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Description and female genital structures of a new species of the demersal calanoid copepod *Ridgewayia* from southern Japan

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(Accepted 26 January 1998)

A new species of the demersal calanoid copepod *Ridgewayia*, *R. boxshalli* n.sp., is described from southern Japan. This is the first record of the genus in Japan. It is distinguishable from other congeners by the antennule and leg 5 of both sexes. In order to identify evolutionary trends, detailed observations were also carried out on the female genital structures using light and scanning electron microscopy for comparison with other calanoids. Their organization is characterized by two egg-laying ducts opening through paired gonopores into a small cavity, the genital atrium, covered by a genital operculum and opening to the outside through a distal atrial slit. No seminal receptacle is present. The unique morphological features and *in situ* feeding habit of *Ridgewayia* are also noted.

KEYWORDS: Copepoda, Calanoida, *Ridgewayia*, demersal, genital structures.

Introduction

Hyperbenthic/epibenthic copepods in Japanese waters have been intensively studied by one of us (S.O.) and his colleagues since 1983. A number of new taxa belonging to the orders Platycopioida, Calanoida and Misophrioida have been discovered. In the Calanoida, the families Arietellidae (Ohtsuka, 1983, 1985; Ohtsuka and Mitsuzumi, 1990; Ohtsuka *et al.*, 1991, 1994), Pseudocyclopidae (Barr and Ohtsuka, 1989), Pseudocyclopiidae (Ohtsuka, 1992), Ridgewayiidae (Ohtsuka *et al.*, 1996), Stephidae (Ohtsuka and Hiromi, 1987) and Tharybidae (Ohtsuka and Nishida, 1997) have hitherto been recorded. Species diversity of hyperbenthic/epibenthic calanoids in shallow Japanese waters is as high as in the Caribbean Sea (Wilson, 1958; Fosshagen, 1968a, b, 1970a, b; Yeatman, 1969; Humes and Smith, 1974; Ferrari, 1995).

This paper presents descriptions of both sexes of a new species of *Ridgewayia* (family Ridgewayiidae) collected at depths of 4–39 m in the Nansei Is., southern Japan. Particular attention is focused on the female genital structures of the genital double-somite, which are greatly diversified in calanoids (Steuer, 1923; Park, 1966; Geptner, 1968; Cuoc *et al.*, 1989; Ohtsuka *et al.*, 1994; Cuoc *et al.*, 1997; Barthélémy

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This paper presents descriptions of both sexes of a new species of *Ridgewayia* (family *Ridgewayiidae*) collected at depths of 4-39 m in the Nansei Is., southern Japan. Particular attention is focused on the female genital structures of the genital double-somite, which are greatly diversified in calanoids (Steuer, 1923; Park, 1966; Geptner, 1968; Cuoc *et al.*, 1989; Ohtsuka *et al.*, 1994; Cuoc *et al.*, 1997; Barthélémy

et al., 1998), but have never been examined in the Ridgewayiidae. The female genital structures of the new species are compared with those of other calanoids.

Material and methods

Copepods were collected off Kakeroma Island, the Nansei Is., Kagoshima Prefecture, southern Japan (28°11.6'N-129°13.7'E, 4–5 m, 9 November 1994) with a hand-net (diameter 30 cm; mesh size 0.1 mm) using SCUBA. The net was towed along the fine sandy bottom. Additional material was gathered off Mage Is., the Nansei Is., Kagoshima Prefecture, southern Japan (30°38.5'N-130°49.0'E, 39 m, 29 May 1997) with a dredge (mouth area 50 cm wide, 15 cm high; mesh size 5 mm). The dredge was towed at *ca* 2 knots for 5 min by the TRV Toyoshio-maru, Hiroshima University. Type specimens are designated from Kakeroma Is. (9/11/1994), and deposited in the Natural History Museum and Institute, Chiba, Japan.

The rostrum, antennule and leg 5 of males and the gut contents of females from Mage Is. (29 May 1997) were examined with scanning electron microscope (Jeol T-20). In addition, gut contents were analysed for two paratypic adults (1♀, 1♂) from Kakeroma Is. and four adults (2♀♀, 2♂♂) from Mage Is. with a differential interference contrast microscope (Nikon Optiphot).

The female genital structures of this new species were studied using light and scanning electron microscopy. For light microscopy, observations were made on semi-thin sections of the genital double-somite of two specimens dehydrated and embedded in Epon. Sections were cut using an LKB UM5 ultramicrotome and stained with Unna Blue. For scanning electron microscopy, external and internal areas were examined respectively on three entire females, and on the isolated urosomes of two other females from off Mage Is. In this last case, after a wide dorsal cut into the genital double-somite, the urosome was treated with 2% sodium hypochlorite in order to eliminate all the soft parts, rinsed in distilled water, and stained in a solution of chlorazol black. All samples for electron microscopy were dehydrated in acetone, critical-point dried, mounted on stubs and coated with gold or gold-palladium. Observations were carried out using a Jeol JSM 35C scanning electron microscope.

Terminology follows Huys and Boxshall (1991)

Family RIDGEWAYIIDAE M. S. Wilson, 1958

Ridgewayia boxshalli n.sp.

(Figures 1–7)

Types. HOLOTYPE: 1♀, dissected and mounted on glass slides, Reg. No. CBM-ZC4501. PARATYPES: 1♀ & 2♂♂, dissected and mounted on glass slides, same locality as holotype, Reg. No. CBM-ZC4502; 3♀♀ & 3♂♂; whole specimens, same locality as holotype, Reg. No. CBM-ZC4503. All types collected at depth of 4–5 m off Kakeroma Is., the Nansei Is., Kagoshima Prefecture, Japan, on 9 November 1994, by S. Ohtsuka.

Other specimens examined. Twenty four females and 18♂♂, collected at a depth of 39 m off Mage Is., the Nansei Is., Kagoshima Prefecture, Japan, on 29 May 1997, by S. Ohtsuka.

Body length. Type specimens from Kakeroma Is.: female: range = 0.71–0.77 mm (mean \pm s.d. = 0.74 ± 0.02 mm, $n=5$); male: 0.67–0.74 mm (0.71 ± 0.03 mm, $n=5$). Specimens from Mage Is.: female: 0.80–0.91 mm (0.86 ± 0.03 mm, $n=15$); male: 0.77–0.85 mm (0.82 ± 0.02 mm, $n=18$).

