

New records of *Halgerda* Bergh, 1880 (Opisthobranchia, Nudibranchia) from the deep western Pacific Ocean, with descriptions of four new species

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ABSTRACT

Four new species of *Halgerda* from the deep western Pacific Ocean are described. *Halgerda fibra* n. sp. was found in the Philippines at depths near 90 m and is also recorded from the New Caledonia region in 90-400 m. The new species differs from other *Halgerda* in its reproductive morphology. The ampulla is larger and more coiled than other *Halgerda* and the vagina is also much larger and more bulbous than other members of the genus. *Halgerda abyssicola* n. sp. was found near Vanuatu at depths of 207-280 m and from the Coral Sea in 385-420 m. Its reproductive morphology is unusual for a species of *Halgerda* in that the penis and vagina are both extremely large and bulbous. *Halgerda azteca* n. sp. was found near Norfolk Ridge, south of New Caledonia at depths from 230-367 m. Its reproductive morphology differs from other *Halgerda* species primarily due to its long, coiled ejaculatory duct and prominent vaginal sphincter. *Halgerda orstomi* n. sp. was found near Vanuatu at depths between 160-251 m; from the Philippines at 92-95 m and from New Caledonia at 120 m. *Halgerda orstomi* has an unusual vaginal sphincter and bulbous vagina which distinguishes it from other *Halgerda* species. The ranges and depths of three additional, previously described *Halgerda* species: *H. brunneomaculata* Carlson & Hoff, 1993, *H. carlsoni* Rudman, 1978 and *H. dalanghita* Fahey & Gosliner, 1999 are also extended.

KEY WORDS

Nudibranch,
Mollusca,
Halgerda,
new species,
Indo-Pacific,
deep-sea.

RÉSUMÉ

Nouvelles données sur le genre Halgerda Bergh, 1880 (Opisthobranchia, Nudibranchia) dans les eaux profondes du Pacifique occidental, et descriptions de quatre espèces nouvelles.

Quatre nouvelles espèces d'*Halgerda* sont décrites du Pacifique occidental, à des profondeurs supérieures à celles connues jusqu'ici pour ce genre récifal et sublittoral. *Halgerda fibra* n. sp., découverte aux Philippines à 90 m de profondeur et dans la région néo-calédonienne de 90 à 400 m, se distingue des autres espèces du genre par la morphologie de son appareil génital : son ampoule hermaphrodite est plus grande et plus entortillée et son vagin est également plus grand et plus bulbeux que chez les autres espèces d'*Halgerda*. *Halgerda abyssicola* n. sp. a été récoltée au Vanuatu par 207-280 m et en mer du Corail par 385-420 m. Sa morphologie génitale est remarquable par le développement inhabituel à la fois du pénis et du vagin, tous les deux particulièrement grands et bulbeux. Celle d'*Halgerda azteca* n. sp., récoltée sur la Ride de Norfolk au Sud de la Nouvelle-Calédonie par 230-367 m, diffère essentiellement par le canal déférent long et entortillé et le sphincter vaginal prononcé. Enfin, *Halgerda orstomi* n. sp. a un sphincter vaginal inhabituel et un vagin bulbeux qui la distinguent de ses congénères ; elle a été récoltée au Vanuatu par 160-251 m, aux Philippines par 92-95 m et en Nouvelle-Calédonie à 120 m de profondeur. De nouvelles données étendent les répartitions géographiques et bathymétriques connues de trois autres espèces déjà décrites : *Halgerda brunneomaculata* Carlson & Hoff, 1993, *H. carlsoni* Rudman, 1978 et *H. dalanghita* Fahey & Gosliner, 1999.

MOTS CLÉS

Nudibranchia,
Mollusca,
Halgerda,
nouvelles espèces,
Indo-Pacifique,
océan profond.

INTRODUCTION

Recent work by Fahey & Gosliner (1999b) reviews the genus *Halgerda* from the tropical Indo-Pacific. That paper examined the phylogenetic relationships among *Halgerda*. Collections of nudibranchs from the deep western Pacific Ocean have produced specimens of four undescribed species, and new records for three previously named taxa. This paper describes the morphology of all these taxa and adds new biogeographical data regarding the genus *Halgerda*. The range and depths of the three previously recorded species are extended beyond that which was described by the original and subsequent authors.

ABBREVIATIONS

CP beam trawl;
DW Waren dredge.

MATERIALS

The present study is based on material from two collections: material deposited in the collections of the Muséum national d'Histoire naturelle (MNHN), Paris, and material deposited in the collections of the California Academy of Sciences, Invertebrate Zoology (CASIZ), San Francisco. The materials at MNHN were collected from MUSORSTOM cruises (the joint expeditions by the Muséum national d'Histoire naturelle, Paris, and the Institut de Recherche pour le Développement). Photos are of specimens collected during the particular campaign specified in each species description.

Materials deposited at CASIZ were collected at various locations in the western Pacific including Okinawa, Philippines, Papua New Guinea, Fiji, Tonga and Indonesia.

SYSTEMATICS

Family HALGERDIDAE Odhner, 1926

REMARKS

The family name Halgerdidae was introduced by Odhner (1926) for *Halgerda* and Asteronotidae was introduced by Thiele (1931) for *Asteronotus*. Odhner in Franc (1968) suggested that both family names are synonymous and included the genera *Aphelodoris*, *Halgerda*, *Sclerodoris* and *Asteronotus*. He employed Asteronotidae for the family despite the fact that Halgerdidae was used earlier and has priority. Others (Willan & Coleman 1984; Wells & Bryce 1993; Rudman 1998) have united most of the cryptobranch dorids into the single family Dorididae with or without employing a series of subfamilies. This approach unites more than 60 genera into a single unwieldy family which does not reflect phylogenetic relationships. Since Halgerdidae is the oldest available name we place *Halgerda* in Halgerdidae pending a more complete phylogenetic analysis (Gosliner & Fahey 1998).

Genus *Halgerda* Bergh, 1880

TYPE SPECIES. — By monotypy: *Halgerda formosa* Bergh, 1880.

REMARKS

Gosliner & Fahey (1998) provide a list of characters thought to be consistent within the genus *Halgerda*. This list was compiled from existing literature (Rudman 1978; Carlson & Hoff 1993; Willan & Brodie 1989) and from examination by the authors of specimens of *Halgerda*. The list included the following characters: a smooth, gelatinous, yet firm body, a large gill that is sparsely pinnate, the openings to the rhinophore and gill pockets are smooth, the radular sac is elongate and curved, and the rhinophoral stalks are long relative to the club. Since the 1998 publication, additional work by the authors and by other workers with additional members of the genus has provided further insight to these characters. For example, rather than the typical elongate radular sac present in more derived members of the

genus, the radular sac of *Halgerda dalanghita* Fahey & Gosliner, 1999, a basal member of the clade, is short (Fahey & Gosliner 1999a). In addition, the phylogeny of *Halgerda* proposed by Fahey & Gosliner (1999b) suggests that the following six additional characters are shared by all members of the genus: the presence of dorsal ridges, ridge color that is different from the general body color; that is, being either orange/yellow or white, white rhinophore bulb color, the presence of gill glands, a rectangular radula shape, and a two-part prostate that is well-differentiated (except for the basal species, *H. dalanghita*). All animals examined for the present study share these six recently described characters along with the previously identified five characters.

Halgerda fibra n. sp.
(Figs 1A-C; 2-4)

HOLOTYPE. — **Philippines**. MUSORSTOM 3, stn CP134, 12°01'N, 121°57'E, 92-95 m, 5.VI.1985, 38 mm (MNHN).

PARATYPES. — **Philippines**. MUSORSTOM 3, stn CP134, 12°01'N, 121°57'E, 92-95 m, 5.VI.1985, 2 sp., 30 mm, 44 mm (MNHN).

ETYMOLOGY. — The specific name is taken from the Latin *fibra* meaning thread or filament. The name refers to the many thin, dark lines on the dorsum, which radiate downward from the distinct tubercles.

OTHER MATERIAL EXAMINED. — **Banc Aztèque**. Sud Nouvelle-Calédonie, SMIB 8, stn DW184, 23°18'S, 168°05'E, 305-320 m, 31.I.1993, 1 sp., 22 mm (CASIZ 119062). — Stn DW182-184, 23°18'S, 168°05'E, 305-367 m, 31.I.1993, 1 sp., 30 mm (MNHN). — Stn DW189, 23°18'S, 168°06'E, 400-402 m, 31.I.1993, 1 sp., 35 mm (MNHN).

Banc Jumeau ouest. Sud Nouvelle-Calédonie, SMIB 8, stn DW174, 23°40'S, 168°01'E, 235-240 m, 29.I.1993, 3 sp., 25 mm, 35 mm, 41 mm (MNHN); 235-240 m, 29.I.1993, 2 sp., 26 mm, 23 mm (MNHN). — Stns DW170-172, 23°41'S, 168°00'E, 230-290 m, 29.I.1993, 3 sp., 26 mm, 30 mm, 37 mm (MNHN). — Stn DW173, 23°41'S, 168°00'E, 234-242 m, 29.I.1993, 1 sp., 37 mm (MNHN). — Stn DW175, 23°41'S, 168°01'E, 235-240 m, 29.I.1993, 1 sp., 29 mm (MNHN).

Banc Kaimon Mau. Sud Nouvelle-Calédonie, SMIB 8, stn DW158, 24°46'S, 168°08'E, 262-290 m, 28.I.1993, 1 sp., 21 mm (MNHN).

Ride de Norfolk. Nouvelle-Calédonie, BATHUS 3, stn CH802, 23°41'S, 168°00'E, 357-550 m,

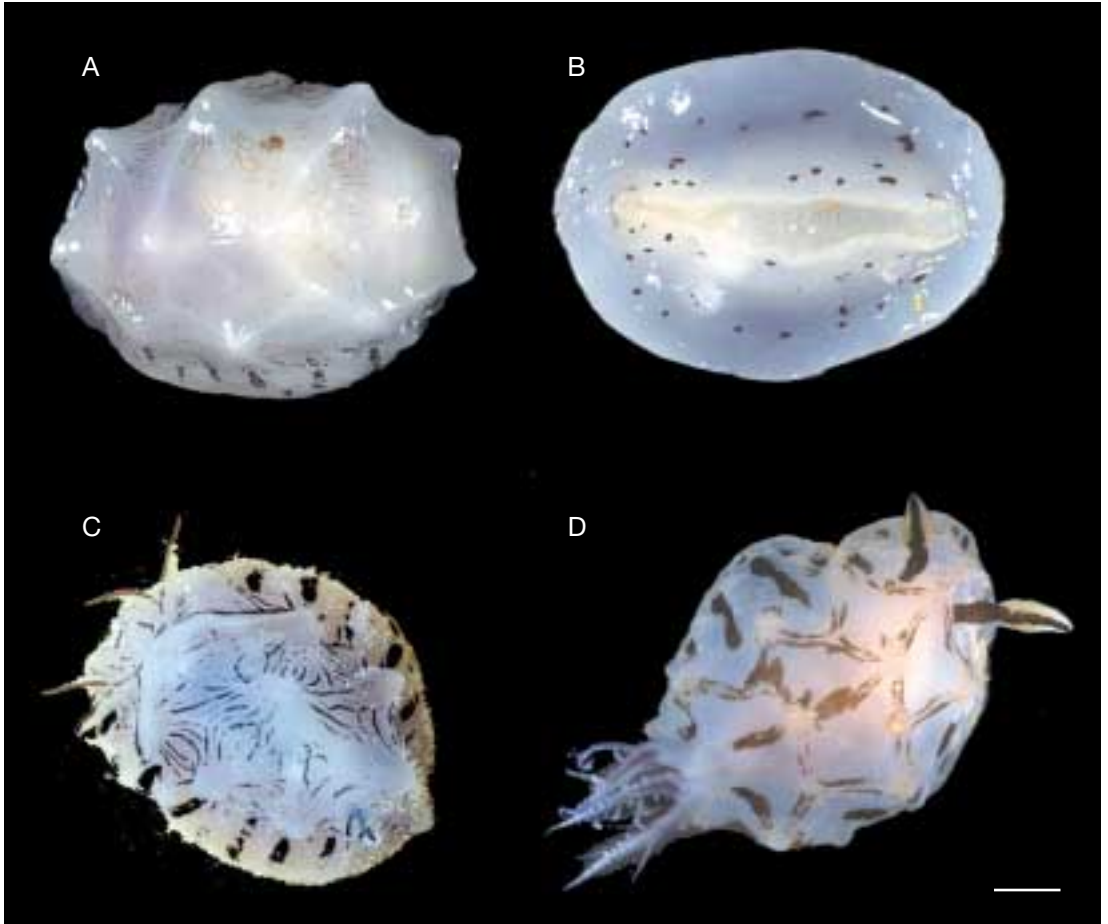


FIG. 1. — Photos of new *Halgerda* species from the deep sea; **A**, *Halgerda fibra* n. sp., living animal, dorsal view (MNHN BATHUS 3); **B**, *Halgerda fibra* n. sp., preserved animal, ventral view (MNHN BATHUS 3); **C**, *Halgerda fibra* n. sp., living animal, dorsal view (MNHN CHALCAL 2 CP20); **D**, *Halgerda abyssicola* n. sp., living animal, dorsal view (MNHN MUSORSTOM 8 CP1132). Scale bar: A, B, 5 mm; C, 2 mm; D, 3 mm.

27.XI.1993, 6 sp., 14 mm, 20 mm, 22 mm, 25 mm, 28 mm, 29 mm (MNHN). — Stn CP804, 23°41'S, 168°00'E, 244-278 m, 27.XI.1993, 9 sp., 18 mm, 20 mm, 20 mm, 22 mm, 25 mm, 30 mm, 36 mm, 37 mm, 40 mm (MNHN). — Stn CH801, 23°39'S, 168°00'E, 270-300 m, 27.XI.1993, 4 sp., 26 mm, 35 mm, 38 mm, 46 mm (CASIZ 119060).

