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## A New Species of *Ridgewayia* (Copepoda: Calanoida) from a Submarine Cave in Palau, Western Pacific

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A new calanoid copepod, *Ridgewayia stygia*, is described from a submarine cave in Palau in the Western Pacific. The new species is most similar to a Caribbean species, *R. fosshageni*, but can be distinguished from the latter by the location of the female genital operculum and the structure of the fifth legs of both sexes. The affinities of the new species appear to lie with the North Atlantic/Mediterranean *R. marki* species-group rather than the Indo-West Pacific *R. typica* species-group. This discovery suggests that, within the Tethys Sea, westward dispersal of marine copepods from the Caribbean Province extended as far as the western Central Pacific rather than only to the eastern Central Pacific.

**Key Words:** Copepoda, Calanoida, *Ridgewayia*, submarine cave, Palau, zoogeography

### Introduction

The family Ridgewayiidae accommodates five genera, the species of which are highly adapted to cavernicolous and/or benthic modes of life (Fosshagen and Iliffe 1998). The genera *Brattstromia* and *Exumellina* are known exclusively from anchialine caves, whereas *Exumella* and *Ridgewayia* are found mainly in the hyper- or epibenthos, and occasionally from caves (Wilson 1958; Fosshagen and Iliffe 1998). Another genus, *Placocalanus*, is regarded as an epibenthic taxon that may be able to burrow into sediments temporarily (Fosshagen 1970; Ohtsuka *et al.* 1996; Fosshagen and Iliffe 1998).

The genus *Ridgewayia* consists of 10 nominal species, including two nominal subspecies, and two as yet undescribed species (Barthélémy *et al.* 1998a; Fosshagen and Iliffe 1998). Unusual behaviors for calanoids, such as association with corals and actinarians, are reported in this genus (Yeatman 1969; Humes and Smith 1974; Ferrari 1995). *Ridgewayia marki marki* (Esterly, 1911) and *R. marki minorcaensis* Razouls and Carola, 1996 were recorded from caves in Bermuda (Esterly 1911; Yeatman 1969; Fosshagen and Iliffe 1985) and Minorca (Razouls and Carola 1996), respectively.

The present paper describes a new species of *Ridgewayia* collected from a sub-

marine cave in Palau. It also includes zoogeographical notes on the genus.

### Material and Methods

Copepods were collected from deep crevices in the walls of a small submarine cave at a depth of 17 m on 23 October 1999 using a hand-held suction-pump. The cave branched off from the main tunnel (more than 50 m long) informally called "Virgin Hole 1" on the west side of Ngemelis Island, Palau (07°7.185'N, 134°14.147'E). The void of the cave was totally dark and almost barren of macrofauna, and the walls and ceilings were densely coated by small sedentary invertebrates, such as two species of thecidlinid brachiopod, a dimyid bivalve *Dimyella* sp., and an unidentified sphinctozoan sponge. The bottom of the cave was filled with muddy calcareous sediment, which included numerous microscopic molluscs and exoskeletons of other organisms dwelling on the walls and ceiling. Copepods were preserved in 10% neutralized formalin/sea-water.

The type specimens are deposited at the National Science Museum, Tokyo, Japan. Terminology follows Huys and Boxshall (1991).

Family **Ridgewayiidae** Wilson, 1958  
Genus ***Ridgewayia*** Thompson and Scott, 1903  
***Ridgewayia stygia*** new species  
(Figs 1–4)

**Material examined.** One female and two males from a submarine cave, "Virgin Hole 1," on west side of Ngemelis Island, Palau (07°7.185'N, 134°14.147'E), depth 17 m, 23 October 1999.

**Types.** Holotype: adult female, dissected and mounted in gum-chloral on glass slides, NSMT-Cr 13084. Paratypes: two adult males, antennule and leg 5 mounted in gum-chloral on glass slides, body proper in vial, NSMT-Cr 13085.

**Description.** *Female (holotype).* Body (Fig. 1A, B) 0.98 mm long. Cephalosome separate from first pediger. Rostrum (Fig. 1B, C) remarkably produced ventrally, rounded at tip, with pair of secretory gland openings subterminally. Labrum (Fig. 1B, C) protruded ventrally, bearing tuft of fine setules on median swelling. Medial papilla present anterior to labrum, beneath rostrum. Second to fourth pedigers with prominent posterior ventrolateral corners (Fig. 1D, arrowed); fourth and fifth pedigers separate; fifth pediger slightly produced posteriorly in dorsal view (Fig. 1A, E), smoothly rounded in lateral view (Fig. 1B). Urosome (Fig. 1E) 4-segmented; genital double-somite slightly asymmetrical, protruding laterally more on left side than on right; seminal receptacle (?) visible by transparency only in left dorsal view; genital operculum (Fig. 1F) located nearly at posterior margin; posterior margin of first 3 urosomites striated; anal somite small; anal operculum convex at tip. Caudal rami (Fig. 1E) symmetrical, almost entirely covered by minute spinules and granules; seta I apparently lacking; seta II spiniform; seta V longest; seta VII hirsute, located dorsally, near bases of setae V and VI.