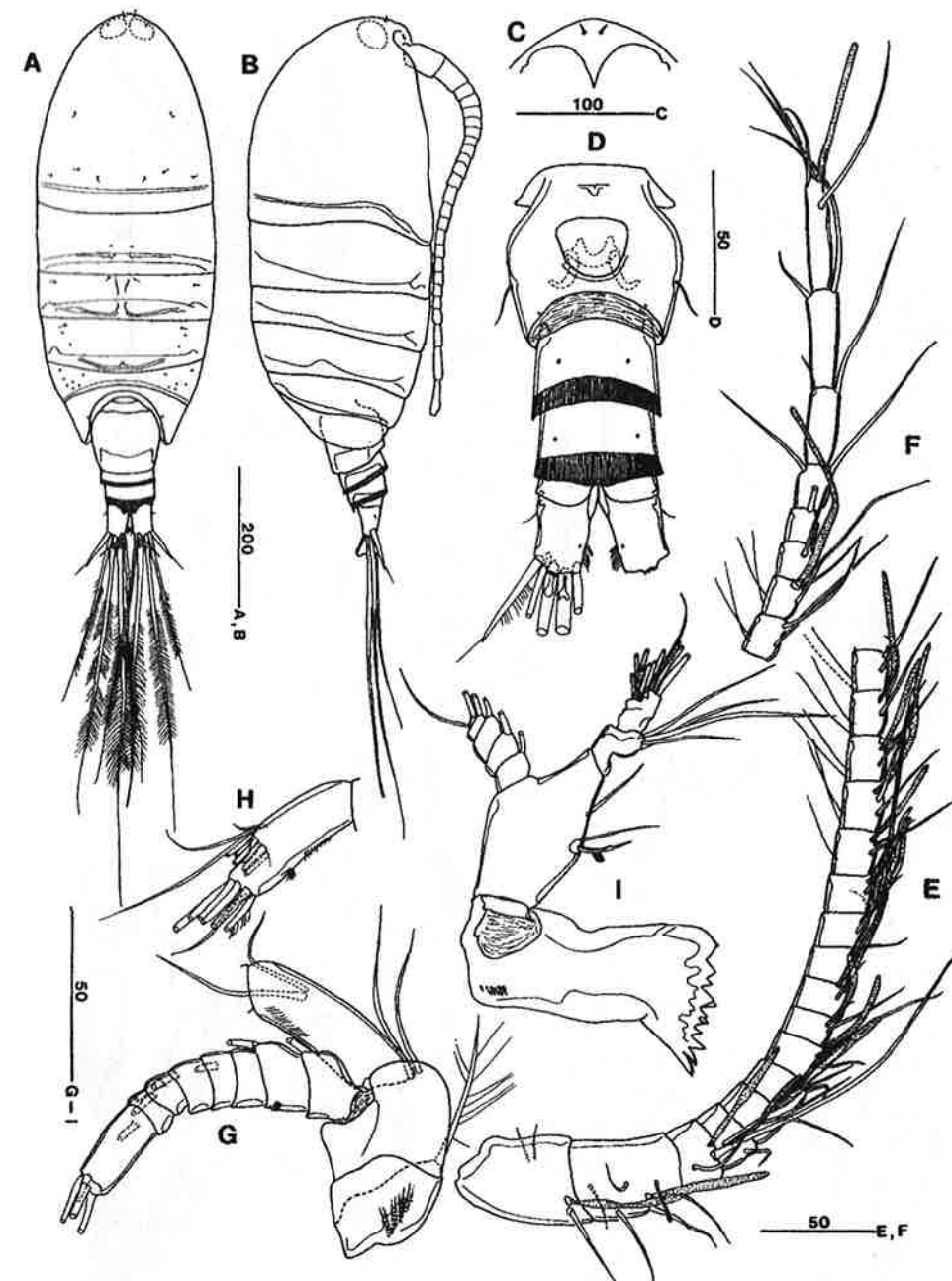


FIG. 1. *Ridgewayia boxshalli* n.sp., female (holotype): (A) habitus, dorsal; (B) habitus, lateral; (C) rostrum; (D) urosome, ventral; (E) antennule, segments 1–17 (I–XIX); (F) antennule, segments 18–25 (XX–XXVIII); (G) antenna, distal endopod segment omitted; (H) distal segment of antennary endopod; (I) mandible. Scale bars in μ m.

Description

Female (holotype). Body (figure 1A, B) robust, 0.75 mm long. Cephalosome distinctly separate from first pedigerous somite. Naupliar eye present. Rostrum