Sud Nouvelle-Calédonie. SMIB 4, stn DW52, 23°41'S, 168°01'E, 235-250 m, 9.III.1989, 1 sp., 33 mm (MNHN). — Stn DW53, 23°40'S, 168°00'E, 250-270 m, 9.III.1989, 1 sp., 40 mm (MNHN). — CHALCAL 2, stn CP20, 24°45'S, 168°09'E, 230 m, 27.X.1986, 1 sp., 12 mm (MNHN).

Nord Nouvelle-Calédonie. BATHUS 4, stn CP938, 19°00'S, 163°26'E, 280-288 m, 8.IX.1994, 4 sp., 15 mm, 21 mm, 25 mm, 26 mm (MNHN). — Stn

DW932, 19°08'S, 163°29'E, 170-190 m, 8.VIII.1994, 1 sp., 23 mm (MNHN). — Stn DW941, 19°02'S, 163°27'E, 270 m, 8.VIII.1994, 1 sp., 23 mm (MNHN). — Stn CP936, 19°04'S, 163°28'E, 252-258 m, 8.IX.1994, 2 sp., 18 mm, 19 mm (MNHN). — Stn DW939, 18°58'S, 163°25'E, 304-320 m, 8.IX.1994, 2 sp., 10 mm, 20 mm (CASIZ 119061).

Nouvelle-Calédonie. MUSORSTOM 4, stn CP191, 19°02'S, 163°28'E, 250 m, 19.IX.1985, 1 sp., 30 mm (MNHN). — Stn DW227, 22°46'S, 167°20'E, 300 m, 30.IX.1985, 2 sp., 16 mm, 11 mm (MNHN). — Stn DW183, 19°02'S, 163°20'E, 280 m, 18.IX.1985, 1 sp., 20 mm (MNHN). — BIOCAL, stn CP84, 20°43'S, 167°01'E, 150-210 m, 6.IX.1985, 1 sp., 14 mm (MNHN).

DISTRIBUTION. — This species is found from New Caledonia to the Philippines (present study) at depths from 90 m in the Philippines to over 400 m near New Caledonia.

DESCRIPTION

External morphology

Transparencies of living animals and preserved specimens were studied. The animals have a firm, smooth body. The body profile is high and the dorsum has ridges arranged in a reticulate pattern (Figs 1A, C; 2). There are pronounced tubercles at the ridge junctions. The gill and rhinophoral pockets are smooth. The ground color of the living animal's dorsum and foot is white with a gray tinge. This color is retained in the preserved state. There are thin, dark lines that radiate downward from the gill pocket and from each tubercle and into the depressions between the ridges. On the edge of the mantle there are numerous, small dark spots or lines (either small, distinct speckles or lines arranged both perpendicular to the border, then parallel to the border nearest to its edge). Animals collected from the Philippines have dark spots arranged in perpendicular lines along the mantle edge, and animals collected from New Caledonia have dark perpendicular lines. On the underside of the body and on the foot are a few of the same small dark spots (Figs 1B; 2).

The rhinophores are long and tapered towards the tips. The rhinophoral base is white with a black line extending up the length on the posterior side of the stalk (Fig. 1C). There are 43-45 rhinophoral lamellae.

The bipinnate gill lies flat over the dorsum and is moderately pinnate. Each of the two main gill raches is divided into three secondary branches and each has a brown stripe on the anterior side and dark spots on the posterior side. The anal papilla is long and has brown pigment on the tip. The dark pigmentation is not retained on some preserved specimens.

Buccal armature

The buccal mass is not pigmented; however, there are small dark spots on the buccal opening.

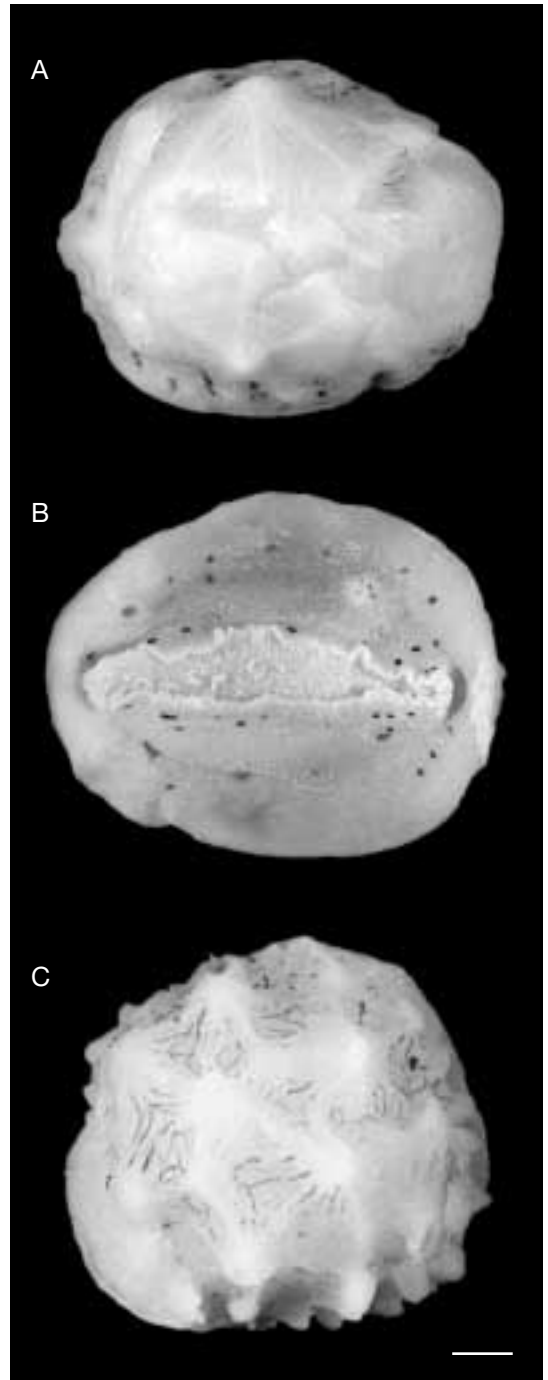


FIG. 2. — *Halgerda fibra* n. sp.; **A**, preserved animal, dorsal view (MNHN BATHUS 3 CH801); **B**, preserved animal, ventral view (MNHN BATHUS 3 CH801); **C**, preserved animal, dorsal view (MNHN MUSORSTOM 3 CP134). Scale bar: A, B, 6 mm; C, 4.5 mm.

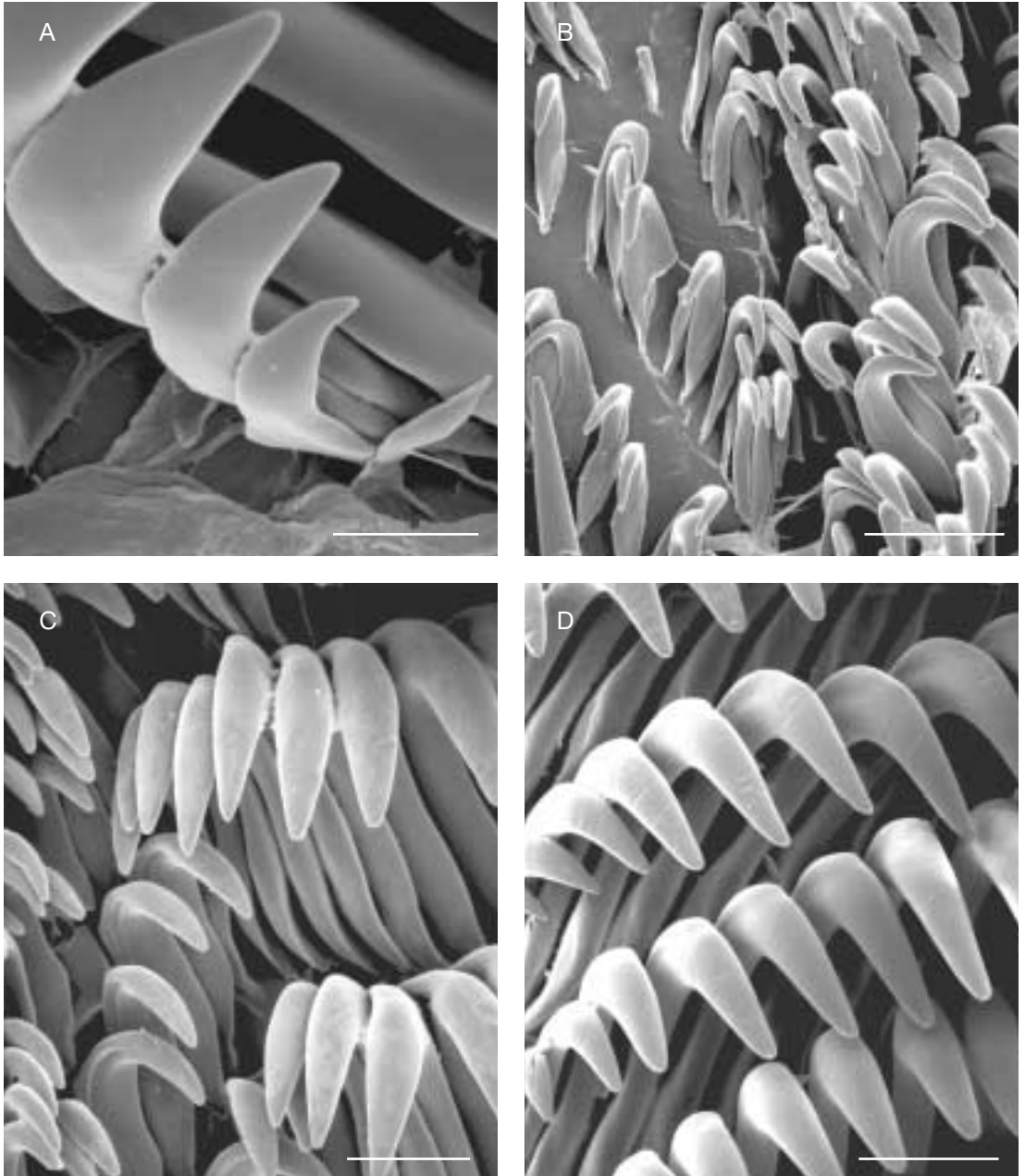


FIG. 3. — Electron micrographs of *H. fibra* n. sp. (MNHN MUSORSTOM 3 CP134) radular morphology; **A**, outer lateral teeth; **B**, inner lateral teeth; **C**, middle lateral teeth; **D**, middle lateral teeth. Scale bars: A, 43 μ m; B, C, 100 μ m; D, 150 μ m.

The radular sac is elongate, curved and lies flat on the posterior end of the buccal mass. The labial cuticle is smooth and devoid of any jaw rodlets.

The radula (Fig. 3) of the holotype (MNHN MUSORSTOM 3 CP134, 38 mm) has a formula of $51 \times 65.0.65$. Two paratypes (MNHN

BATHUS 3 CP804, 22 mm & MNHN SMIB 4 DW52, 33 mm) each had a radular formula of $41 \times 51.0.51$. The three outer teeth (Fig. 3A) are much smaller than the inner and middle lateral teeth and have no denticles. The eight or so inner lateral teeth (Fig. 3B) are smaller and have shorter hooks than the middle lateral teeth and the rows are arranged in a V-shaped pattern. The middle lateral teeth (Fig. 3C, D) are hamate with long, pointed hooks. They have a flattened flange that overlaps the adjacent tooth.

Reproductive system

The reproductive system (Fig. 4, MNHN BATHUS 3 CH801) is triaulic. The ampulla is flattened, moderately elongate and lies flat on the prostate in the holotype and one paratype. In two other specimens (CASIZ 119062 SMIB 4 DW184, 22 mm & MNHN SMIB 4 DW52, 33 mm) the ampulla is extremely large and coiled. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is slightly larger than the prostate gland. The short vas deferens separates from the ampulla and widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well-differentiated as in most other members of *Halgerda*. The prostate coils behind the bursa, and in some specimens, the prostate partially covers the bursa with a thin membrane. The muscular portion of the vas deferens leaves the distal prostate in a long, thick duct, that loops twice, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the oval receptaculum seminis near the last quarter of its length. The duct connecting the receptaculum and the bursa is very long and coiled. The oval receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The long, wide vaginal duct emerges from the base of the bursa copulatrix. Near the vagina exit there is a large muscular portion of the bulbous vagina. The common genital atrium is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

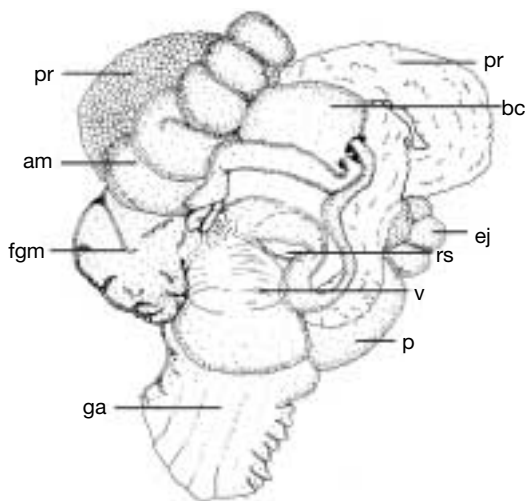


Fig. 4. — Drawing of *H. fibra* n. sp., reproductive morphology. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **ej**, ejaculatory duct; **fgm**, female gland mass; **ga**, genital aperture; **p**, penis; **pr**, prostate; **rs**, receptaculum seminis; **v**, vaginal sphincter. Scale: 7.5 ×.