Sides of prosome, distal margins of urosomites, proximal antennular segments, and all post-antennular appendages tinged with reddish brown.

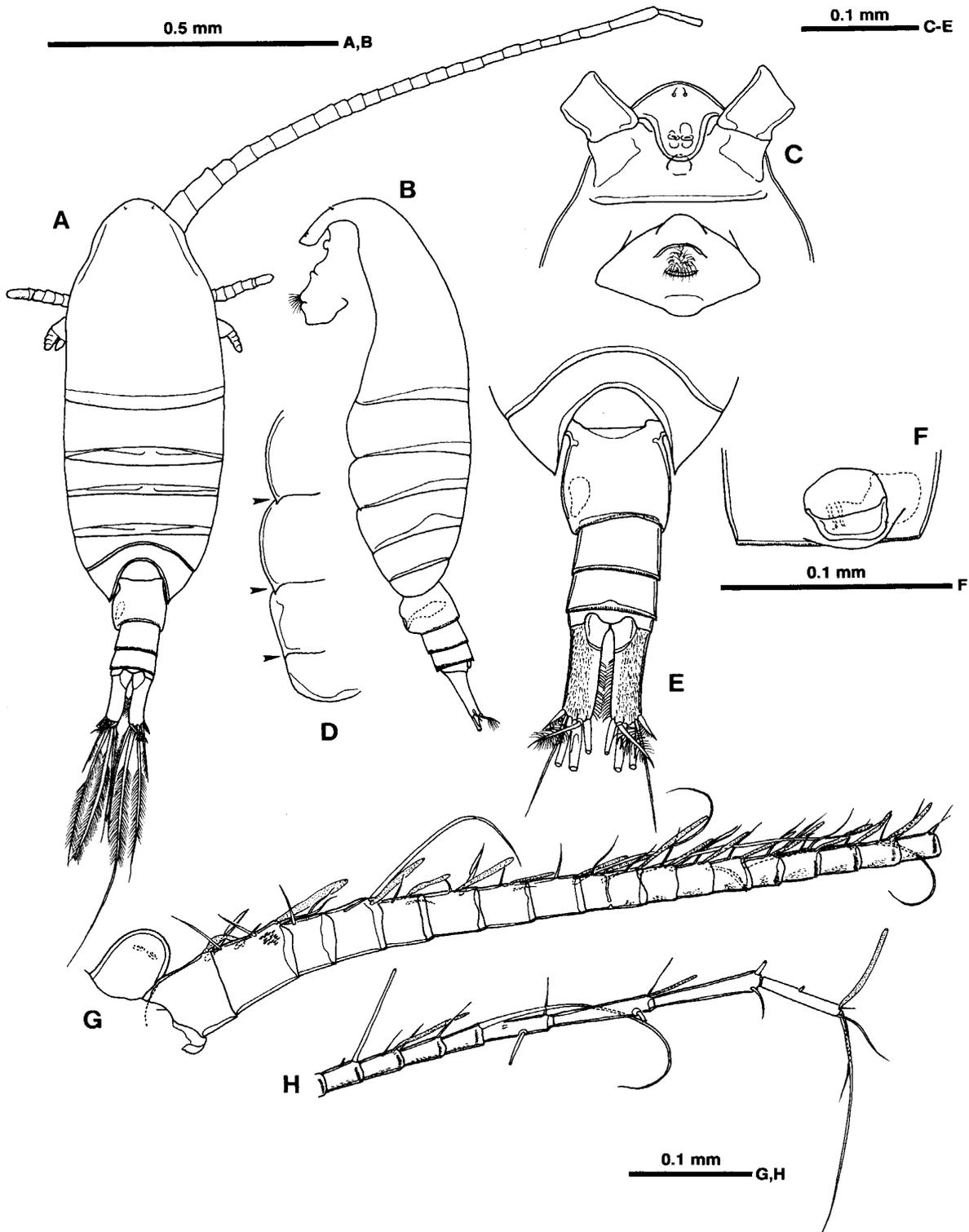


Fig. 1. *Ridgewayia stygia* n. sp., adult female (holotype). A. Habitus, dorsal view. B. Habitus, lateral view. C. Rostrum and labrum, ventral view. D. Ventrolateral corners of second to fourth pedigers, pointed posterior corners arrowed. E. Urosome, dorsal view. F. Genital operculum. G. Antennular segments I to XIX. H. Antennular segments XX to XXVII-XXVIII.