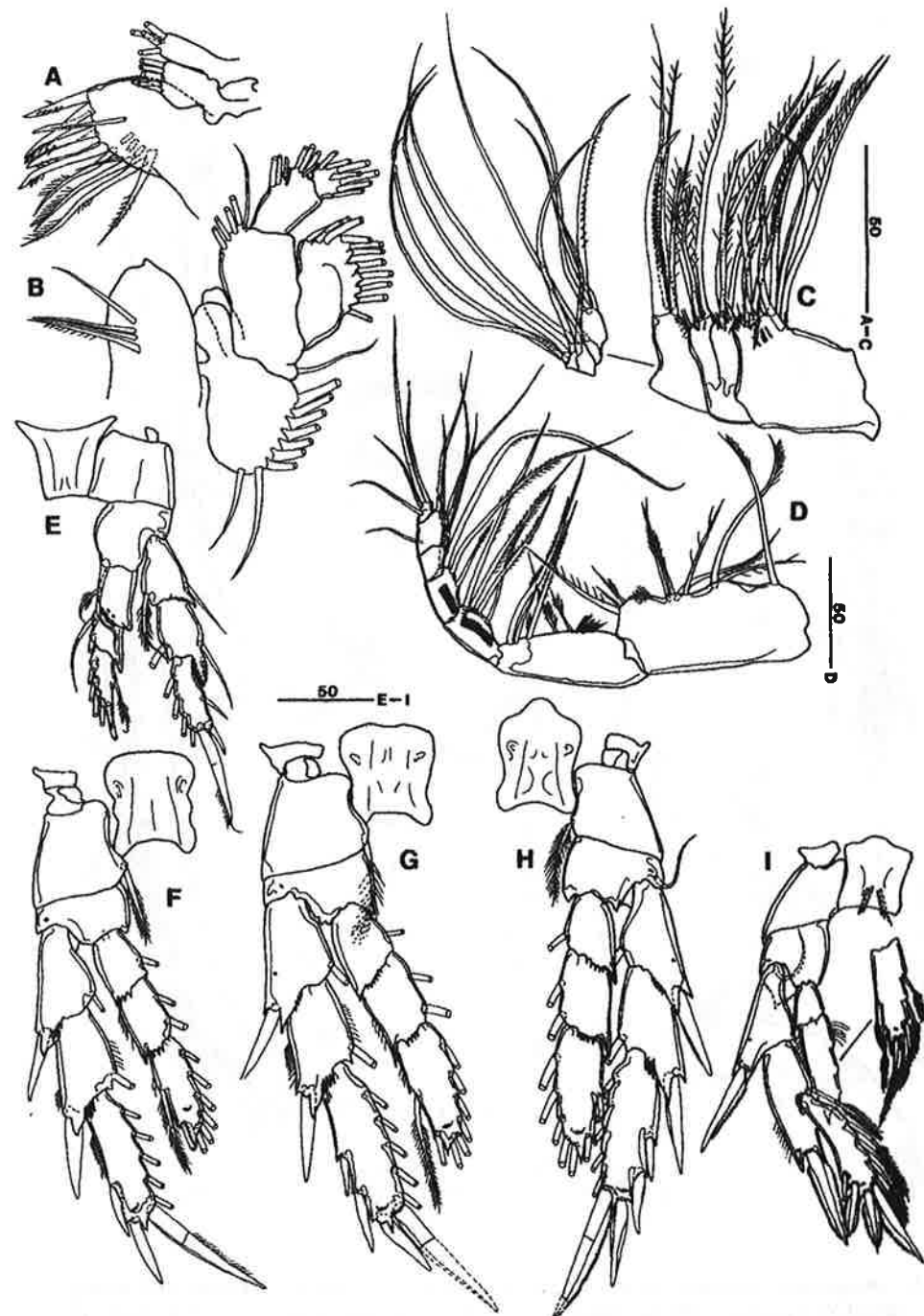


FIG. 2. *Ridgewayia boxshalli* n.sp., female (holotype): (A) praecoxal, coxal and basal endites of maxillule; (B) maxillule, parts of setae omitted; (C) maxilla; (D) maxilliped; (E) leg 1, anterior; (F) leg 2, anterior; (G) leg 3, anterior; (H) leg 4, anterior; (I) leg 5, anterior. Scale bars in μm .

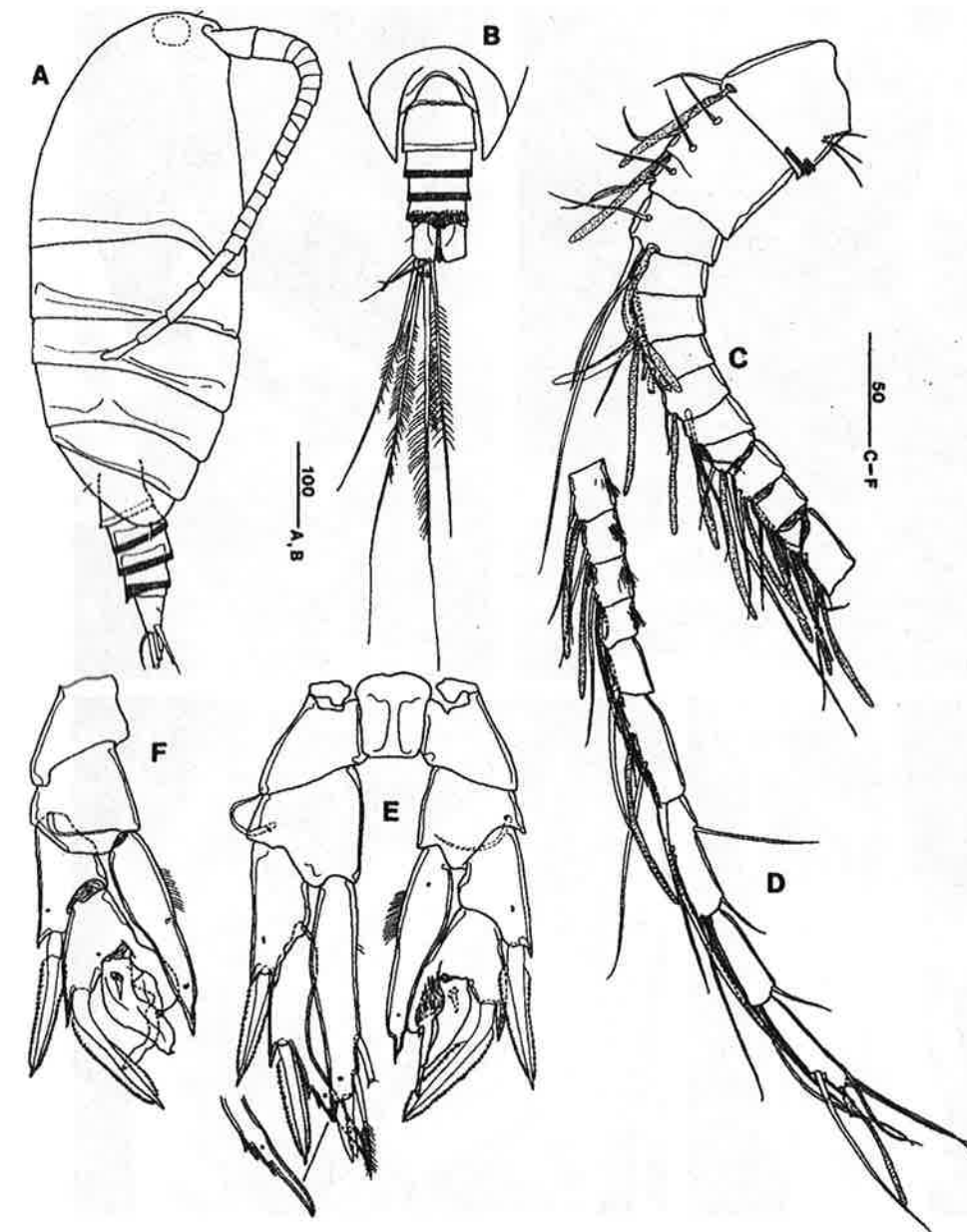


FIG. 3. *Ridgewayia boxshalli* n.sp., male (paratypes): (A) habitus, lateral; (B) prosomal end and urosome, dorsal; (C) antennule, segments 1-13 (I-XV); (D) antennule, segments 14-22 (XVI-XXVIII); (E) leg 5, anterior; (F) left leg 5, posterior. Scale bars in μm .