DISCUSSION

The external markings on the dorsum of *Halgerda fibra* are unique among members of the genus. Due to some external and internal morphological similarities with *Halgerda willeyi* Eliot, 1904 a comparison is made between these two species. In addition, due to some external similarities with the original description of *Halgerda graphica* Basedow & Hedley, 1905, and *H. johnsonorum* (Carlson & Hoff 2000), a contrast is drawn between all three species.

First, in comparing the external morphology of these species, the following similarities and contrasts are noted: the general body shape of all four species is similar in that they are broad ovals; three of the species, *Halgerda fibra*, *H. willeyi* (Eliot, 1904) and *H. graphica* (Basedow & Hedley, 1905), have a high body profile and a surface texture that is firm and gelatinous; *Halgerda johnsonorum* has a low body profile and a soft, flaccid surface texture (Carlson & Hoff 2000). Both *Halgerda willeyi* and *H. fibra* have distinct dorsal ridges that have rounded tubercles at the junctions. Although both species can have dark pigment in the depressions between the

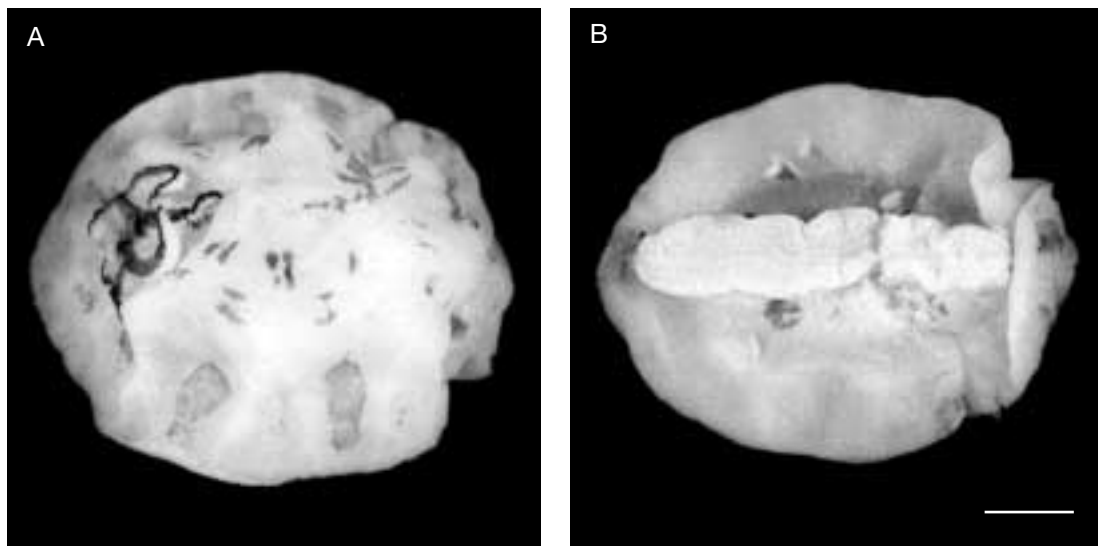


FIG. 5. — *Halgerda abyssicola* n. sp., preserved animal, (MNHN MUSORSTOM 8 CP1132); **A**, dorsal view; **B**, ventral view. Scale bar: 4 mm.

ridges, this pigment is arranged in two distinct patterns. The thick dark pigment on the dorsum of *H. willeyi* lies in the ridge depressions, parallel to the ridges that are also lined with orange. In *H. fibra*, the dark pigment is arranged as finely drawn lines that radiate down from the tubercles and gill pocket. While both species have dark pigment at the mantle border, *Halgerda willeyi* has distinct dark lines perpendicular to the border, whereas *H. fibra* can have either small, distinct speckles or lines arranged both perpendicular to the border, then parallel to the border nearest to its edge.

Halgerda graphica has distinct ridges, but no tubercles at the junctions. The dark pigment on the dorsum is a distinct spot in the center of each ridge depression. There are no other dark lines on the dorsum. On the underside of both *H. fibra* and *H. graphica* are irregularly spaced dark spots. Eliot (1904) described black spots on the genital orifices of *H. willeyi*, but no other pigment on the underside. *Halgerda johnsonorum* has very low-lying ridges with no noticeable tubercles on the dorsum. The dark pigment is similar to *H. willeyi* in that it lies in the ridge depressions alongside secondary lines of yellow and perpendi-

cular to the ridges. There are dark lines perpendicular to the mantle edge, on the foot, and a few leading into the genital pore of *H. johnsonorum*. The dark pigment on the rhinophores of these species also differs. *Halgerda fibra* has one single dark line on the posterior side of the rhinophores, extending from the base to the tip of the club. *Halgerda willeyi* also has a dark line on the posterior side of the rhinophores, and in addition, there is dark pigment covering the club. *Halgerda graphica* has dark pigmentation on the club only. *Halgerda johnsonorum* has dark spots randomly scattered over the entire rhinophoral stalk.

The branchial plume of three species, *Halgerda fibra*, *H. willeyi* and *H. graphica*, is similar in that there are six branches. In both *H. fibra* and *H. willeyi*, there are two main plumes that each divide into three subdivisions. *Halgerda johnsonorum* has four main plumes with the posterior two being secondarily divided (Carlson & Hoff 2000). The branchial coloration differs among the four species. The gill of *H. graphica* is dark, whereas the gill of both *H. fibra* and *H. willeyi* has only a dark stripe on the anterior side of each plume. *Halgerda johnsonorum* has dark spots all over the gill.

The radula is also different. The three outer lateral teeth of three *Halgerda* species, *H. fibra*, *H. graphica* and *H. willeyi*, are small and simple, with no denticles. The six outer teeth of *H. johnsonorum* are reduced with the outer three flattened and the penultimate is bifid (Carlson & Hoff 2000). The radular formulae for *H. fibra* is $51 \times 65.0.65$ (38 mm specimen) and $41 \times 51.0.51$ (22 and 33 mm specimens), for *H. graphica* the published formula is $40 \times 40.0.40$ (45 mm specimen), for *H. johnsonorum* the formula is $37 \times 46.0.46$ (20 mm specimen) and for *H. willeyi* no formula is published. There are differences between the reproductive systems of three species (*Halgerda fibra*, *H. willeyi* and *H. johnsonorum*). The reproductive system of the fourth species, *Halgerda graphica*, was never described by the original authors, and further specimens have not been reported in the literature since.

The ampulla of each of the three described species, *Halgerda fibra*, *H. willeyi*, and *H. johnsonorum*, differs in length and in placement on the reproductive system. *Halgerda fibra* has either a flattened ampulla that is mid-length between that of *H. willeyi* and *H. johnsonorum*, or it has a very thick, coiled ampulla. In either case, the ampulla rests against the prostate gland. *H. willeyi* has a large, long, convoluted ampulla that is not embedded in the prostate. The ampulla of *H. johnsonorum* is short, slightly coiled and mostly embedded in the prostate. The uterine duct of each of the three species also differs in length. The uterine duct of *Halgerda fibra* is long, convoluted and is not covered by the bursa copulatrix whereas the duct of *H. willeyi* is long and loops completely around the bursa. The uterine duct of *H. johnsonorum* has one simple loop. The bursa is entirely covered by the prostate in both *H. fibra* and in *H. johnsonorum* and mostly covered in *H. willeyi*. The penial sheath of the three species differs in length and width. The sheath of *H. fibra* is long and wide, as in *H. johnsonorum*, whereas the penial sheath of *H. willeyi* is short, then widens before it enters the common genital vestibule. The vaginal duct of *H. fibra* is wide and long, with a muscularized portion at its exit into the bulbous vagina. The vaginal ducts of *H. willeyi* and *H.*

johnsonorum are both thin and long, with a small muscular portion at the exit of the duct of *H. willeyi* only. There is a common genital atrium in all three species.

The combination of the external, reproductive and radular morphology of *Halgerda fibra*, distinguish it as a new species.

Halgerda abyssicola n. sp.
(Figs 1D; 5-7)

HOLOTYPE. — **Vanuatu**. MUSORSTOM 8, stn CP1084, 15°50.9'S, 167°17'E, 207-280 m, 5.X.1994, 1 sp., 17 mm (MNHN).

PARATYPE. — **Banc Nova**. Coral Sea, MUSORSTOM 5, stn DW304, 22°10'S, 159°26'E, 385-420 m, 12.X.1986, 1 sp., 26 mm (MNHN).

ETYMOLOGY. — The specific name is taken from the latinised form of the Greek *abyssos* meaning the deep sea and the Latin *cola* meaning dweller. This species was found at depths between 207-420 m.

DISTRIBUTION. — This species is found in the Coral Sea, east to Vanuatu (present study) at depths from 207 to 420 m.

DESCRIPTION

External morphology

Transparencies of living animals and preserved specimens were studied. The animals have a firm, smooth body. The body profile is high and the dorsum has ridges arranged in a reticulate pattern (Figs 1D; 5). There are pronounced tubercles at the ridge junctions. The gill and rhinophoral pockets are smooth. The ground color of the dorsum and foot is white with a gray tinge in both the living animals and in the preserved state. There are dark lines that outline both sides of each ridge. The ridges and tubercles are pale yellow-white. There is thick, dark pigment in lines perpendicular to the mantle edge, and there are dark spots along the mantle margin. There are the same dark spots on the underside of the body and on the foot.

The rhinophores are tapered towards the tips. The rhinophore base is white with a thick, dark line extending down the length on the posterior side of the stalk. There are 43-45 rhinophoral lamellae.

The bipinnate gill is sparsely pinnate. There are two anterior and two posterior gill branches.

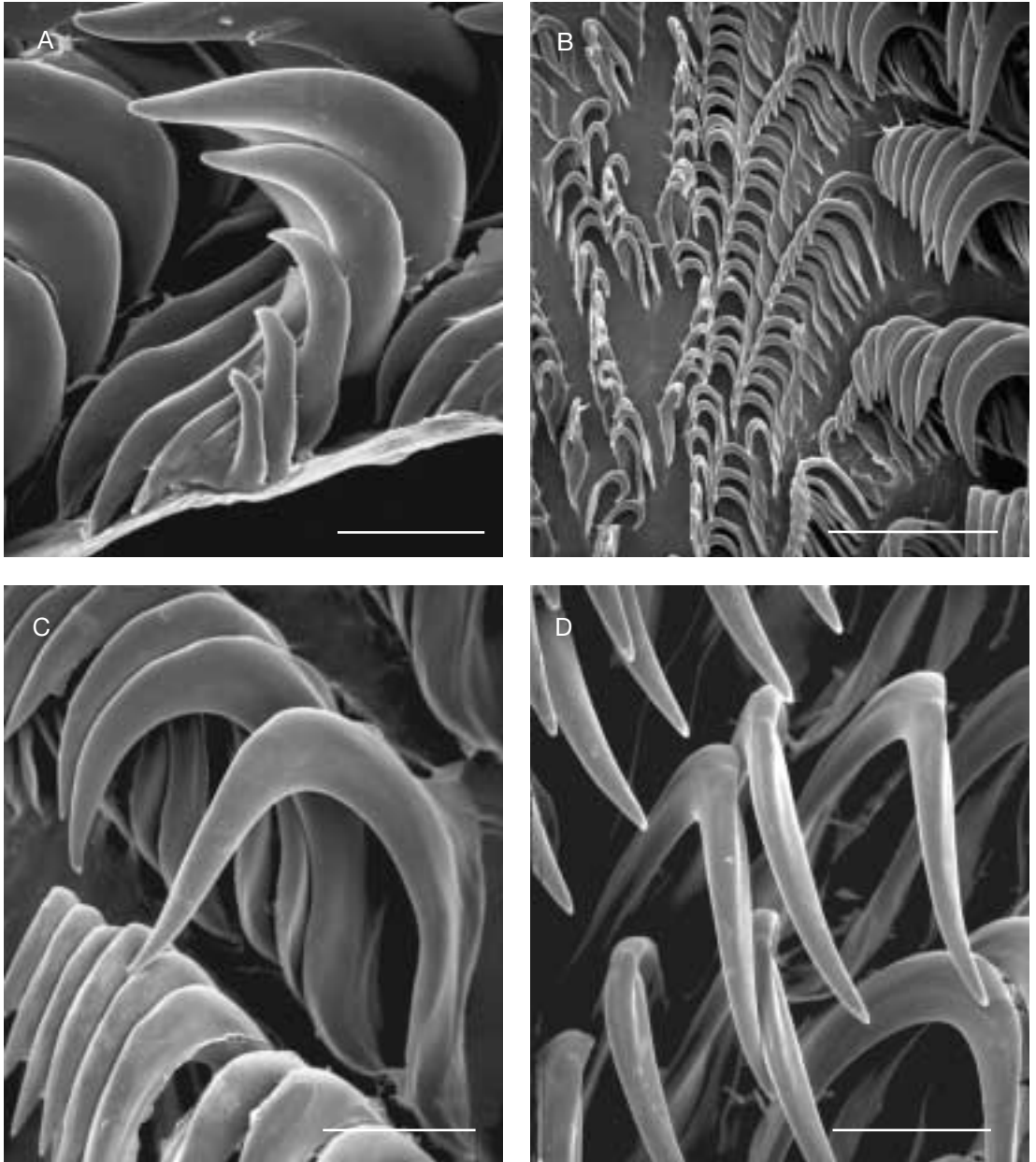


FIG. 6. — Electron micrographs of *H. abyssicola* n. sp. (MNHN MUSORSTOM 8 CP1084), radular morphology; **A**, outer lateral teeth; **B**, inner lateral teeth; **C**, middle lateral teeth; **D**, middle lateral teeth. Scale bars: A, 75 μ m; B, 150 μ m; C, 75 μ m; D, 100 μ m.

Each of the two posterior branches is divided into three secondary branches and each has a dark stripe on the anterior side. The anal papilla is long and has dark pigment on the tip.