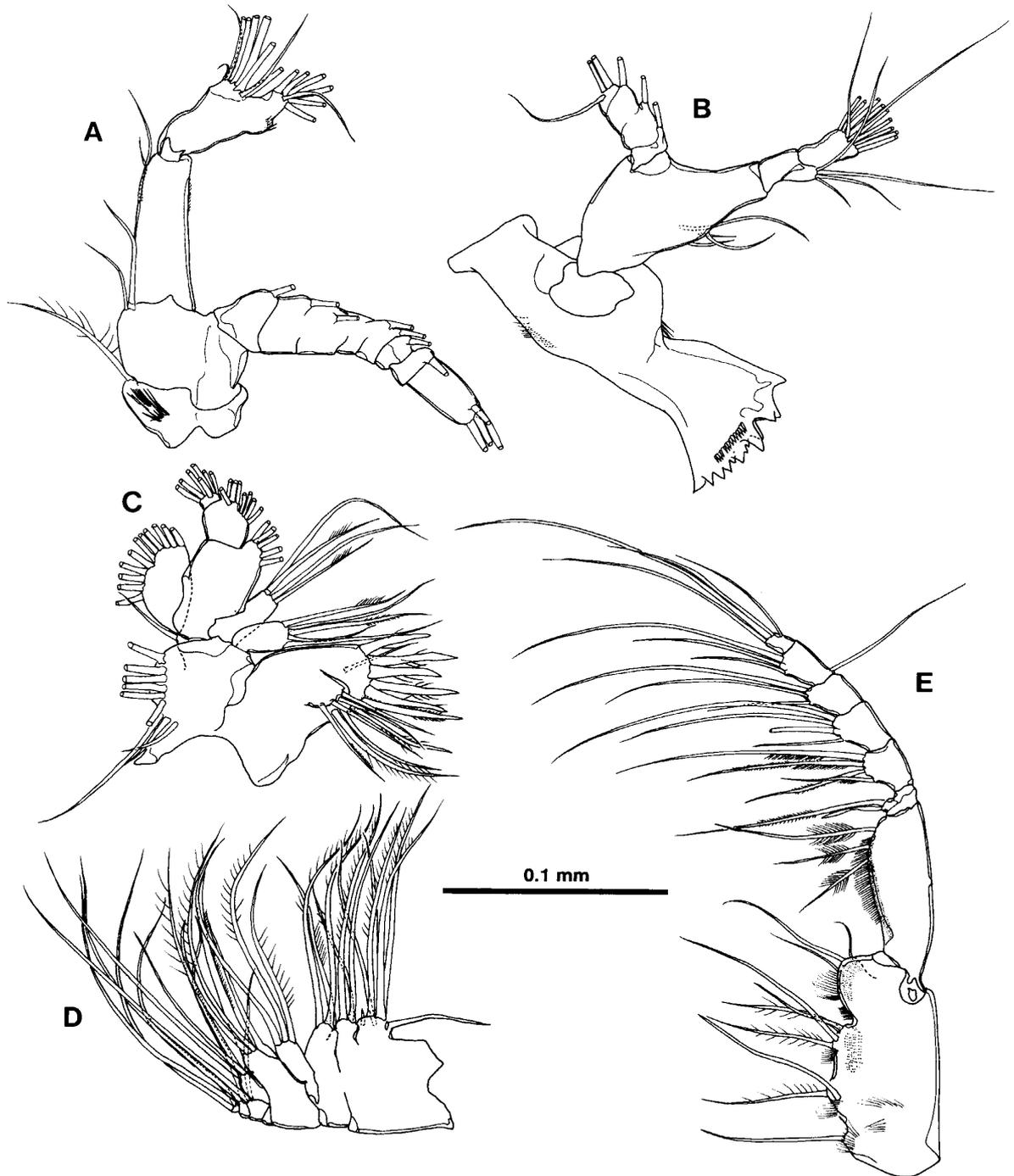


Fig. 2. *Ridgewayia stygia* n. sp., adult female (holotype). A. Antenna. B. Mandible. C. Maxillule. D. Maxilla. E. Maxilliped.

Antennule (Fig. 1G, H) 26-segmented, with 9th (X) and 10th (XI) segments partly fused. Patch of spinules present at anterodistal corner of compound second (II-III) segment. Transverse row of spinules on each segment from 13th (XIV) to 22nd (XXIII). Armature elements and fusion pattern as follows:

I-1+ae, II-III-4+ae, IV-2, V-2+ae, VI-2+ae, VII-2+ae, VIII-2+ae, IX-

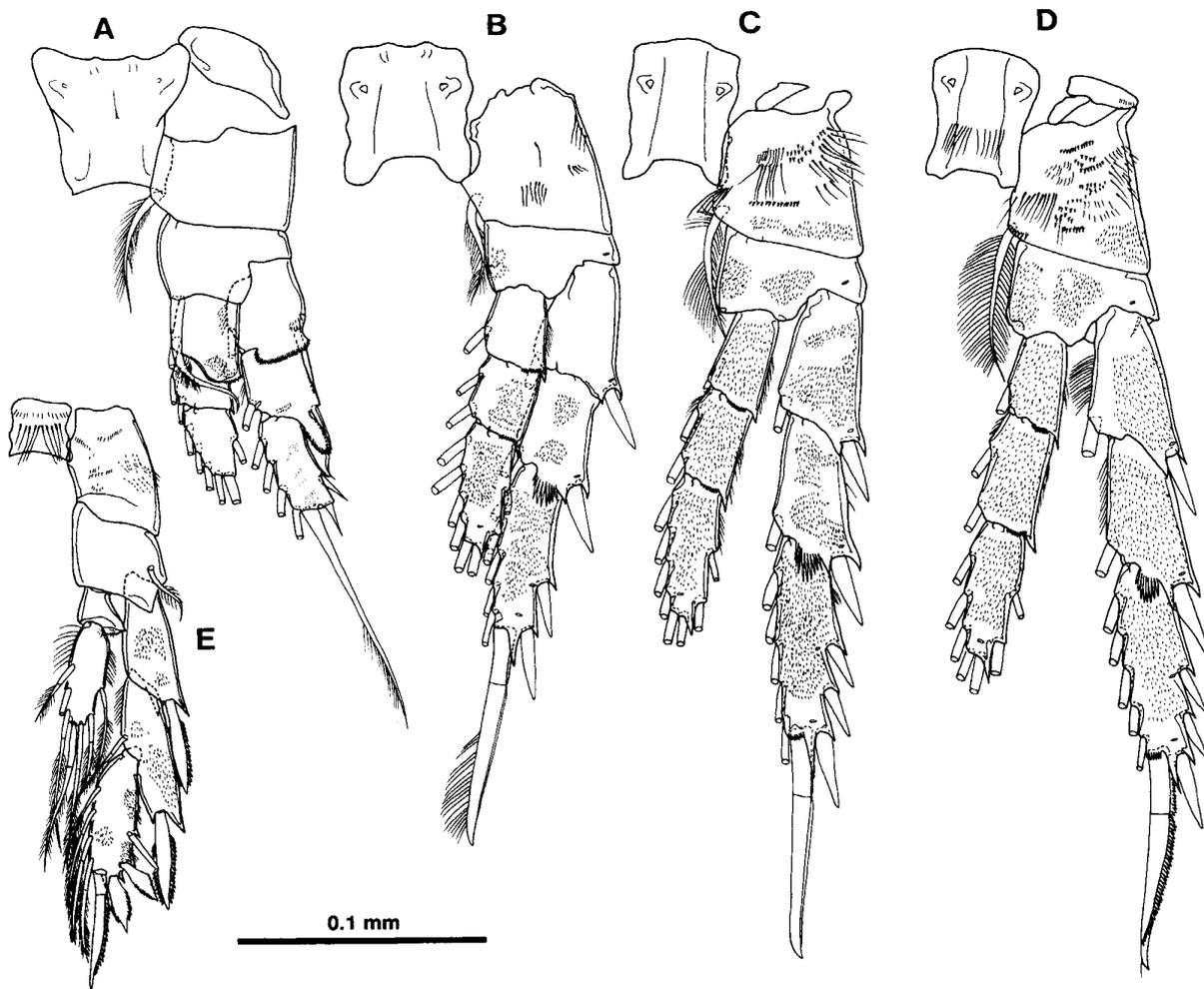


Fig. 3. *Ridgewayia stygia* n. sp., adult female (holotype). A. Leg 1, anterior surface. B. Leg 2, anterior surface. C. Leg 3, anterior surface. D. Leg 4, anterior surface. E. Leg 5, posterior surface.

2+ae, X-XI-4+2ae (X-2+ae, XI-2+ae), XII-2+ae, XIII-2+ae, XIV-2+ae, XV-2+ae, XVI-2+ae, XVII-2+ae, XVIII-2+ae, XIX-2, XX-2, XXI-2+ae, XXII-1, XXIII-1, XXIV-1+1, XXV-1+1+ae, XXVI-1+1, XXVII-XXVIII-5+ae.

Antenna (Fig. 2A) with 2-segmented endopod and indistinctly 8-segmented exopod. Coxa bearing spinulose seta and patch of setules; basis with 2 setae of unequal length. Setal formula of exopod 1, 1, 1, 1, 1, 1, 1, 4. First endopod segment with 2 setae subterminally; second segment bilobed, proximal and distal lobes with 9 and 7 setae, respectively.

Mandible (Fig. 2B) with heavily sclerotized gnathobase bearing 9 teeth; basis with 4 setae along inner margin; exopod indistinctly 4-segmented, setal formula 1, 1, 1, 3; endopod 2-segmented, proximal and distal segments bearing 4 and 11 setae, respectively.

Maxillule (Fig. 2C) well developed; precoxal arthrite bearing 1 anterior and 4 posterior setae and 1 minute, 4 spinulose, and 5 heavily sclerotized setae along inner margin; coxal epipodite with 2 short proximal and 7 long distal setae; basal