(figures 1C, 4A) sharply pointed without filament. Fourth and fifth pedigerous somites separate. Fifth pedigerous somite symmetrical, produced posteriorly into round lobe on each side reaching half of genital double-somite. Urosome (figure 1D) four-segmented; genital double-somite swollen midlaterally, bearing pair of long hair-sensilla ventrolaterally. Genital operculum located ventromedially (see

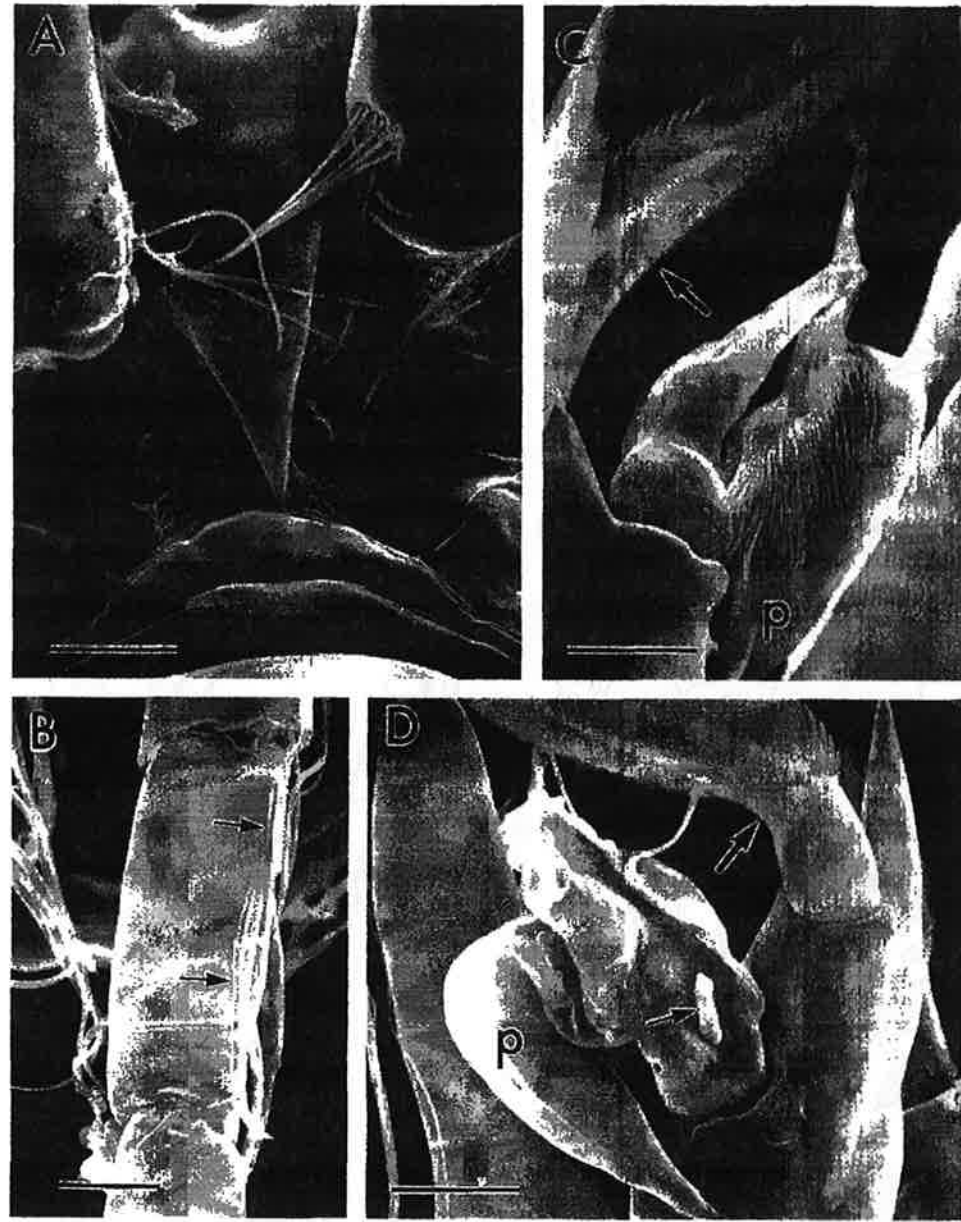


FIG. 4. SEM photomicrographs of *Ridgewayia boxshalli* n.sp., males: (A) rostrum; (B) nineteenth segment (ancestral segments XXI–XXIII) of right antennule, anterior process arrowed; (C) third exopod segment of left leg 5, anterior, (p) inner distal process on second exopod segment, inward curved spine of second exopod segment arrowed; (D) second and third segments of left leg 5, posterior, (p) inner distal process on second exopod segment, inward curved spine of second exopod segment indicated by large arrow, posterior spine of third exopod segment by small arrow. Scale bars = 10 μ m.

description of female genital structures); second and third urosomal somites flanged with minute spinules along posterior margin; third urosomal somite produced dorso-medially into bifurcate tip covering anal somite; anal somite almost telescoped into