Radular morphology

The buccal mass is not pigmented. The radular sac is elongate and protrudes from the buccal mass. The labial cuticle is smooth and devoid of

any jaw rodlets. The radula (Fig. 6) of the holotype (MNHN MUSORSTOM 8 CP1084) has a formula of $35 \times 57.0.57$ and the paratype (MNHN MUSORSTOM 5 DW304) has a formula of $39 \times 37.0.37$. The three outer teeth (Fig. 6A) are much smaller than the inner and middle lateral teeth and only the outermost tooth has very small, blunt denticles. The second and third teeth have no denticles. The 10 or so inner lateral teeth (Fig. 6B) are much smaller and have shorter hooks than the middle lateral teeth and the rows are arranged in a V-shaped pattern. The middle lateral teeth (Fig. 6C) are hamate with extremely long, pointed hooks. They have a flattened base that overlaps the adjacent tooth.

Reproductive system

The reproductive system (Fig. 7) is triauleic. The ampulla is thick, long and lies against the female gland mass. The ampulla narrows into the post-ampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass of the animal examined appeared to be not fully mature owing to its small size. The short vas deferens separates from the ampulla and widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well-differentiated as in most other members of *Halgerda*. The muscular portion of the vas deferens leaves the distal prostate in a long, thick, convoluted duct, that loops three times, then enters the large, wide penial bulb. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is long and coiled. The round receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The prostate does not cover the bursa copulatrix, but wraps around it as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is long. At its exit is the top of a large, bulbous vagina. The common genital atrium is wide and large.

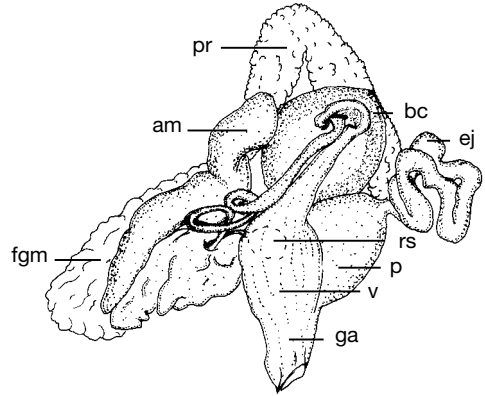


Fig. 7. — Drawing of *H. abyssicola* n. sp., reproductive morphology. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **ej**, ejaculatory duct; **fgm**, female gland mass; **ga**, genital atrium; **p**, penis; **pr**, prostate; **rs**, receptaculum seminis; **v**, vagina. Scale: 7.5 \times .

DISCUSSION

The external morphology of *Halgerda abyssicola* has some external similarity to *H. okinawa* (Carlson & Hoff 2000). These similarities include body profile and coloration, presence of tubercles, and rhinophoral coloration. Due to these external similarities, a comparison is made between these two species.

Both species have a smooth, firm, high body profile with ridges and depressions as typical for the genus. Both have tubercles at the junctions of the ridges, but *H. abyssicola* has lower, less pronounced tubercles. Both have smooth rhinophoral and gill sheaths. The rhinophores of both species are long, with a slight posterior angle. The highly pinnate gill of *H. okinawa* is divided into four main branches whereas the gill of *H. abyssicola* is sparsely pinnate and is divided into three main branches.

The external coloration of the two species is similar in that both have a translucent white body, and the upper part of the tubercles is yellow. *Halgerda okinawa* has dark pigmentation lining the tubercles and along the ridges, whereas *H. abyssicola* has dark pigmentation lining the ridges only. The other dark pigmentation on *H. abyssicola* appears as thick streaks that begin below the dorsal ridges and run perpendicular to the mantle edge. Dark spots can be seen on both animals, with those of

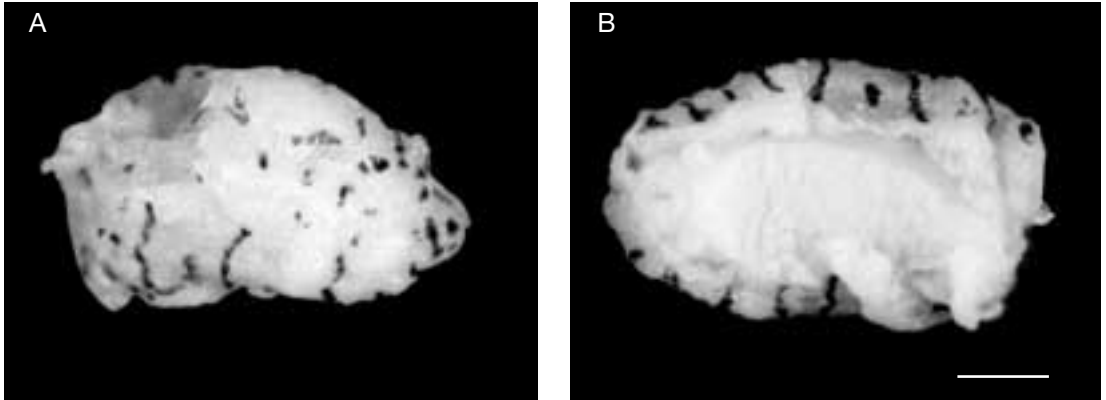


FIG. 8. — *Halgerda azteca* n. sp., preserved specimen (MNHN SMIB 8 DW182-184); **A**, dorsal view; **B**, ventral view. Scale bar: 3 mm.

H. abyssicola along the mantle edge only and those of *H. okinawa* all over the dorsum.

The rhinophore coloration of both species is similar. The base is translucent and the club is yellow. There is a dark line on the posterior side of the rhinophores of both species, but the line is much thicker on *Halgerda abyssicola*.

The gill coloration is very different between the two species. *Halgerda okinawa* has a bright to pale yellow gill with dark spots scattered over all branches. *Halgerda abyssicola* has a translucent white gill with a dark stripe on the anterior side. The radula of both species is similar in that the three outer teeth are reduced and not denticulate. The outermost tooth of *Halgerda abyssicola* can have very small, blunt denticles.

There are also some similarities between the reproductive systems of the two species. The reproductive systems are similar in that the bursa copulatrix is large and enfolded by a glandular prostate that does not cover the bursa. The differences between the reproductive morphologies are as follows: the vas deferens differs between the species, with that of *Halgerda okinawa* being thin and having one fold before it reaches the large penial sheath. The vas deferens of *H. abyssicola* is quite thick, long and coiled several times before reaching the large penial sheath. The vaginal duct also differs between the two species. *Halgerda okinawa* has a vaginal duct that widens only slightly at the distal end, whereas the duct of *H. abyssicola*

is long, tubular and widens considerably into the vagina. Both the vagina and the penial sheath of *H. abyssicola* are bulbous and the same size.

The external and reproductive morphology of *Halgerda abyssicola* distinguishes it as a new species.

Halgerda azteca n. sp.
(Figs 8-10)

HOLOTYPE. — Banc Aztèque. Sud Nouvelle-Calédonie, SMIB 8, stns DW182-184, 23°18'S, 168°05'E, 314-367 m, 31.I.1993, 1 sp., 10 mm (MNHN).

PARATYPES. — Banc Aztèque. Sud Nouvelle-Calédonie, SMIB 8, stns DW182-184, 23°18'S, 168°05'E, 314-367 m, 31.I.1993, 1 sp., 15 mm (MNHN).

Banc Jumeau east. Sud Nouvelle-Calédonie, SMIB 8, stns DW170-172, 23°41'S, 168°00'E, 230-290 m, 29.I.1993, 3 sp., 28 mm, 16 mm, 12 mm (CASIZ 119059).

ETYMOLOGY. — The specific name refers to the locality, banc Aztèque, where the type specimens were collected near New Caledonia.

DISTRIBUTION. — This species is found at Norfolk Ridge near the southern end of New Caledonia (present study) at depths from 230 to 367 m.

DESCRIPTION

External morphology

The preserved animals studied have a firm, smooth body. The body profile is high and the

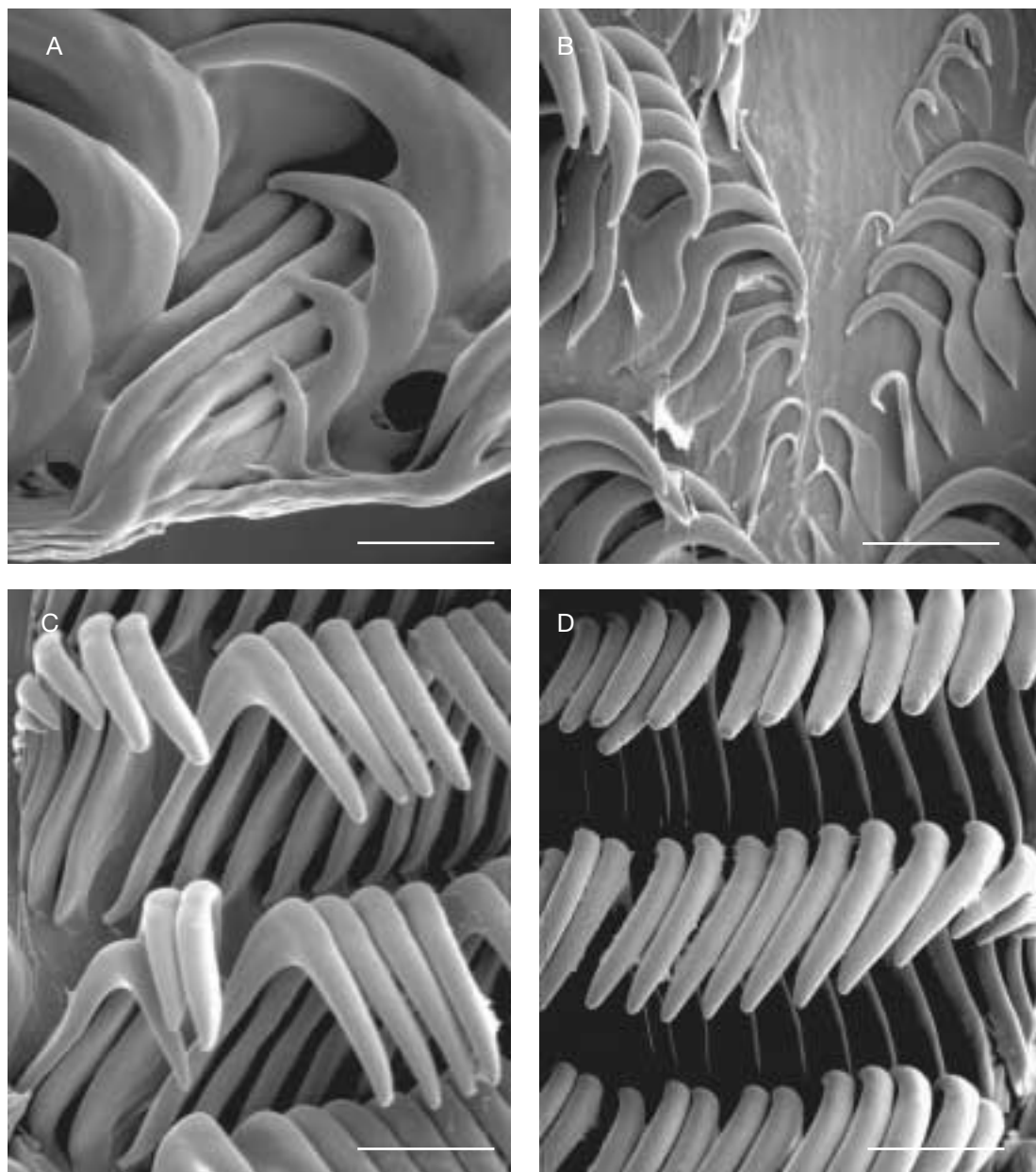


FIG. 9. — Electron micrographs of *H. azteca* n. sp. (MNHN SMIB 8 DW182-184), radular morphology; **A**, outer lateral teeth; **B**, inner lateral teeth; **C**, middle lateral teeth; **D**, middle lateral teeth. Scale bars: A, B, 60 μ m; C, D, 150 μ m.

dorsum has ridges arranged in a reticulate pattern (Fig. 8). There are pronounced tubercles at the ridge junctions. The gill and rhinophoral pockets are smooth. The ground color of the dorsum and

foot is white. There are spots of dark pigment on the dorsum and along the mantle edge. Along the mantle edge of the preserved animal there are also perpendicular dark lines that extend nearly to the

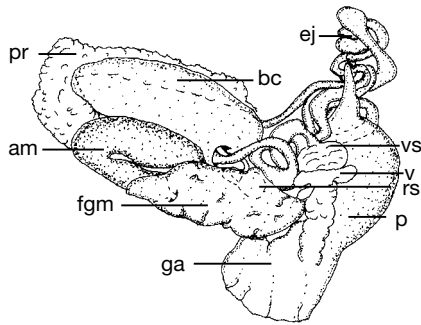


FIG. 10. — Drawing of *H. azteca* n. sp. reproductive morphology. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **ej**, ejaculatory duct; **fgm**, female gland mass; **ga**, genital atrium; **p**, penis; **pr**, prostate; **rs**, receptaculum seminis; **v**, vagina; **vs**, vaginal sphincter. Scale: 10 ×.

mid dorsum. The rhinophores are tapered towards the tips. No pigmentation is present on the preserved animals.

The bipinnate gill has two main branches, each divided into two secondary branches and sparsely pinnate. There is dark stripe on the anterior side of each branch. The anal papilla is white.

Buccal armature

The buccal mass is not pigmented. The radular sac is elongate and protrudes from the buccal mass. The labial cuticle is smooth and devoid of any jaw rodlets. The radular formula of the animal examined (MNHN SMIB 8 DW182-184) is $27 \times 43.0.43$. The four outer teeth (Fig. 9A) are much smaller than the inner and middle lateral teeth and have no denticles. The middle lateral teeth (Fig. 9C, D) are hamate with long, pointed hooks. They have a flattened base that overlaps the adjacent tooth. The seven or eight inner lateral teeth (Fig. 9B) are smaller than the middle lateral teeth and are arranged in V-shaped rows.