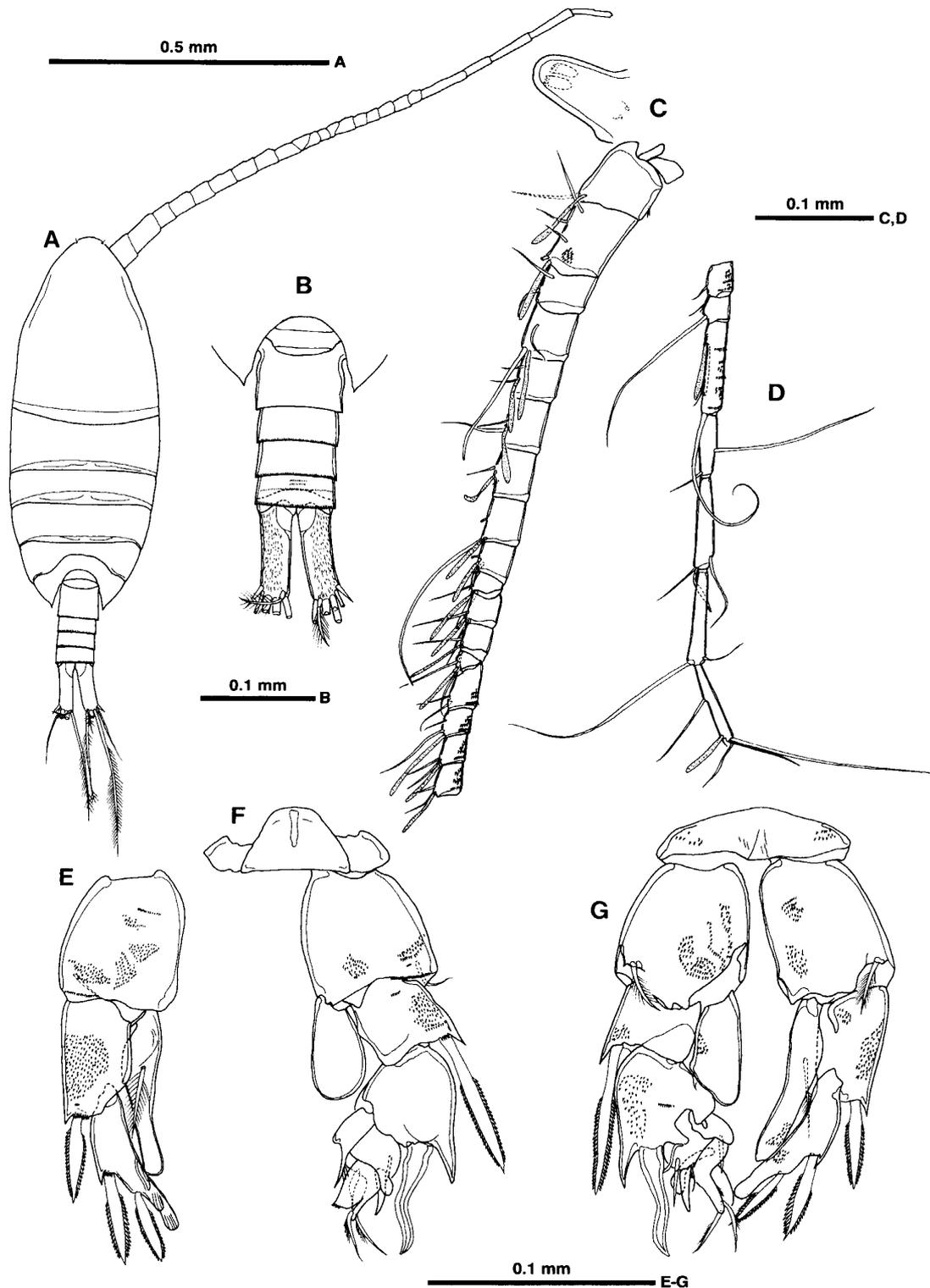


Fig. 4. *Ridgewayia stygia* n. sp., adult male (paratypes). A. Habitus, dorsal view. B. Urosome, dorsal view. C. Rostrum and antennular segments I to XVIII. D. Antennular segments XIX to XXVII-XXVIII. E. Right leg 5, anterior surface. F. Left leg 5, anterior surface. G. Leg 5, posterior surface.

exite bearing seta; coxal and 2 basal endites having 5, 4, and 5 setae, respectively; exopod unisegmented, with 11 setae along outer margin; endopod 2-segmented, setal formula (4+4), 7.

Maxilla (Fig. 2D) with precoxa and coxa incompletely fused; first precoxal endite with 5 long and 1 proximally directed setae in addition to one rudimentary element; setal formula of second precoxal to basal endites 3, 3, 3, 4. Endopod indistinctly 4-segmented; setal formula 3, 2, 2, 3.

Maxilliped (Fig. 2E) with setal formula of syncoxal endites 1, 2, 4, 3; each endite ornamented with patch of setules; basis bearing 3 inner setae and row of setules along entire inner margin; first endopod segment distinctly separate from basis; setal formula of endopod segments 2, 4, 4, 3, (3+1), 4.

Seta and spine formula of legs 1 to 4 (Fig. 3) as in *Ridgewayia boxshalli* Barthélémy, Ohtsuka and Cuoc, 1998 except for presence of inner coxal seta of leg 1 (see Barthélémy *et al.* 1998a: table 1, with correction of misprinted outer basal spine (I) of legs 4 and 5 to seta (1)). Leg 1 (Fig. 3A) with first endopod segment finely serrate along distal margin. Legs 2 to 4 (Fig. 3B–D) ornamented with numerous setules and/or minute prominences on both sides; distal margin of second exopod segment sharply serrate. Intercoxal sclerite of legs 4 and 5 furnished with transverse row of setules. Outer basal seta of leg 4 small. Leg 5 (Fig. 3E) similar to that of *R. boxshalli*, except for presence of setules/prominences on coxa and rami.

