found between the two transpacific populations by analysis of mitochondrial DNA. More recently, Lessios and Robertson (2006) studied the

mitochondrial DNA of 20 species of transpacific reef fish and found that 18 of these species showed some level of recent gene flow across the barrier. The genetic analysis performed by Lessios and Robertson (2006) demonstrated that dispersal occurred stochastically in time and with respect to species dispersed; and that gene flow occurred in both directions. Such evidence raises the possibility that the Ridgewayiids from the Galapagos and Palau are the result of post-Tethyan dispersal.

Many uncertainties remain which will be subject to future research, chief among these are: 1) the timing of the dispersal of the *marki* species-group ridgewayiids in the Pacific, 2) whether this dispersal was from East to West or vice versa, and 3) whether the two species of ridgewayiids in the Galapagos are the result of one or two different colonization events. Ohtsuka et al. (2000) recognizes that the species richness of *Ridgewayia* is yet to be determined due to paucity of sampling. Research filling in this gap and genetic studies of the various *Ridgewayia* species will be essential for determining the biogeographic history of this genus. Further exploration in the Galapagos Archipelago may lead to the discovery of more species of ridgewayiids, and it is almost certain that further exploration in the Caribbean and Indo-west Pacific will lead to similar new discoveries.

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