Reproductive morphology

The reproductive system (Fig. 10) is triauleic. The ampulla is tubular, rather short and lies flat against the female gland mass. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is about the same size as the prostate

gland. The short vas deferens separates from the ampulla and widens into the glandular prostate. The prostate consists of two distinct glandular types and they are not as well differentiated as in most other members of *Halgerda*. The muscular portion of the vas deferens leaves the distal prostate in a long, convoluted duct, that loops several times into a tall, twisted mass over the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long, thick and coiled. The spherical receptaculum seminis is much smaller than the large, thin-walled spherical bursa copulatrix. The prostate does not cover the bursa copulatrix, but wraps around it as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is very long and convoluted. At its exit is a sphincter at the top of a glandular portion of the bulbous vagina. The glands are isolated on either side of the vagina. The common genital atrium is wide and large.

DISCUSSION

Although this species has some similar external characters to other *Halgerda* species, no photo or description was available to confirm its color characters. The dark pigmentation that remains on the animal through preservation is most similar to *Halgerda willeyi* and *H. johnsonorum* (Carlson & Hoff 2000). For this reason, these animals are compared.

First, in comparing the external morphology of these species, the following similarities and contrasts are noted.

The general body shape of all three species is similar in that they are broadly ovate. Two of the species, *Halgerda azteca* and *H. willeyi*, have both a high body profile and a surface texture that is firm and gelatinous. *Halgerda johnsonorum* has a low body profile and a softer, more flaccid surface texture.

Both *Halgerda willeyi* and *H. azteca* have distinct dorsal ridges that have rounded tubercles at the junctions. Although both species have dark pigment in the depressions between the ridges, this pigment is arranged in two distinct patterns. The

thick dark pigment on the dorsum of *Halgerda willeyi* lies in a complex pattern in the depressions along with orange lines. In *Halgerda azteca* the dark pigment remains as finely drawn lines that radiate down the sides of the dorsum to the mantle edge in no particular pattern. Both species have these distinct dark lines perpendicular to the mantle border. *Halgerda johnsonorum* has very low-lying ridges with no noticeable tubercles on the dorsum. The dark pigment on this animal is similar to *H. willeyi* in that it lies in the ridge depressions alongside secondary lines of yellow and perpendicular to the ridges. There are dark lines perpendicular to the mantle edge. On the underside of *Halgerda azteca* are irregularly spaced dark spots. Eliot (1904) described black spots on the genital orifices, but no other pigment on the underside of *H. willeyi*. *Halgerda johnsonorum* has dark spots on the foot, and a few leading into the genital pore.

There are differences among the rhinophores of the three species. No pigmentation is present on the preserved specimens of *Halgerda azteca*. *Halgerda willeyi* has a dark line on the posterior side of the rhinophores, and in addition, there is dark pigment covering the club. *Halgerda johnsonorum* has dark spots randomly scattered over the entire rhinophoral stalk.

The gill of *Halgerda azteca* has two main branches each divided into two secondary branches. *Halgerda willeyi* has two main plumes that each divide into three subdivisions. *Halgerda johnsonorum* has four main plumes with the posterior two being secondarily divided. The gill coloration differs among the three species. The gill of both *H. azteca* and *H. willeyi* has a black stripe on the anterior side of each plume. *Halgerda johnsonorum* has dark spots all over the gill.

The radular differences among the three species are as follows: *Halgerda azteca* has four outer teeth reduced, simple with no trace of denticles; the three outer lateral teeth of *H. willeyi* are small and simple, with no denticles; the six outer teeth of *H. johnsonorum* are reduced with the outer three flattened and the penultimate is bifid.

There are significant differences among the reproductive morphologies of three species. Firstly, the ampulla of each of the three species differs in length

and in placement on the reproductive system. *Halgerda azteca* has a flattened ampulla that is intermediate in length to that of *H. willeyi* and *H. johnsonorum*, and rests against the female gland mass. *Halgerda willeyi* has a large, long, convoluted ampulla that is not embedded in the prostate. The ampulla of *H. johnsonorum* is short, slightly coiled and mostly embedded in the prostate. The uterine duct of each of the three species also differs in length. The uterine duct of *Halgerda azteca* is long, convoluted and is not embedded under the bursa copulatrix whereas the duct of *H. willeyi* is long and loops completely around the bursa. The uterine duct of *H. johnsonorum* has one simple loop. The bursa is surrounded by the glandular prostate in *H. azteca*. The bursa in *H. johnsonorum* is entirely covered by the prostate and mostly covered in *H. willeyi*. The ejaculatory duct of *H. azteca* is distinct. It is extremely long, coiled and protrudes from the genital mass. In contrast, the ejaculatory ducts of both *H. willeyi* and *H. johnsonorum* are thin and extremely short in comparison, and tucked against the genital mass. The penial sheath of the three species differs in length and width. The sheath is wide and bulbous in *H. azteca* and in *H. johnsonorum*, whereas the penial sheath of *H. willeyi* is short, then it widens before it enters the common genital vestibule. The vaginal duct of *H. azteca* is wide and long, with a muscularized portion at its exit into the bulbous vagina. The vaginal ducts of *H. willeyi* and *H. johnsonorum* are both thin and long, with a small muscular portion at the exit of the duct of *H. willeyi*. *Halgerda azteca* also has a glandular portion of the vagina, which is not present in either of the other two species. There is a common genital atrium in all three species.

The unusual reproductive morphology combined with the radular differences and dark external pigmentation clearly separate *Halgerda azteca* as a new species.

Halgerda orstomi n. sp.
(Figs 11-13)

HOLOTYPE. — Vanuatu. MUSORSTOM 8, stn CP1140, 15°48'S, 167°09'E, 235-251 m, 11.X.1994, 1 sp., 13 mm (MNHN).

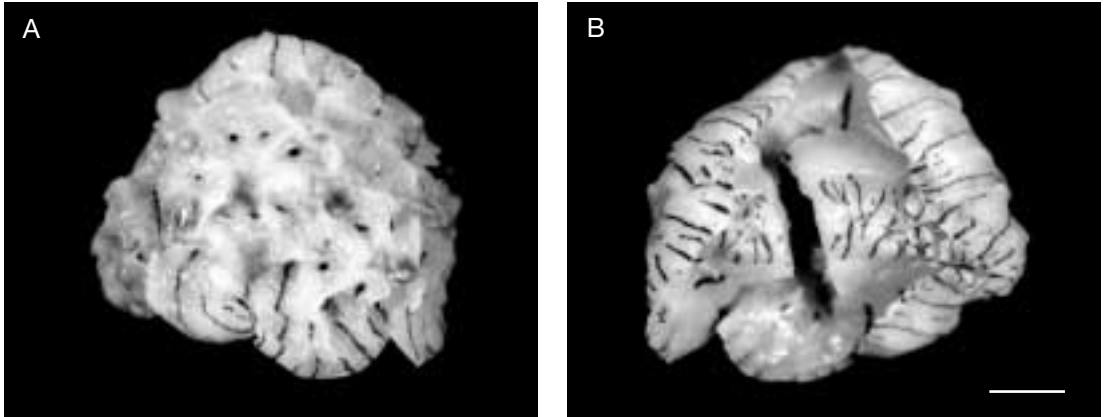


FIG. 11. — *Halgerda orstomi* n. sp., preserved specimen (MNHN MUSORSTOM 8 CP1140); **A**, dorsal view; **B**, ventral view. Scale bar: 2.5 mm.

PARATYPES. — **Vanuatu**. MUSORSTOM 8, stn CP1132, 15°38'S, 167°03'E, 160-182 m, 11.X.1994, 2 sp., 14 mm, 20 mm (MNHN). — Stn CP1133, 15°39'S, 167°03'E, 174-210 m, 11.X.1994, 1 sp., 11 mm (MNHN).

ETYMOLOGY. — The specific name, a patronym, refers to the Institut de Recherche pour le Développement, the acronym of which (now IRD, then ORSTOM) is combined with the Muséum national d'Histoire naturelle, Paris, in the MUSORSTOM expeditions.

OTHER MATERIAL EXAMINED. — **Philippines**. MUSORSTOM 3, stn CP134, 12°01'N, 121°57'E, 92-95 m, 5.VI.1985, 1 sp., 22 mm (MNHN). **Nouvelle-Calédonie**. MUSORSTOM 4, stn DW204, 22°37'S, 167°06'E, 120 m, 27.IX.1985, 1 sp., 20 mm (MNHN).

DISTRIBUTION. — This species is presently recorded from Vanuatu and the Philippines, at depths from 92 to 251 m.

DESCRIPTION

External morphology

The preserved animals studied have a firm, smooth body. The body profile is high and the dorsum has low ridges arranged in a reticulate pattern (Fig. 11). There are pronounced tubercles at the ridge junctions. The gill and rhinophoral pockets are smooth. The ground color of the dorsum and foot is white with a gray tinge in preservation. The tubercles have retained dark pigmentation in a ring near the apex. The holotype has a single dark spot in the depressions between the ridges.

The paratype has dark lines of pigmentation. On both the mantle and foot margins of both animals are a series of dark lines that lie perpendicular to the edge. The rhinophores are long and tapered towards the tips. The rhinophoral base is gray-white with a spot of dark pigmentation on the posterior side. Dark pigmentation circles the length of the stalk. The club is dark with a white apex.

The bipinnate gill is moderately pinnate. Each of the four main gill branches is divided into three secondary branches. The base color is gray-white. Each branch has a streak of brown pigmentation the length of the anterior side. The posterior side is covered with dark spots. The anal papilla is long, white at the apex and has some dark pigment near the base.

Buccal armature

The buccal mass is not pigmented; however, there are small dark spots at the buccal opening. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and curves downward, behind the posterior end of the buccal mass. The radula of the holotype (MNHN MUSORSTOM 8 CP1140) has a formula of 43 × 47.0.47. The three to four outer-most teeth (Fig. 12A, B) are much smaller than the inner and middle lateral teeth and have short, finely divided denticles. The 20 or so inner lateral teeth

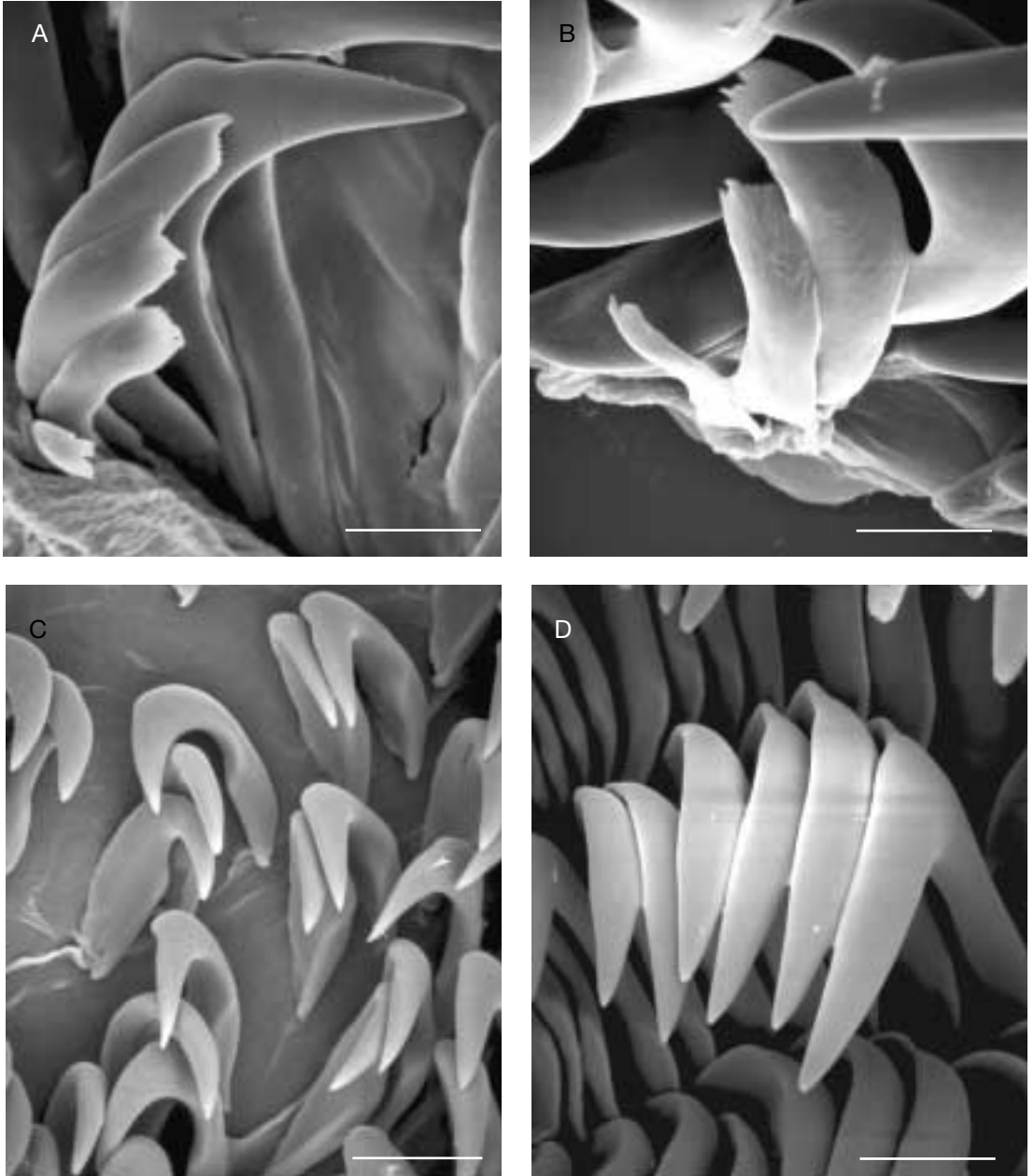


FIG. 12. — Electron micrographs of *H. orstomi* n. sp. (MNHN MUSORSTOM 8 CP1140), radular morphology; **A**, outer lateral teeth; **B**, outer lateral teeth; **C**, inner lateral; **D**, middle lateral teeth. Scale bars: A, C, 30 μ m; B, 20 μ m; D, 43 μ m.