*Male (paratypes)*. Body (Fig. 4A) 0.90, 0.98 mm long, similar in size and color to that of female. Urosome (Fig. 4B) 5-segmented; anal somite small, almost telescoped into preceding one; caudal rami as in female.

Right antennule (Fig. 4C, D) weakly geniculate, consisting of 24 free segments. Geniculation present between 19th (XX) and 20th (XXI–XXIII) segments. Armature elements and fusion pattern as follows: I–1+ae (seta missing), II–III–4+ae, IV–2 (seta missing), V–2+ae, VI–2+ae, VII–2+ae, VIII–2+ae, IX–2+ae, X–2+ae, XI–2+ae, XII–2+ae, XIII–2+ae, XIV–2+ae, XV–2+ae, XVI–2+ae, XVII–2+ae, XVIII–2+ae, XIX–2, XX–2, XXI–XXIII–3+ae+process (seta missing?), XXIV–1+1, XXV–1+1+ae, XXVI–1+1, XXVII–XXVIII–5+ae. Tenth (XI) and 13th (XIV) segments triangular in shape. Patch of spinules present anteriorly on compound second segment; transverse row of spinules on each segment from 14th (XV) to 18th (XIX); 20th segment compound (XXI–XXIII), bearing 3 transverse spinular rows, these presumably indicating margins of original segments.

Leg 5 (Fig. 4E–G) with intercoxal sclerite and both coxae completely fused to form common base on posterior surface (Fig. 4G), incompletely fused on anterior surface (Fig. 4F). Right leg with 2-segmented exopod and unisegmented endopod; first exopod segment distally produced into acute triangular process, with serrate outer spine reaching beyond base of first spine of second segment; second exopod segment smoothly curved inward, bearing 2 outer spines; base of first spine of second segment serrated on anterior surface; terminal and subterminal rounded swellings on second exopod segment pad-like, with several longitudinal ridges; endopod elongate, almost reaching to base of second outer spine of second exopod segment, with plumose seta located at one third of length and patch of minute denticles on posterior side. Left leg with 3-segmented exopod and 1-segmented endopod; outer spine on first exopod segment reaching slightly beyond outer distal process on second segment; acute process and serrate anterior margin present at base of spine; outer spine on second segment elongate, irregularly curved, reach-

ing almost to tip of terminal elements on third segment; third segment complex, lamellar, bearing 4 elements on posterior side and 1 on anterior side proximally, and 2 spinulose elements distally; endopod unarmed, with patch of minute spinules at outer midlength.

**Gut contents.** The gut of the holotypic female was packed with fragments of small crustaceans and unidentified remains.

**Remarks.** The new cavernicolous species is tinged with reddish brown as is another cave-dwelling species, *Ridgewayia marki marki* (Yeatman 1969). The hyperbenthic species *R. klausruetzleri* Ferrari, 1995 appeared colorless in the water, but reddish in direct sunlight (Ferrari 1995). In contrast, hyperbenthic species such as *R. fosshageni* Humes and Smith, 1974 and *R. boxshalli* were colorless (Humes and Smith 1974; Ohtsuka pers. obs.). Since exclusively stygobiont crustaceans tend to be colorless (Ilfie *et al.* 1984; Fosshagen and Ilfif 1985; Wilkens *et al.* 1986), it is possible that colored cavernicolous species of *Ridgewayia* occur both inside and outside caves. Yeatman (1969) suggested that *R. marki marki* is a stygobiont and sometimes feeds outside caves at night.

The female of *Ridgewayia stygia* appears to have a left seminal receptacle, whereas that of *R. boxshalli* completely lacks seminal receptacles (Barthélémy *et al.* 1998a). Humes and Smith (1974: Fig. 5) illustrated a similar seminal receptacle-like structure on the left ventral side of the female genital double-somite of *R. fosshageni* but did not mention it in the text. In addition, the female of *R. marki marki* is reported to lack it (Barthélémy *et al.* 1998a). Since *R. stygia*, *R. fosshageni*, and *R. marki* belong to the same species-group (see below: Discussion, Comparison), the sac-like structure in the female genital double-somite of *R. stygia* and *R. fosshageni* should be reexamined in detail.

In the family Ridgewayiidae the genera *Placocalanus* and *Brattstromia* have seminal receptacles, whereas *Exumella* and *Exumellina* lack them (Barthélémy *et al.* 1998a). Such variation in the structure of female genital systems within the Ridgewayiidae contrasts with the consistency shown by other families such as the Candaciidae, Centropagidae, Pontellidae, and Temoridae, all of which lack seminal receptacles (Barthélémy *et al.* 1998b). In the family Acartiidae the genus *Acartiella* lacks seminal receptacles while the genus *Acartia* has paired ones (Barthélémy 1999). The loss of seminal receptacles seems to have occurred convergently many times within the Calanoida.

**Etymology.** The new specific name *stygia* (Latin *stygius* meaning infernal) alludes to the cave-dwelling habit of the new species.