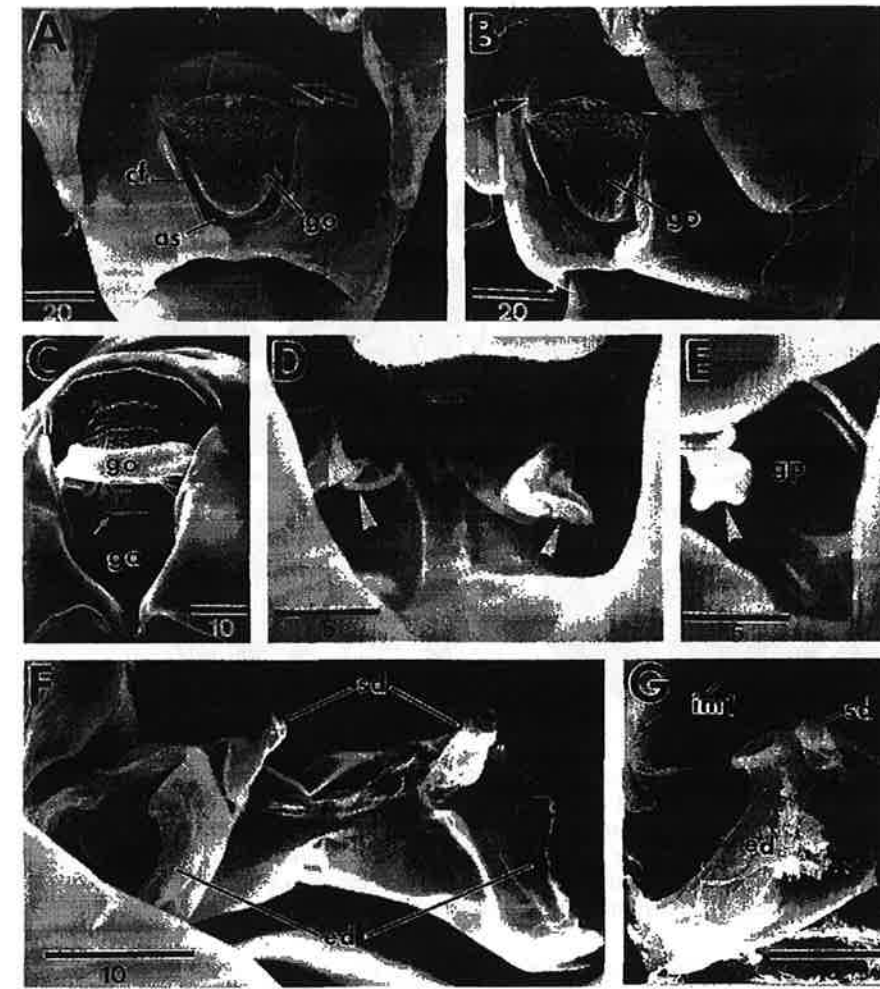


FIG. 5. SEM photomicrographs of *Ridgewayia boxshalli* n.sp., non-inseminated females: (A–E) external ventral views; (A–B) genital double-somite, ventral and left lateral view respectively; (C) detail of the genital area. Note the cuticular field (white arrow) under the operculum (go) and the genital atrium (ga); (D–E) details of the wall of the genital atrium showing two cuticular expansions (D, E, white arrowheads) and the left gonoporal plate (E, gp); (F–G) internal dorsal views; (F) genital area, egg-laying ducts (ed) and shell ducts (sd); (G) detail of the left egg-laying duct. as, atrial slit; cf, cuticular fold; im1, zone of insertion of the left opercular muscle. Scale bars in μ m.

preceding somite. Caudal rami symmetrical, seta I minute, located at anterior third, seta II spiniform with fine setule subterminally, seta III–VI plumose, seta VII located posterodorsally.

Antennule (figure 1E, F) nearly reaching end of prosome, 25-segmented. Fusion pattern and armature as follows: I-1 (seta) + ac (aesthetasc), II-IV-6 + ac, V-2 + ac, VI-2 + ac, VII-2 + ac, VIII-2 + ac, IX-2 + ac, X-2 + ac, XI-2 + ac, XII-2 + ac, XIII-2 + ac, XIV-2 + ac, XV-2 + ac, XVI-2 + ac, XVII-2 + ac, XVIII-2 + ac, XIX-2, XX-2 + ac, XXI-2 + ac; XXII-1, XXIII-1, XXIV-1 + 1, XXV-1 + 1, XXVI-1 + 1,

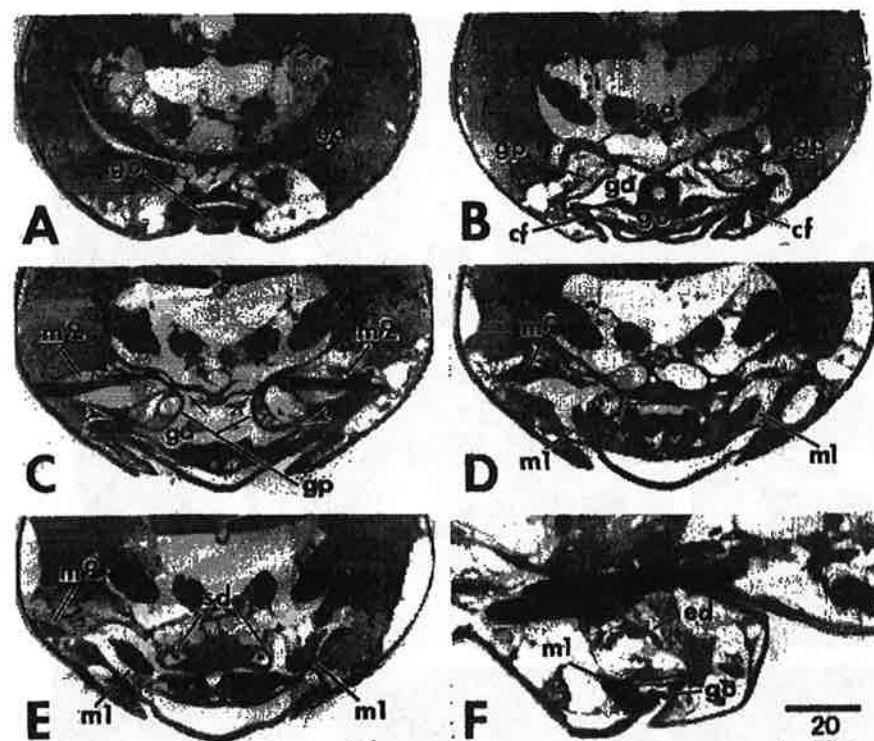


FIG. 6. *Ridgewayia boxshalli* n.sp., females. Photomicrographs of transverse and longitudinal sections through the genital double-somite: (A-E) serial transverse section (section A posteriormost, E anteriormost); (F) longitudinal section. Note the insertion of the genital operculum (go) under the cuticular fold (cf) (A, B), the presence of the opercular (m1) and egg-laying duct muscles (m2) (C-F) and the gonoporal slits (C, arrows) of the roof of the genital atrium. Abbreviations as for figure 5. Scale bar in μm .

XXVII-XXVIII-5+ae. Thirteenth (XV) to 19th (XXI) each bearing 1 or 2 long setules along posterior margin.