(Fig. 12C) are smaller and have shorter hooks than the middle lateral teeth and the rows are arranged in a V-shaped pattern. The middle late-

ral teeth (Fig. 12D) are hamate with long, pointed hooks. They are flattened at mid-point and overlap the adjacent tooth.

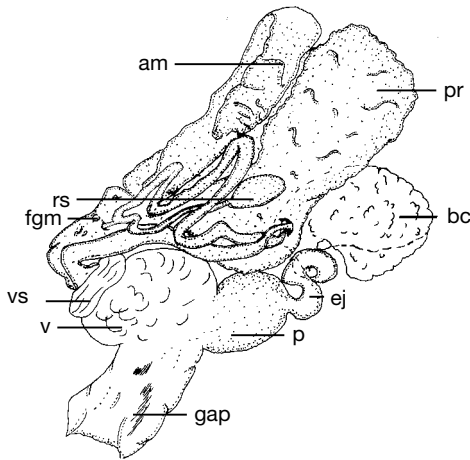


FIG. 13. — Drawing of *H. orstomi* n. sp. reproductive morphology. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **ej**, ejaculatory duct; **fgm**, female gland mass; **gap**, genital atrium pigment; **p**, penis; **pr**, prostate; **rs**, receptaculum seminis; **v**, vagina; **vs**, vaginal sphincter. Scale: 20 \times .

Reproductive system

The reproductive system (Fig. 13) is triauleic. The ampulla is an angular tube, moderately elongate and lies flat against the female gland mass. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is about the same size as the prostate gland. The short vas deferens separates from the ampulla and widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well-differentiated as in most other members of *Halgerda*. The muscular portion of the vas deferens leaves the distal prostate in a moderately long, convoluted duct, that loops once, then enters the wide penial bulb. The relatively short uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis midway along its length. The duct connecting the receptaculum and the bursa is very long and coiled. The pyriform receptaculum seminis is much smaller than the thin-walled bursa copulatrix. The prostate completely covers the bursa copulatrix. The vaginal duct that emerges from the base of the bursa copulatrix is long and thick. At its exit at the top of the very large, bulbous vagina is a large sphincter. The common genital

atrium is wide, large and has dark pigmentation on the interior that can be seen through the wall of the atrium.

DISCUSSION

The external markings on the dorsum of *Halgerda orstomi* are unique among other members of the genus. Due to some internal morphological similarities with *Halgerda formosa* Bergh, 1880, a comparison is made between these two species. First, in comparing the external morphology of these species, the following similarities and contrasts are noted.

Both *Halgerda orstomi* and *H. formosa* (Bergh 1880; Fahey & Gosliner 1999a) have distinct ridges. *Halgerda orstomi* has pronounced tubercles with dark pigmentation at the ridge junctures, but *H. formosa* has low, indistinct ridges. Both *Halgerda orstomi* and *H. formosa* have dark spots in the depressions between the ridges, and dark perpendicular lines along the mantle edge. However, the spots on the dorsal surface of *Halgerda orstomi* are more numerous and of a more consistent size than those of *H. formosa*. The lines of dark pigmentation in the ridge depressions of the paratype are uniform in thickness. The dark marginal lines are also more numerous and evenly spaced on *H. orstomi* and are also present on the foot margin. There are no lines on the foot of *Halgerda formosa*, but there are some dark spots remaining in preservation. The pigmentation on the rhinophores also differs between the two species. *Halgerda orstomi* has a single dark spot on the posterior side of the base, and dark pigmentation circling the club but not on the apex. *Halgerda formosa* has dark patches on the posterior side of the stalk and dark pigmentation on the club that extends to the apex. The gills also differ between the two species. *Halgerda orstomi* and *H. formosa* have four main branches that each divides into three secondary branches. Each branch of the gill of both species has a streak of dark pigmentation the length of the anterior side. The gill of *Halgerda orstomi* has dark spots covering the posterior side and *Halgerda formosa* has dark pigmentation circling the tips of the

branches. The anal papilla of *Halgerda orstomi* is long, white at the apex and has some dark pigment near the base. The anal papilla of *H. formosa* is long and has dark pigmentation on the apex.

There are differences in the radular morphology of the two species. *Halgerda orstomi* has four denticulate outer lateral teeth, whereas *H. formosa* has two denticulate outer teeth (Bergh 1880) or two smooth outer teeth (Rudman 1978). The twenty inner lateral teeth of *H. orstomi* are smaller than the middle lateral teeth and in *H. formosa*, the inner seven to eight teeth are smaller than the middle lateral teeth.

The similarities and differences in the reproductive morphology of the two species are as follows:

- the ampulla of *Halgerda orstomi* is a flattened tube that folds back upon itself one-third the distance from its end. The ampulla of *H. formosa* is a rounded, elongate tube that does not fold, but has slight bends along its length;
- the duct connecting the receptaculum and the bursa is long and convoluted in both species;
- the vaginal ducts of both species are moderately thick, but the duct of *Halgerda orstomi* is very long, while the duct of *H. formosa* is short;
- both species have a distinct sphincter at the exit of the vaginal duct into the vagina. However, the sphincter of *Halgerda orstomi* is wide and sits like a beret on top of the vagina, and the sphincter of *H. formosa* is narrow and constricts above the bulbous vagina;
- the vagina in both species is bulbous, but *Halgerda orstomi* has a very large, rounded vagina that is larger than the penial bulb. The vagina of *Halgerda formosa* is narrower and constricts before joining the similarly-sized penis at the common atrium;
- the ejaculatory duct of *Halgerda orstomi* is moderately long when compared to the duct of *H. formosa* which is extremely long and convoluted;
- the two-part prostate of both *Halgerda orstomi* and *H. formosa* is well-differentiated. The prostate of both species covers the bursa copulatrix;
- the genital atrium of *Halgerda orstomi* has dark pigmentation on the inside that is visible from

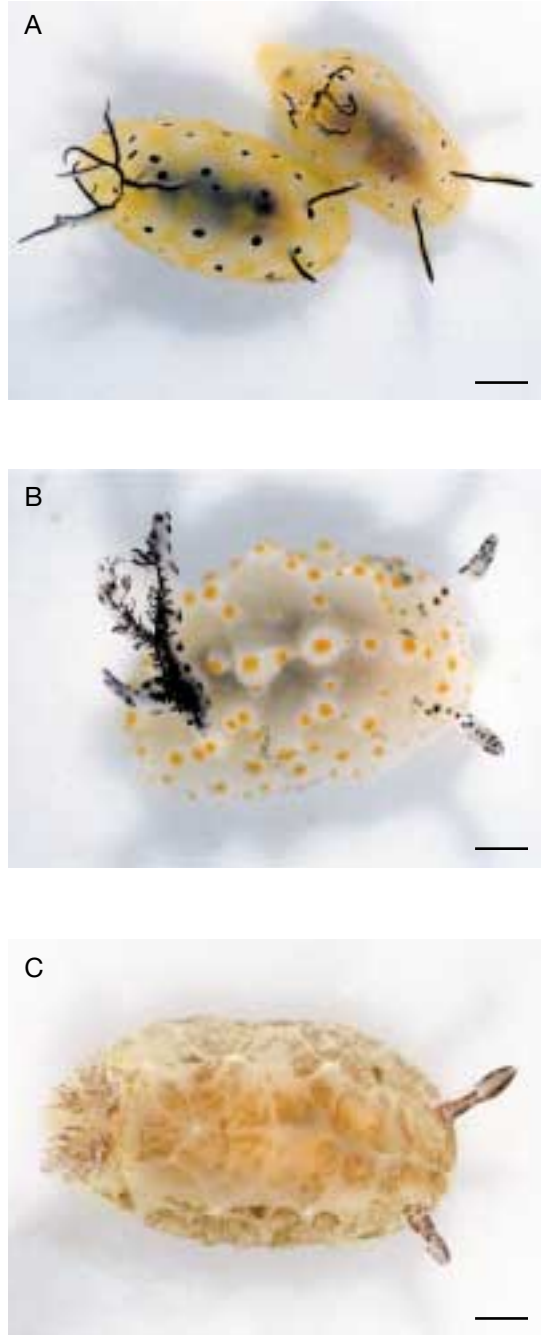


FIG. 14. — Three previously described *Halgerda* species; living specimens from the deep sea; **A**, *H. brunneomaculata* (MNHN MUSORSTOM 10 CP1364); **B**, *H. carlsoni* (MNHN MUSORSTOM 10 CP1364); **C**, *H. dalanghita* (MNHN MUSORSTOM 10 CP1364). Scale bars: A, 3 mm; B, 2 mm; C, 2.5 mm.

the exterior. The genital atrium of *H. formosa* does not have dark pigmentation.

Although there are some similarities between the two species, it is evident that *Halgerda orstomi* is a new species with distinct characteristics particular to it.

The known geographical and bathymetrical ranges of these species differs markedly. *Halgerda formosa* has been found in the Indian Ocean, from South Africa to Western Australia at depths above 60 m. *Halgerda orstomi* has been found in the western Pacific Ocean at depths exceeding 160 m.

Halgerda brunneomaculata Carlson & Hoff,
1993
(Figs 14A; 15; 16A, B)

MATERIAL EXAMINED. — **South of Viti Levu.** Fiji, MUSORSTOM 10, stn CP1364, 18°11.9'S, 178°34.5'E, 80-86 m, 15.VIII.1998, 4 sp., 10 mm, 12 mm, 14 mm, 15 mm (MNHN).

Horseshoe Cliffs. 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 3 m, coll. R. F. Bolland, 17.V.1991, 1 sp., 6 mm (CASIZ 079223).

Swain Reefs. Great Barrier Reef, Australia, 21°14'S, 152°30'E, 1-10 m, coll. A. Ferreira, 7.XII.1977, 1 sp., 8 mm (CASIZ 076337).

DISTRIBUTION. — This species has been found previously on Guam and in the Northern Mariana Islands. The present study extends the range to Fiji, Okinawa, Papua New Guinea (transparency examined for the present study) and the Great Barrier Reef, Australia.

DESCRIPTION

External morphology

Transparencies of living animals and preserved animals were studied. The animals have a firm, smooth body. The body profile is relatively low and the dorsum has low ridges arranged in a reticulate pattern (Fig. 14A). There are low tubercles at the ridge junctions. The gill and rhinophoral pockets are smooth. The ground color of the dorsum and foot is translucent white and the viscera can be seen through the dorsum. In the living animals the ridges and the tubercles are bright yellow. In the depressions between the ridges are a single dark spot, although on some smaller animals there are two smaller spots. On the underside of the body and on the foot are a few of the

same small dark spots. The edge of the mantle and the foot are yellow.

The rhinophores are extremely long and tapered towards the tips. The rhinophore base is white with a thick black line extending down the length on the posterior side of the stalk. The club is yellow. There are 25-27 rhinophoral lamellae.

The unipinnate gill is extremely long and sparsely pinnate. Each of the two main gill rachae is divided into three secondary branches and each has a thick brown stripe on the anterior side. The anal papilla is long and has some brown pigment at the anal pore on some animals.

Buccal armature

The buccal mass is not pigmented; however, there are small dark spots at the buccal opening. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and lies flat on the posterior end of the buccal mass. The radula of the specimen dissected (MNHN MUSORSTOM 10 CP1364) has a formula of $44 \times 39.0.39$. The five outer teeth (Fig. 15A, B) are much smaller than the inner and middle lateral teeth and have long, finely divided denticles. The eight or so inner lateral teeth (Fig. 15C) are smaller and have shorter hooks than the middle lateral teeth and the rows are arranged in a V-shaped pattern. The middle lateral teeth (Fig. 15D) are hamate with long, pointed hooks. They have a flattened base that overlaps the adjacent tooth.