## Discussion

### Comparison

The new species from the Palau submarine cave is assigned to the *Ridgewayia marki* species-group, which is currently recorded from the Caribbean region and the Mediterranean (*R. marki marki*; *R. schoemakeri* Wilson, 1958; *R. fosshageni*; *R. klausruetzleri*, and *R. marki minorcaensis*). The species-group can be characterized by the presence of an inner coxal seta on leg 1, 2 outer spines on the second exopod segment of the right male leg 5, and the relatively simple, unarmed endopod of the male left leg 5 (Ummerkutty 1963; Ferrari 1995; Barthélémy *et al.* 1998a; present

study). Another species-group, the *R. gracilis* species-group (*R. gracilis* Wilson, 1958; *R. wilsonae* Fosshagen, 1970), shares the former two characters with the *R. marki* species-group and can be distinguished solely by the last character: the left endopod of male leg 5 with several finger-like extensions. In addition, the linguiform rostrum with a rounded tip and the relatively long caudal rami are also shared by members of this species-group.

The new species is most similar to *Ridgewayia fosshageni*, sharing the following characters with it: (1) the absence of setules on the left ventrolateral side of the female genital double-somite (present in *R. marki marki* and *R. klausruetzleri*); (2) the caudal rami almost entirely covered by minute spinules dorsally and ventrally; (3) the antennules of both sexes reaching beyond the end of the urosome (reaching at most to the genital double-somite in female *R. shoemakeri*); (4) the presence of an elongate, irregularly curved outer spine on the second exopod segment of left leg 5 of the male, which extends beyond the tip of the third segment (short in *R. marki marki*, *R. m. minorcaenesis*, and *R. klausruetzleri*); (5) the first exopod segment of right leg 5 of the male being longer than wide (nearly as long as wide in *R. shoemakeri*). Differences in length of the antennule among the members of the *R. marki* species-group may be related to their habitat: epibenthic or hyperbenthic. A similar variation in relative antennular length has been observed among species of other cavernicolous/benthic calanoid copepods such as *Enantiosis* Barr, 1984 and *Pseudocyclops* Brady, 1872 (Barr and Ohtsuka 1989; Fosshagen pers. comm.).

The new species is readily distinguishable from *R. fosshageni* by: (1) the genital operculum of the female being located near the distal margin of the double-somite (in the middle of the double-somite in *R. fosshageni*); (2) 7 setae on the second endopod of the female leg 5 (6 in *R. fosshageni*); (3) the outer spine of the second exopod segment of female leg 5 reaching at most to the second spine of the third segment (beyond the third spine in *R. fosshageni*); (4) the shape of the left endopod and third exopod segment of male leg 5.

### Zoogeography

The following seven species of the genus *Ridgewayia* are known from the Indo-West Pacific: *R. typica* Thompson and Scott, 1903; *R. canalis* (Gurney, 1927); *Ridgewayia* sp. *sensu* Krishnaswamy (1953) (as *Suezia* sp.); *R. krishnaswamyi* Ummerkutty, 1963; *R. flemingeri* Othman and Greenwood, 1988; *R. boxshalli* and *R. stygia* n. sp. These species, except for the present new species, are assigned to a single group, the *R. typica* species-group, characterized by sharing the following characters: (1) absence of a coxal seta on leg 1; (2) 4 or 5 elements on the right endopod of male leg 5; (3) only a single outer spine on the second exopod segment of right leg 5 of the male (Barthélémy *et al.* 1998a). Interestingly, *R. stygia* from Palau is more similar to the members of North Atlantic/Mediterranean *R. marki* species-group than to the Indo-West Pacific *R. typica* species-group (see above Comparison).

The present finding reconfirms the existence of a faunistic link between the Indo-West Pacific and the North Atlantic/Mediterranean, in particular between the western Central Pacific and Caribbean. The origin of this connection may date back to the Mesozoic (cf. Ekman 1953; Wilson 1958; Nishimura 1981; van der Spoel 1983). Ohtsuka and Reid (1998) discussed the zoogeographical relationships of present zooplankters occurring in both the Indo-West Pacific and the Caribbean region and suggested that there are two possible origins of such taxa, either: (1) as