Antenna (figure 1G, H) with one plumose seta on coxa; basis bearing two setae of almost equal length; exopod indistinctly eight-segmented, setal formula 1,1,1,1,1,1,1,4; endopod two-segmented, first segment bearing two subterminal setae, second segment with nine middle and seven terminal setae. Mandible (figure 1I) with gnathobase bearing eight teeth, two dorsalmost of which sharply pointed, and a tuft of minute spinules near base of palp; basis bearing four inner setae, proximal of which thicker than others and plumose, protruded at inner distal corner; exopod five-segmented, setal formula 1,1,1,1,2; endopod two-segmented, first segment with four distal inner setae, second segment bearing 11 setae.

Maxillule (figure 2A, B) well-developed; praecoxal arthrite bearing six spiniform, two slender, three spinulose (figure 2A) and four posterior (figure 2B) setae; coxa with nine setae on epipodite, two proximal of which shorter than others, and five setae on endite; basis with one short seta on exite, four setae on first endite and five setae on second endite; exopod unisegmented, bearing 11 setae along outer margin; endopod two-segmented, setal formula 4+4,7. Maxilla (figure 2C) compact; first praecoxal endite bearing five spinulose and one short spiniform setae; second praecoxal and two coxal endites each with three spinulose setae; basis with one heavily

distally into outer blunt process; second and third endopod segments sharply pointed at outer distal corner. Legs 2-4 (figure 2F-H) similar, but basal seta present only in leg 4; third exopod segment carrying two outer spines in leg 2 and 3 in legs 3 and 4; first and second exopod and endopod segments serrated along distal margin. Leg 5 (figure 2I) with intercoxal sclerite bearing pair of setular rows on posterior surface; first exopod segment produced at outer distal corner; outer spine on second exopod segment reaching beyond third segment; third exopod segment narrow basally, arising from middle portion of preceding segment; first endopod segment unarmed.

Male (2 dissected paratypes). Body (figure 3A) as in female, 0.72 and 0.74 mm in length. Urosome (figure 3B) five-segmented; genital to anal somites flanged distally with minute spinules.

Right antennule (figure 3C, D) 22-segmented, weakly geniculate; fusion pattern and armature as follows; I-1+ae, II-IV-6+ae, 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-1, XX-1+process, XXI-XXIII-2+ae+2 processes (see figure 4B), XXIV-XXV-2+2+ae, XXVI-1+1, XXVII-XXVIII-5+ae. First segment (I) with spinular rows and slender, long setules posteriorly; 9th (XI) and 12th segments (XIV) constricted posteriorly; 14th (XVI) to 17th (XIX) segments bearing tuft of fine setules posteriorly.

Leg 5 (figure 3E, F) considerably modified; intercoxal sclerite without setular rows as in female; coxa unarmed; basis with outer seta on posterior surface. Right leg (figure 3E) with two-segmented exopod and one-segmented endopod; first exopod segment with outer spine reaching beyond base of proximal spine of third exopod segment; second exopod segment curved inward, tapering distally into pointed process, bearing one spine and three minute prominences along outer margin; endopod elongate, bearing two terminal spines which incompletely fused to segment at base, and two plumose subterminal setae. Left leg (figure 3E, F) with three-segmented exopod and one-segmented endopod; first exopod segment bearing large outer spine reaching beyond distal tip of endopod; second exopod segment with outer spine curved inward and inner process, distal end of which bearing spiniform process reaching beyond tip of third exopod segment, partially covering the third exopod segment (figure 4C); third exopod segment complicated, tapering distally, lamelliform, with short spine and membranous process proximally on posterior surface (figure 4D); endopod tapering distally, bearing row of fine setules medially.

Variation

The body lengths of both sexes are smaller in the type specimens from Kakeroma Is. (9 November 1994) than in the other specimens from Mage Is. (29 May 1997). No remarkable differences were, however, found between the specimens from both localities. The absence of a coxal seta on leg 1 is confirmed in all the dissected specimens from both Kakeroma and Mage Is.

The spiniform process at the distal end of the second exopod segment of the male left leg 5 was straight in a paratype (figure 3E) but curved outward in another paratype (figure 3F). This spiniform process was straight in two dissected adult males from Mage Is.

Female genital structures

External area. The genital area is located medioventrally, on the posterior part of the genital double-somite (figures 1D, 5A, B). It is trapezoidal with a strong



FIG. 7. *Ridgewayia boxshalli* n.sp., females: (A, B) photomicrographs of gut contents, crustacean spine; (c) diatom fragments (d). Scale bars = 10 μ m.

sclerotized spiniform and three spinulose setae; endopod indistinctly four-segmented, setal formula 3,2,2,3. Maxilliped (figure 2D) with coalescent praecoxa and coxa; first to fourth syncoxal endites bearing one, two, four and three setae, respectively; basis with three setae; first endopod segment incorporated into basis, with two setae; second to sixth endopod segments carrying 4,4,3,3+1 and four setae, respectively; second and third endopod segments each with spinular row, second segment bearing round process with minute prominences near base of setae.

Legs 1–5 with three-segmented rami except for the two-segmented endopod of leg 5. Seta and spine formula of legs 1–5 shown in table 1. Leg 1 (figure 2E) with unarmed coxa; basis bearing curved inner seta (see Grooming organs on maxilliped and leg 1 discussed below); second exopod segment produced distally into outer serrate process; first endopod segment bearing minute spinules distally, protruded

Table 1. Seta and spine formulae of legs 1–5 of female of *Ridgewayia boxshalli* n.sp. Roman and Arabic numerals indicate spines and setae respectively.

	coxa	basis	exopod			endopod		
			1	2	3	1	2	3
Leg 1	0-0	0-1	I-1; I-1;	II,1,4	0-1; 0-2;	1,2,3		
Leg 2	0-1	0-0	I-1; I-1;	II,1,5	0-1; 0-2;	2,2,4		
Leg 3	0-1	0-0	I-1; I-1;	III,1,5	0-1; 0-2;	2,2,4		
Leg 4	0-1	I-0	I-1; I-1;	III,1,5	0-1; 0-2;	2,2,3		
Leg 5	0-0	I-0	I-0; I-1;	III,1,4	0-0; 2,2,3			

anterior pad (arrow in figure 5A,B) and is covered by a genital operculum (go in figure 5A, B) presenting on its internal face an important cuticular rectangular field (figure 5C; white arrow). The operculum is free laterally and posteriorly and covers a cavity, the genital atrium, opening to the outside by an atrial slit (as in figure 5A). The lateral edges of the operculum, thinner than the median part, are inserted under the cuticular fold (cf in figure 5A) delimiting the genital area (figures 5A, 6A–B). On the roof of the atrium, two cuticular expansions (arrowheads) are clearly visible (figures 5D, E). On both sides of these expansions are situated the gonoporal plates (gp) which form the lateral walls of the genital atrium (figures 5E, 6B, C). In this proximal part, the genital atrium tends to form two narrow lateral extensions (figure 6C; arrowheads).