Reproductive system

The reproductive system (Fig. 16A, B) is triaulic. The ampulla is tubular, moderately elongate and lies flat against the bursa copulatrix. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is about the same size as the prostate gland, although it appears that the animal examined was not fully mature due to its size. The short vas deferens separates from the ampulla and widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well-differentiated as in most other members of *Halgerda*. The muscular por-

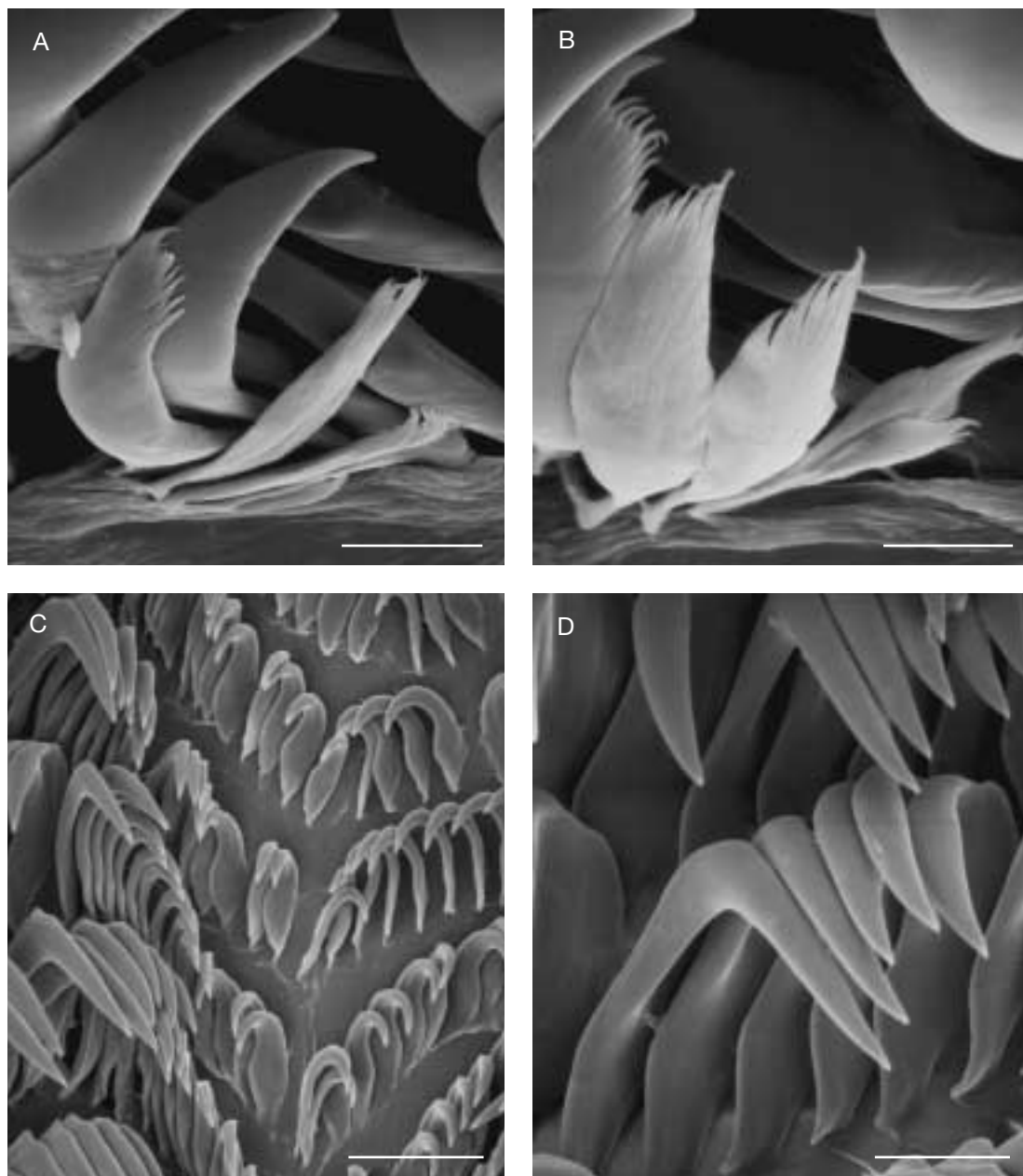


FIG. 15. — Electron micrographs of radula, deep-sea *Halgerda brunneomaculata* (MNH CP1364); **A**, outer lateral teeth; **B**, outer lateral teeth; **C**, inner lateral teeth; **D**, middle lateral teeth. Scale bars: A, 25 μ m; B, 15 μ m; C, 75 μ m; D, 60 μ m.

tion of the vas deferens leaves the distal prostate in a long, convoluted duct, that loops twice, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and

joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long and coiled. The pyriform receptaculum seminis is much smaller than the

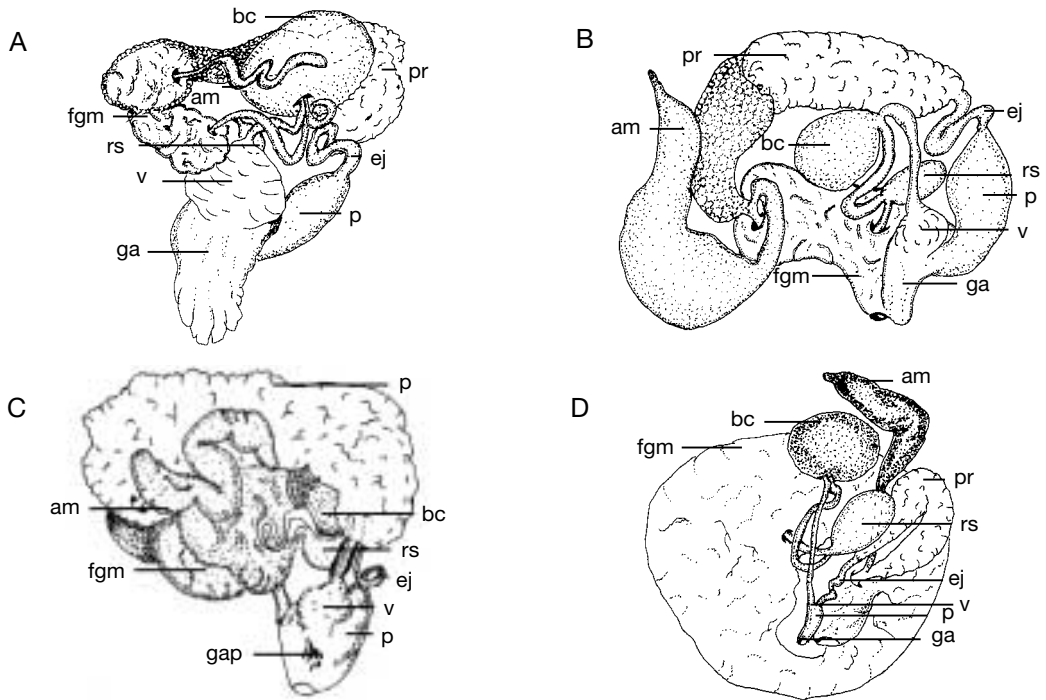


FIG. 16. — Drawings of reproductive systems of the three previously described *Halgerda* species; **A**, *H. brunneomaculata* (Fiji, MNHN CP1364); **B**, *H. brunneomaculata* (Okinawa, CASIZ 079223); **C**, *H. carlsoni* (Fiji, MNHN CP1364); **D**, *H. dalanghita* (Fiji, MNHN CP1364). Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **ej**, ejaculatory duct; **fgm**, female gland mass; **ga**, genital aperture; **gap**, genital aperture pigment; **p**, penis; **pr**, prostate; **rs**, receptaculum seminis; **v**, vagina. Scale: A, B, 20 x; C, D, 10 x.

thin-walled spherical bursa copulatrix. The prostate does not cover the bursa copulatrix, but wraps around it as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is long and convoluted. At its exit is the top of the bulbous vagina. The common genital atrium is wide and large.

DISCUSSION

Halgerda brunneomaculata was previously recorded from 2 to 18 m around Guam and from the Coral Sea (eastern Australia) at 25 m. It is reported for the first time from Fiji at depths of over 80 m. The range of *H. brunneomaculata* is also extended westward to Okinawa and south to Papua New Guinea.

The deep water specimens of *Halgerda brunneomaculata* (MNHN) differ from the shallow water specimens from Okinawa (CASIZ 079223) ex-

amined for comparison and from the original description of *H. brunneomaculata* (Carlson & Hoff, 1993) from Guam. These differences are primarily in the reproductive morphology, although the differences are within the expected range of variation for individual species of the genus.

The external morphology of all animals is nearly identical. All specimens have the same body profile with low ridges and low or non-existent tubercles. All specimens have yellow ridges and a black spot in the ridge depressions. The specimens all have irregularly spaced dark spots on the underside of the mantle and the deep water specimen has spots on the sides of the foot. The specimens of *Halgerda brunneomaculata* from Guam is the only one described with a yellow translucent ground color. Both the Okinawa and the deep water animals have a translucent white ground color. All specimens have unipinnate gills that are sparsely pinnate with a thick, dark stripe on the

anterior side of each branch. The rhinophores of the specimens differ slightly in that the animals from Guam and the deep water animals have a distinct dark stripe on the posterior side of the rhinophore, whereas the Okinawa animal has two perpendicular stripes, which run along the sides of the rhinophores. The deep water animals have yellow mantle and foot borders, and the specimens of *H. brunneomaculata* from Guam do not. The animal from Okinawa has a white mantle border.

The described reproductive morphology differs markedly among the specimens. The deep water animal has a long, tubular ampulla, whereas the Guam specimen has a broad and somewhat flattened ampulla. The Okinawa animal also has a broad and rather flattened ampulla but it is relatively larger than that of the Guam specimens. The bursa copulatrix of both the deep water animal and the Okinawa animal is surrounded by a long, glandular portion of the prostate, whereas in the animal described from Guam, the prostate nearly covers the bursa. The ejaculatory duct of the animals ranges from long, thin and convoluted in the Guam animals, to long, thicker and convoluted in the deep water animals to finally, shorter, thick with only one fold in the Okinawa animal. The penis of both, the deep water animal and the Okinawa animal is bulbous, and the penis of the animal from Guam is more tubular. The vaginal duct of all three animals is long, but it is quite sinuous and convoluted in the animal from Guam. The vagina of both the deep water animal and the Okinawa specimen is large and bulbous, whereas the vagina of the Guam specimens widens only slightly as it joins the penial sheath.

The radular morphology of the animals from all three localities is nearly identical. The outer five teeth are reduced and apically pectinate. The inner five to six teeth are smaller than the middle lateral teeth and the middle lateral teeth are hamate with a flange at the base that overlaps the adjoining tooth.

Examination of animals from various localities of the Indo-Pacific has revealed some interesting variations in both the external and internal morphologies of *Halgerda brunneomaculata*. In summary, these variations include some features

unique to the deep water animals: a yellow mantle and foot border, a long, tubular ampulla and a longer, thicker, convoluted ejaculatory duct. The deep water animals from Fiji also share common features with animals found in Okinawa: both have long, glandular portions of the prostate that surround the bursa copulatrix and animals from both localities have a large, bulbous penis and vagina. The differences between the animals from the different localities appear to be minor and within the range of variability noted in the genus. The specimens are no doubt the same species and further examination of specimens from Guam should be undertaken to confirm the observations described by Carlson & Hoff (1993).

Halgerda carlsoni Rudman, 1978
(Figs 14B; 16C; 17)

MATERIAL EXAMINED. — **South of Viti Levu.** Fiji, MUSORSTOM 10, stn CP1364, 18°11.9'S, 178°34.5'E, 80-86 m, 15.VIII.1998, 1 sp., 15 mm (MNHN).

Pangaimotu Island. South side of Maungai Peninsula, Vava'u Group, Tonga, 18°42'S, 174°00'W, 1-27 m, coll. R. Van Syoc, 21.VII.1985, 3 sp., 26 mm, 33 mm, 55 mm (CASIZ 072235).

The Bomber. Between Wongat Island and Tabat Island, north coast near Madang, Papua New Guinea, 23 m, coll. T. Gosliner, 13.XI.1990, 1 sp., 20 mm (CASIZ 075256).

Naen Island. Manado, Sulawesi, Indonesia, 27 m, coll. by P. Fiene, 17.V.1991, 1 sp., 27 mm (CASIZ 078623); 20 m, coll. P. Fiene, 19.V.1989, 1 sp., 16 mm (CASIZ 070293); no depth given, coll. P. Fiene & M. Severns, V.1988, 1 sp., 18 mm (CASIZ 087271).

Seregaki Beach. 1.3 km ENE of Maeki-zaki, Ryukyu Islands, Okinawa, 26°30.4'N, 127°52.6'E, 21 m, coll. R. Bolland, 27.VII.1989, 1 sp., 30 mm (CASIZ 069905).

Great Astrolabe Reef. Fiji, 18°45.06'S, 178°27.99'E, 30 m, coll. by J. Koven, 6.VI.1998, 1 sp., 20 mm (CASIZ 114170).

DISTRIBUTION. — This species has previously been found in Fiji (Rudman 1978) and Papua New Guinea (Gosliner, Behrens & Williams 1996). This study extends the range to Tonga, Sulawesi, and Okinawa.

DESCRIPTION

External morphology

Photo slides of living animals and preserved animals were studied. The animals have a firm,

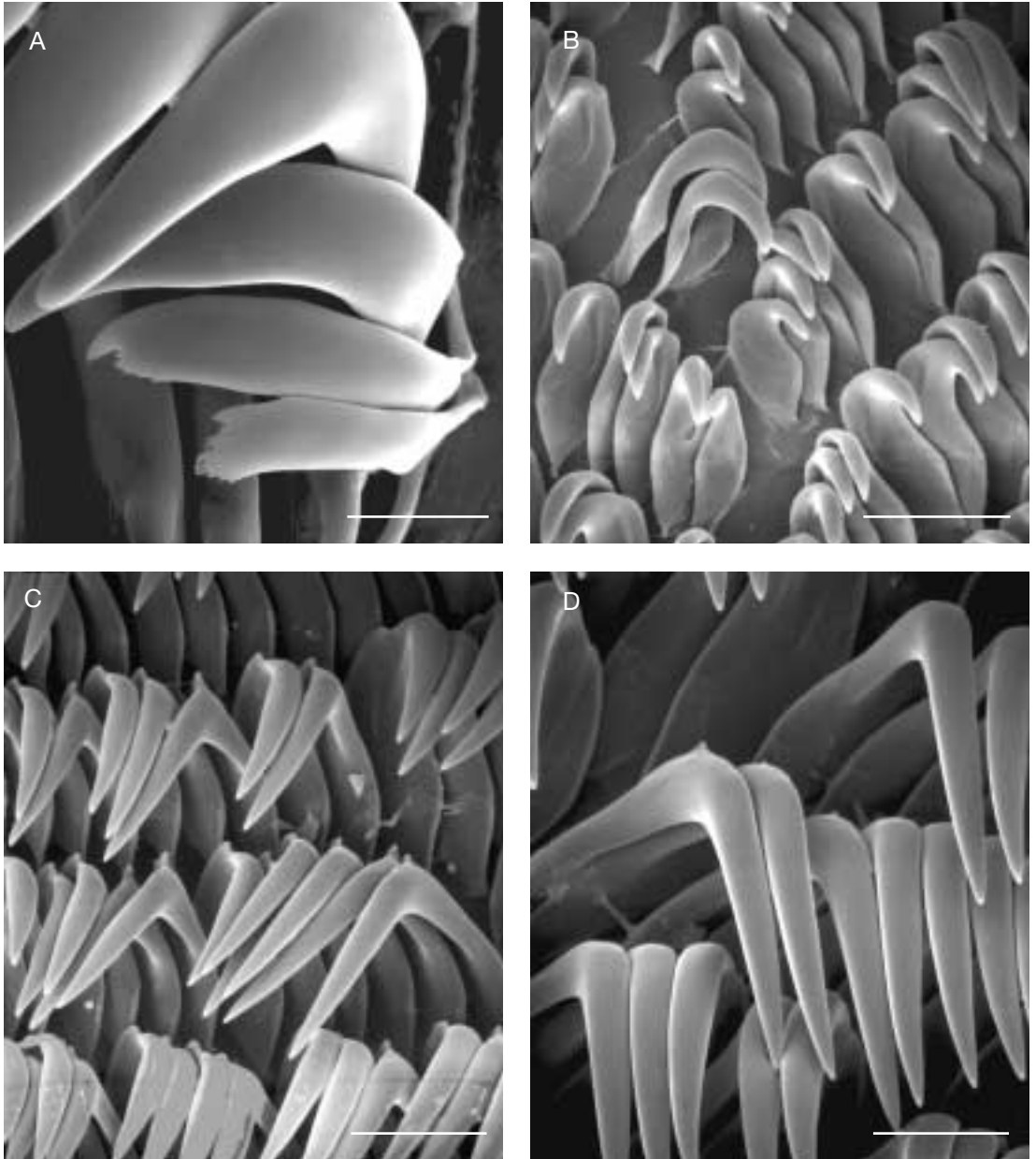


FIG. 17. — Electron micrographs of radula, *Halgerda carlsoni* (MNHN CP1364); **A**, outer lateral teeth; **B**, inner lateral teeth; **C**, middle lateral teeth; **D**, middle lateral teeth. Scale bars: A, 20 μ m; B, 43 μ m; C, 75 μ m; D, 60 μ m.