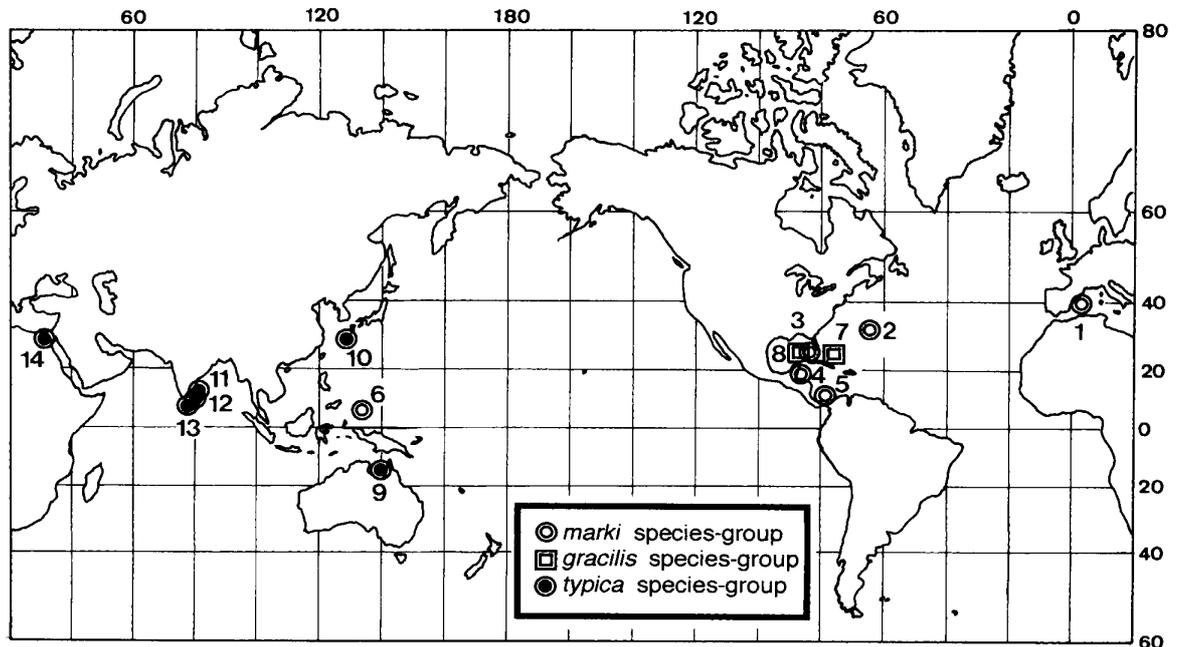


Fig. 5. Distribution of *Ridgewayia* species. 1–6: *R. marki* species-group; 7–8: *R. gracilis* species-group; 9–14: *R. typica* species-group. 1. *R. marki minorcaensis*; 2. *R. marki marki* and *R. sp. sensu* Yeatman (1969); 3. *R. shoemakeri*; 4. *R. klausruetzleri*; 5. *R. fosshageni*; 6. *R. stygia*; 7. *R. wilsonae*; 8. *R. gracilis*; 9. *R. flemingeri*; 10. *R. boxshalli*; 11. *R. sp. sensu* Krishnaswamy (1953); 12. *R. typica*; 13. *R. krishnaswamyi*; 14. *R. canalis*.

Tethyan relicts; or (2) by one-way dispersal of ancestors from the Indo-Malayan region to the western Atlantic via Panama and/or other passages during the Miocene and Pliocene. In some cases these can be distinguished by the following criteria: (1) the number of species in both areas; (2) the presence or absence of species in the eastern North Atlantic; (3) the mode of life (planktonic vs benthic/cavernicolous); (4) the presence or absence of evolutionary novelties in Caribbean taxa (cf. Nishimura 1981; Huys and Boxshall 1991; Jaume and Boxshall 1996; Ohtsuka and Reid 1998; Ohtsuka *et al.* 1998, in press). In *Ridgewayia* the species richness in both areas is not yet determined due to paucity of sampling. *Ridgewayia* is an exclusively hyperbenthic or cavernicolous taxon; although a strict cladistic analysis has not yet been employed to examine relationships among ridgewayiids, it may verify only the monophyly of each of the *R. typica*, *R. marki*, and *R. gracilis* species-groups. Hence *Ridgewayia* can be regarded as a Tethyan relict, clearly exhibiting a full Tethyan track (Fig. 5).

It is important to emphasize that *Ridgewayia stygia* is more closely related to the western North Atlantic/Mediterranean *R. marki* species-group than to the Indo-West Pacific *R. typica* species-group. Understanding this relationship requires a feasible model for the origin and evolutionary history of *Ridgewayia*. Perhaps the origin of the *Ridgewayia* species-groups dates back at least to the Cretaceous, at which time several different biogeographic units had already been established in the Tethys Sea (Kauffman 1973). When the Tethys Sea existed as a circum-tropical current system, a westward dispersal was dominant (van der Spoel 1983). Therefore the Central Pacific fauna may have been influenced strongly by the

Caribbean Province and more weakly by the Mediterranean Province (see Kauffman 1973: Fig. 2). Some supporting evidence comes from stygobiont crustaceans that exhibit an ampho-Atlantic/Eastern Pacific track (Stock 1993). However the present finding seems to suggest that these influences extended out to the Western Pacific including Palau, rather than only to the Eastern and Central Pacific including Hawaii. The following hypothesis is a possible explanation of the present distribution of *Ridgewayia*. The ancestor of *R. stygia* migrated from the Caribbean to the western Central Pacific, whereas that of the *R. typica* species-group was already present in the North Indian Ocean Subprovince. The Japanese-East Asian Subprovince north of the Tethyan Realm, where another species belonging to the *R. typica* species-group (*R. boxshalli*) is found at present, seems to have been more influenced by the North Indian Ocean Subprovince than by the Caribbean Province. The present distribution of the *R. marki* species-group could provide support for the supposed connection between the Caribbean Province and the Western Mediterranean Subprovince during the existence of the Tethyan Sea.

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