Internal area. In dorsal internal view, two cuticular egg-laying ducts (ed) are present in the median part of the area (figures 5F, G). Each duct is closed, and forms a gutter, the double wall of which delimits a narrow space corresponding to the gonoporal slit of the roof of the genital atrium (figure 6C; arrows). Proximally, this double wall indicates the insertion zone of the thin oviductary epithelium. Lastly, two tubular excrescences are connected to the anterior part of the egg-laying ducts. Semi-thin sections show that these excrescences probably correspond to the two shell ducts (sd in figure 6E) and that each egg-laying duct is provided with a strong muscle (m2) arising lateroventrally in the body (figure 6C). Two other muscles inserted at level of the hinge of the genital operculum (m1) are also present (figure 6D–F). The insertion zone (im1) of these opercular muscles is clearly visible in SEM observations (figure 5G).

Etymology

The specific name of the new species is named in honour of Dr Geoffrey A. Boxshall (The Natural History Museum, London).

Discussion

Relationships

At present the genus *Ridgewayia* accommodates only nine nominal and two as yet undescribed species: *R. typica* Thompson and Scott, 1903 (♀♂), *R. canalis* (Gurney, 1927) (♂), *R. krishnaswamyi* Ummerkutty, 1963 (♀♂), and *R. sp.* sensu Krishnaswamy, 1953 (♂) from the Indian Ocean; *R. flemingeri* Othman and Greenwood, 1988 (♂) and *R. boxshalli* n.sp. (♀♂) from the Pacific Ocean; *R. marki* (Esterly, 1911) (♀♂), *R. gracilis* Wilson, 1958 (♀♂), *R. wilsonae* (as *R. wilsoni*) Fosshagen, 1970 (♀♂), *R. fosshageni* Humes and Smith, 1974 (♀♂), *R. klausruetzleri* Ferrari, 1995 (♀♂), and *R. sp.* sensu Wilson (♂), 1958 from the Atlantic Ocean. Ummerkutty (1963) divided the genus into three morphologically different groups: *R. typica*, *R. krishnaswamyi* and the American species (*R. marki*, *R. gracilis*, *R. shoemakeri*). However, five nominal species (three from the Atlantic and two from the Pacific) have been added to the genus since Ummerkutty (1963) discussed the three groups, which led us to reconsider the relationships between the congeners. Three distinct species groups can be newly recognized: an Indo-West Pacific species group (= *typica* species group) and two western Atlantic species groups (= *marki* and *gracilis* species groups) (Ferrari, 1995). These species groups are readily distinguishable by the structures of the first leg and male leg 5. The *typica* species group is characterized by the absence of an inner coxal seta of leg 1, and 4–5 terminal and

subterminal elements on the endopod and only a single outer spine on the second exopod segment of the right male leg 5. The *marki* and *gracilis* species groups share the presence of an inner coxal seta of leg 1, and 2 outer spines on the second exopod segment of the right male leg 5. In addition the American species groups can be distinguished by the morphology of the left endopod of the male leg 5 (Ferrari, 1995).

However the following features are convergently found in these groups: (1) fusions of antennular segments in both sexes; (2) fusion of coxae and intercoxal sclerite in male leg 5. Ancestral segments II–III and IV of the female antennule are separate in *R. fosshageni*, *R. gracilis*, and *R. klausruetzleri* of the *marki* species group, *R. wilsonae* of the *gracilis* species group, and *R. krishnaswamyi* of the *typica* species group, but fused in *R. boxshalli* and *R. typica* of the *typica* species group. Ancestral segments XXIV and XXV of the male right antennule are separate in *R. fosshageni*, *R. klausruetzleri*, *R. marki* and *R. shoemakeri* of the *marki* species group, but fused in *R. boxshalli*, *R. canalis*, *R. krishnaswamyi*, *R. typica* and probably *R. flemingeri* of the *typica* species group, and *R. gracilis* and *R. wilsonae* in the *gracilis* species group. Fusion patterns of ancestral segments II–III and IV of the left male antennule are perhaps the same as in the female antennules. Fusion of coxae and intercoxal sclerite of the male leg 5 is found in *R. fosshageni*, *R. gracilis*, *R. klausruetzleri*, *R. marki*, and *R. shoemakeri* of the *marki* species group and *R. wilsonae* of the *gracilis* species group, and *R. flemingeri* of the *typica* species group.

The present new species apparently belongs to the *typica* species group, and is most closely related to the Australian species, *R. flemingeri* in bearing the inward curved spine on the second exopod segment of the male left leg 5. It, however, differs from *R. flemingeri* in the male leg 5; (1) the right endopod of the male leg 5 bearing two inner setae in *R. boxshalli* but three in *R. flemingeri*; (2) the left endopod slender and reaching almost the tip of the terminal exopod segment in *R. boxshalli*, but conical, reaching the middle of the terminal exopod segment in *R. flemingeri*; (3) the structure of the terminal exopod segment of the left leg 5.

Morphology

Grooming organs on maxilliped and leg 1. In the family Ridgewayiidae an organ called 'von Vaupel Klein organ' on leg 1, which consists of a curved, inner basal seta and an outer tubercle with spinules on the endopod (Ferrari and Steinberg, 1993), is found in the genera *Ridgewayia*, *Exumella* (Fosshagen, 1970) and *Brattstromia* (Fosshagen and Iliffe, 1991). According to von Vaupel Klein (1972), this organ is assumed to play a role in grooming. This hypothesis is strongly supported by a high-speed cinematographic observation of feeding modes of the pelagic calanoid genus *Eucalanus*, which also bears such an organ on leg 1 (Giesbrecht, 1892, plate 11), by Price *et al.* (1983): the antennules are drawn across the maxillipeds at the bend created by the proximal joint. Perhaps the organ on leg 1 groom antennules together with maxillipeds because the syncoxa and basis of maxillipeds bear a structure resembling that on leg 1: curved setae and tuft of minute spinules at the distal corner of the syncoxa, and one or more spinular rows along the inner margin of the basis (e.g. Nishida and Ohtsuka, 1997, figure 1D). The maxilliped spinular rows are present usually on the basis, but exceptionally on the second and third endopod segments in *Ridgewayia boxshalli* or on the third and fourth endopod segments in *R. flemingeri*.