smooth body. The body profile is high and the dorsum has ridges arranged in a reticulate pattern (Fig. 14B). There are pronounced tubercles at the ridge junctions. The gill and rhinophoral pockets

are smooth. The ground color of the dorsum and foot is translucent white. The dark viscera can be seen through the dorsum. In the living animals, the dorsum is densely covered with small bright

orange to reddish-orange spots that give the body an orange glow. The tubercles are tipped with bright orange to reddish-orange. Below the orange color is a ring of bright white. The edge of the mantle is white and has large orange to reddish-orange tubercles, in between which are smaller dots of the same color.

The rhinophores are long and tapered towards the tips. The rhinophore stalk is white with black spots scattered over the length. There are 15-38 rhinophoral lamellae, depending on the size of the animal. The larger the animal, the more lamellae. The tip of the rhinophore is white.

The bipinnate gill has six sparsely pinnate branches. Along the anterior side of each branch are numerous dark spots that are arranged in a line. Additional dark spots are scattered over the branches. On the interior of each branch are glandular structures that are arranged in columns that run the length of each branch.

The underside of the animal is translucent white, and the foot is lined with orange.

Radular morphology

The radular sac is elongate and curves away from the buccal mass. The radular formulae of the specimens examined are as follows: MNHN MUSORSTOM 10 CP1364, $55 \times 56.0.56$; CASIZ 075256, $50 \times 41.0.41$; CASIZ 072235, $63 \times 66.0.66$. The labial cuticle is smooth and there are no jaw rodlets. The three outer teeth (Fig. 17A) are much smaller than the inner and middle lateral teeth and have both blunt and pointed denticles. The six or so inner lateral teeth (Fig. 17B) are smaller and have shorter hooks than the middle lateral teeth and the rows are arranged in a V-shaped pattern. The middle lateral teeth (Fig. 17C, D) are hamate with long, pointed hooks. They have a flattened base that overlaps the adjacent tooth.

Reproductive system

The reproductive system (CASIZ 075256, Fig. 16C) is triaulic and was examined in three specimens. The ampulla is tubular, moderately elongate and protrudes away from the prostate.

The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is about the same size as the prostate gland. The short vas deferens separates from the ampulla and widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well-differentiated as in most other members of *Halgerda*. The muscular portion of the vas deferens leaves the distal prostate in a long, convoluted duct, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis approximately one third its length from the base. The duct connecting the receptaculum and the bursa is very long and convoluted. The pyriform receptaculum seminis is somewhat smaller than the thin-walled spherical bursa copulatrix, although larger than in most other species of *Halgerda*. The prostate does not cover the bursa copulatrix completely as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is moderately long and tubular. At its exit at the top of the bulbous vagina is a glandular portion. The common genital atrium is wide and large. Next to the genital opening is the opening of the female gland mass.

DISCUSSION

Halgerda carlsoni Rudman, 1978, previously recorded from Fiji at depths under 7 m, is reported for the first time from 80 to 86 m. Additional records of this species are noted from Papua New Guinea, Tonga, Indonesia and the type locality in Fiji.

Rudman (1978) described *Halgerda carlsoni* from Suva Harbour, Fiji. The three specimens he described were found at depths from approximately 3 to 7 m. The external and radular morphology of the animals examined for the present study is consistent with the thorough description provided by Rudman. The only difference noted was in the radular morphology. The three outer teeth of the animals from Papua New Guinea (CASIZ 075256) and Tonga (CASIZ 072235) were

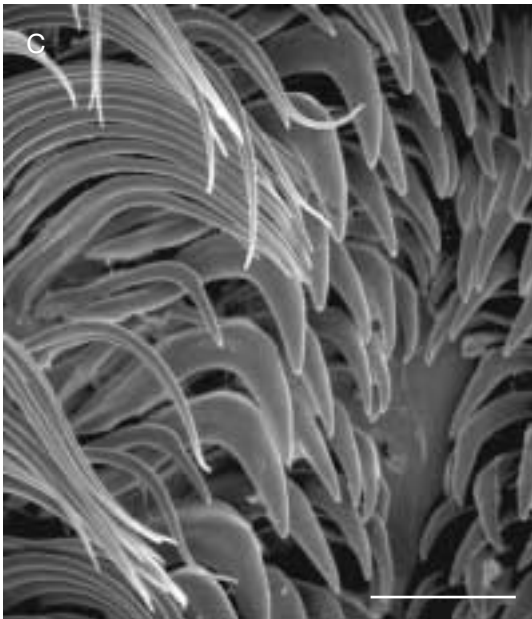
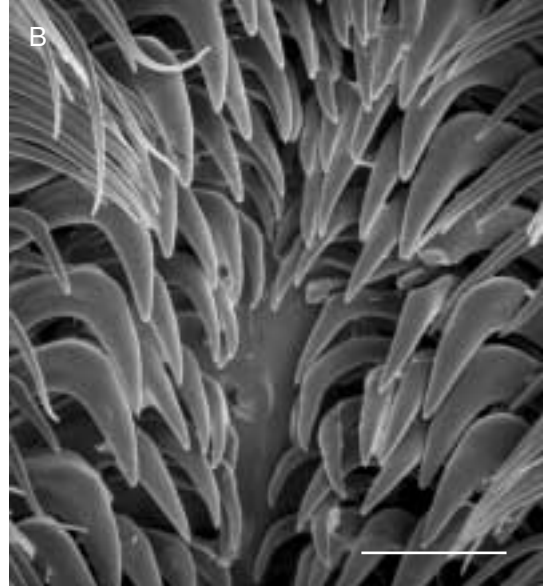
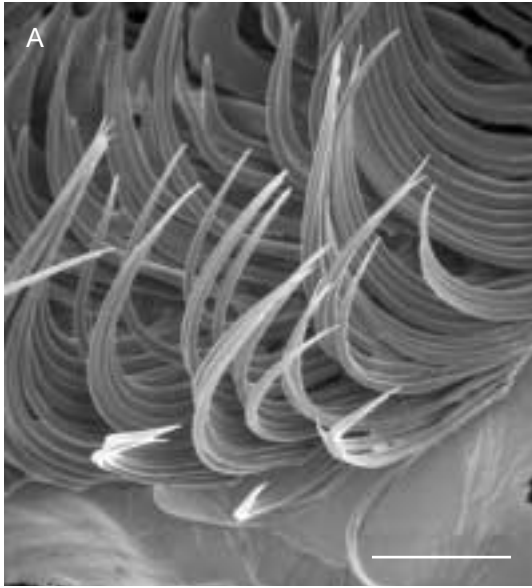


FIG. 18. — Electron micrographs of radula: *Halgerda dalanghita* (MNHN CP1364); **A**, outer lateral teeth; **B**, inner lateral teeth; **C**, middle lateral teeth. Scale bars: 100 μ m.

Eliot, 1904 and *H. willeyi*. All the animals examined in the present study from Papua New Guinea (CASIZ 075256), Fiji (MNHN MUSORSTOM 10 CP1364, CASIZ 114170) and Tonga (CASIZ 072235) have a similar reproductive system. The vagina of all the animals from Papua New Guinea, Fiji and Tonga has a glandular portion at the top where the vaginal duct enters.

Halgerda dalanghita Fahey & Gosliner, 1999
(Figs 14C; 16D; 18)

MATERIAL EXAMINED. — South of Viti Levu, Fiji, MUSORSTOM 10, stn CP1364, 18°11.9'S, 178°34.5'E, 80-86 m, 15.VIII.1998, 1 sp., 20 mm (MNHN).

DISTRIBUTION. — This species is previously known from the Philippines, Papua New Guinea and South Africa. The present study extends the range to Fiji.

DESCRIPTION

External morphology

Photo slides of living animals and preserved animals were studied. The animals have a smooth,

found to be degenerate and denticulate, whereas the animals from Fiji were described as having degenerate, but not denticulate outer teeth.

Rudman (1978) did not describe the reproductive system of the Fijian specimens in detail, but remarked that it was similar to his description (1978) of the morphology of *Halgerda wasinensis*

firm body. The body profile is relatively low and the dorsum has a series of angled ridges arranged in a reticulate pattern (Fig. 14C). There are no conical tubercles at the junctions of the ridges, as is common in some other *Halgerda* species. The ground color of the animal in photos is yellowish-brown. In the living animals, the ridges are pale tan, and the depressions between the ridges have mottled dark pigmentation. The pale yellow viscera can be seen in the photo and through the dorsum of the preserved animal. On the underside of the mantle and on the sides of the foot are dark spots.

The upright rhinophores are tapered towards the tip with dark coloration on the posterior side extending the length of the stalk. The background color is white and the club is nearly circled in dark pigmentation.

The gill has six branches that are highly pinnate. The ground color is white like the rhinophores and each branch has dark lines on the posterior side. The anal papilla is long and white.

Buccal armature

The buccal mass is not pigmented and the radular sac is short. The radular formula is $35 \times 21.0.21$. The outer and middle lateral teeth (Fig. 18A, C) are extremely elongate which are atypical of dorid hamate teeth. The five or so inner lateral teeth are hamate (Fig. 18B). The rows of teeth are arranged in a straight line across the radula.

Reproductive morphology

The reproductive system (Fig. 16D) is as described by Fahey & Gosliner (1999). In summary, the ampulla is long, flattened with a single bend and lies tightly against the female gland mass. The short vas deferens separates from the ampulla then widens into a large, elongate glandular prostate that has two parts that are not well-differentiated. The prostate does not cover the bursa copulatrix but is tubular and folds once behind it. The receptaculum seminis is comparatively larger than in most other *Halgerda* species. The ejaculatory duct is a long duct that widens slightly into the penial bulb. The vaginal duct is long and thin. It widens slightly into the vagina, which is not glandular.

The common genital atrium is smaller than in most other *Halgerda* species.

DISCUSSION

Previous records of *Halgerda dalanghita* have been noted from the Batangas Province of the Philippines, Papua New Guinea and South Africa (Fahey & Gosliner 1999a) at depths from 2 to 20 m. This new record of *H. dalanghita*, found in Fiji at depths greater than 80 m extends its range eastward. In addition, it quadruples the recorded depth for this species.

The previously recorded specimens have a different external coloration than that of the deep water animal. Animals found in shallower waters have brighter coloration that ranges from lemon yellow to orange. The animal from the deeper water has more muted brownish coloration.

Radular and reproductive morphology does not vary between the deep and shallow water specimens.

Bathymetric diversification of Halgerda

The genus *Halgerda* is generally thought to be a shallow water clade, associated primarily with reef environments. Previous authors have noted a bathymetric range from less than 1 m to approximately 60 m. This study is the first time that *Halgerda* species have been reported from depths greater than 60 m.

At depths of approximately 80 to 90 m, there is an overlap of shallow water species. For example, *Halgerda dalanghita*, previously recorded from 2-20 m is also found at depths from 80-86 m. *Halgerda carlsoni*, previously recorded from 3-30 m, is found at depths from 80-86 m. *Halgerda brunneomaculata*, previously recorded from 2-18 m, is also recorded from 80-86 m. At depths exceeding 100 m, four species of *Halgerda* have been recorded: *H. fibra*, *H. abyssicola*, *H. azteca* and *H. orstomi*. None of these species have been previously recorded at shallow depths. It is interesting to note that the bright color patterns seen on shallow water species are largely retained on the animals living at depths of 80-90 m. However, the bright orange color of *H. dalanghita* previously noted by Fahey & Gosliner (1999a)

for the shallow water animals is somewhat muted on the deeper water specimen. The color on these deeper animals is a dull, brownish-orange. The coloration of the exclusively deep water species is also less spectacular. Most of the external color is dark spots or lines, with no bright colors at all. Further collections of *Halgerda* from deeper bathymetric ranges will be of interest to see if animals tend to retain their coloration, or are more likely to lose the bright colors with depth.

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