Unique adhesive organ of leg 1. The large serrate process on the distal outer corner of the second exopod segment of leg 1 is found in both sexes of *R. boxshalli*.

This process seems to be unique to the genus. Although its functions are unknown, it may be a prehensile organ to cling to substrata such as algae and associated animals because marginal prominences of the process are posteriorly directed to be useful for attachment. Unfortunately such a resting behaviour had not been observed in the laboratory (Humes and Smith, 1974). A variety of modifications of leg 1 is found in demersal calanoid copepods. Demersal/cavernicolous calanoid copepods such as *Pseudocyclops* (family Pseudocyclopidae) and *Boholina* (family Boholinidae) bear a similar process on the counterpart of *Ridgewayia* (Nicholls, 1944; Tanaka, 1966; Barr and Ohtsuka, 1989; Fosshagen and Iliffe, 1989). As an additional example, some species of *Placocalanus* (family Ridgewayiidae) bear a large hook-like process on the basis (Fosshagen, 1970b; Ohtsuka *et al.*, 1996). These structures may be adaptations for their benthic life as in benthic harpacticoid copepods. This is supported by a fact that pelagic harpacticoids, such as *Clytemnestra*, *Euterpina*, *Macrosetella* and *Microsetella*, usually bear legs 1 suitable only for swimming while many benthic harpacticoids have legs 1 specialized for feeding and grasping (cf. Boxshall, 1979; Huys and Boxshall, 1991; Huys and Böttger-Schnack, 1994; Huys *et al.*, 1996).

Female genital structures. In *Ridgewayia boxshalli* female genital structures are similar to those observed (unpublished results) in *R. marki*, *Exumella mediterranea*, *Exumellina bucculenta* a new monospecific genus (Fosshagen and Iliffe, in press), and in several centropagoids (Cuoc *et al.*, 1989; Barthélémy *et al.*, 1998). Indeed all these calanoids present a well delimited genital area and are devoid of a seminal receptacle. The only appreciable difference in *R. boxshalli* is the more proximal junctions of the shell ducts with the egg-laying ducts. Therefore, it contrasts with the other Ridgewayiidae, *Placocalanus* and *Brattstromia*, in which the presence of seminal receptacles has been mentioned (Fosshagen and Iliffe, 1991; Ohtsuka *et al.*, 1996) in accord with a genital organization reminiscent of other operculated calanoids, Calanidae or Aetideidae for example (unpublished results).

This organization of genital structures in *R. boxshalli* differs from that in some families, such as the Boholinidae, Hyperbionychidae, Arietellidae and Metridinidae (Ohtsuka *et al.*, 1993, 1994; Cuoc *et al.*, 1997), except for the egg-laying ducts. In these families, there is neither a single operculum nor a genital atrium but the seminal receptacles are both connected with the gonopores and the copulatory pores. This pattern represents a state near that of the hypothetical ancestral calanoid proposed by Huys and Boxshall (1991).

Functionally, the opening mechanism of the egg-laying ducts is the same as described in all other calanoids studied up to now (Cuoc *et al.*, 1989; Cuoc *et al.*, 1997; Barthélémy *et al.*, 1998). *R. boxshalli* must be considered as similar to most of the Centropagoidea (Cuoc *et al.*, 1989; Barthélémy *et al.*, 1998) concerning the function of the genital atrium, which serves as a storage site for the seminal products discharged from the spermatophore during insemination and fulfills the role of seminal receptacle. The deposition of seminal products is probably facilitated by the raising of the operculum by the contraction of the opercular muscles. The two cuticular expansions of the roof of the genital atrium may serve as anchorage-points for the seminal products. The oocytes are fertilized in the atrial cavity when they come into contact with the seminal products. The process of fertilization differs from that observed in the Metridinidae (Cuoc *et al.*, 1997) in which only the necessary fraction of seminal products stored in the receptacles fertilizes the oocytes simultaneously liberated.

The morphology of the genital area suggests that a copulation is necessary before each egg clutch in order to replace the spermatozoa store of the atrium, as reported in marine species such as *Temora stylifera* (Ianora et al., 1989) and *Centropages typicus* (Ianora et al., 1992).

Ecology

Distribution. The distribution of *Ridgewayia* is restricted to the tropical and subtropical shallow waters in the Indo-West Pacific and western Atlantic Oceans (Wilson, 1958). *Placocalanus*, belonging to the same family Ridgewayiidae, also shows a similar distribution pattern although it is not yet discovered in the Indian Ocean (Ohtsuka et al., 1996). Within the Calanoida, association with cnidarians is known only in *Ridgewayia* (Humes and Smith, 1974; Huys and Boxshall, 1991). Swarming behaviour has also been reported from *Ridgewayia* (Ferrari, 1995) but was not observed for *R. boxshalli* during SCUBA diving off Kakeroma Is., where the type specimens were collected. The long antennules of the new species, relatively rare in hyperbenthic calanoids (Bowman and González, 1961), indicate that it is hyperbenthic rather than epibenthic. *Ridgewayia* species, such as *R. marki* also occur in marine caves (Esterly, 1911; Yeatman, 1969) as do other genera in the Ridgewayiidae, such as *Exumella* and *Brattstromia* (Fosshagen and Iliffe, 1991; Jaume and Boxshall, 1995).

In situ feeding habit. The feeding habits of *Ridgewayia* were little known. Its mouthparts, in particular the maxilla and maxilliped, indicate that it is basically a particle feeder. In the guts of *R. boxshalli* a wide variety of pennate and centric diatom fragments (figure 7A, B), small crustacean fragments (figure 7A), amorphous matter and unidentified particles were found, indicative of its particle-feeding habits. The guts of all six specimens from Kakeroma and Mage Is. were packed with pennate diatom fragments, suggesting that *R. boxshalli* usually feeds on epibenthic diatoms. Epibenthic diatoms are an important food also for some hyperbenthic/epibenthic calanoid copepods such as *Pseudocyclops* (Ohtsuka, 1992), *Pseudocyclops* (Fosshagen, 1968a) and *Stephos* (Ohtsuka and Hirno, 1987).

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