

**Redescription of *Halgerda graphica* Basedow and Hedley, 1905,  
with Observations on External Morphological Variation within  
Selected Species of *Halgerda* (Mollusca: Nudibranchia)**

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*Halgerda graphica* Basedow and Hedley, 1905 is redescribed based on examination of two specimens; one collected in 1904 from Middle Harbour, Sydney, Australia, housed at the Australian Museum, Sydney, and another specimen collected in 1990, from Port Moorowie, near the type locality (Kangaroo Island, South Australia). The reproductive system is described and illustrated for the first time. This species has frequently been misidentified due to having similar external morphology to other *Halgerda* species. A comparison is made to those species. *Halgerda graphica* has a unique combination of external and internal characters that confirm it as a distinct *Halgerda* species. The external characters include a “hieroglyphic” pattern of yellow and black markings on the notum, small, similar-size dark spots on the ventral surface, a small, sparse, dark-colored gill and rhinophores with a white base, dark tip and a dark line on the posterior side. The external color variations of *Halgerda dichromis* Fahey and Gosliner, 1999, *H. okinawa* Carlson and Hoff, 2000 and *H. willei* Eliot, 1904 are also described, illustrated and compared to externally similar species. It is the unique combination of external morphological characters such as the color and pattern on the notum, the structure and color of the gills and rhinophores that help to distinguish each species, although examination of internal morphology can confirm the identification.

Basedow and Hedley (1905) described the nudibranch *Halgerda graphica* from two specimens dredged off Antechamber Bay, Kangaroo Island, South Australia. They had at the time examined a third specimen, which, although not included in the original description, they indicated that it belonged to their new species. The original description of the external and radular morphologies of the specimens were quite detailed, but the authors did not provide a description of the reproductive morphology. This species did not show up again until 1990. In the meantime, other authors (e.g., Coleman 1975, 2001; Kay 1979; Kay and Young 1969; Wells and Bryce 1993) have erroneously attributed the name *Halgerda graphica* to other species.

The present study describes two additional specimens of *Halgerda graphica*; the single specimen mentioned by Basedow and Hedley, collected in approximately 1904 at Middle Harbour, Sydney, and an additional specimen collected by N. Holmes in 1990 from Port Moorowie, Yorke Peninsula, South Australia.

The nudibranch genus *Halgerda* Bergh, 1880 has been studied extensively in recent years (Rudman 1978; Willan and Brodie 1989; Carlson and Hoff 1993, 2000; Gosliner and Fahey 1998;

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Fahey and Gosliner 1999a, 1999b, 2000, 2001a, 2001b). Since 1998, the number of described species increased from 14 to 35. Among *Halgerda* species are several that display external color variation in specimens from similar habitats and from varying geographic ranges. Four species, in particular, seem to be most commonly confused: *Halgerda graphica*, *H. willeyi*, *H. okinawa* Carlson and Hoff, 2000, and *H. dichromis* Fahey and Gosliner, 1999. The present study illustrates the color variations that can cause misidentification of these four species in the field and then makes comparisons with the externally most similar species. Field notes and photographic records of many observers, both amateur and professional, provide the basis of the discussion on external color variation presented in this paper.

#### DESCRIPTIONS OF TAXA

##### **Labiostomata Valdés, 2002**

##### **Family Discodorididae Bergh, 1891**

##### **Genus *Halgerda* Basedow and Hedley, 1905**

(Type species: *Halgerda formosa* Bergh, 1880, by monotypy)

##### ***Halgerda graphica* Basedow and Hedley, 1905**

(Figs 1–3)

**TYPE MATERIAL.**— The type material is probably lost; it is not at the Australian Museum. The type locality is Kangaroo Island, South Australia. The authors (Basedow and Hedley 1905) mention an additional specimen deposited at the Australian Museum, Sydney (C18168, Location #016276, collector not named) from Middle Harbour near Sydney, in September 1904. This specimen was examined and is both described below and hereby designated as the neotype.

**OTHER MATERIAL EXAMINED.**— South Australian Museum, TD16542, one specimen, dissected, Port Moorowie, Yorke Peninsula, South Australia. 10 m deep, collected by Nigel Holmes, 15 December 1990.

**EXTERNAL MORPHOLOGY.**— Because there are no photographs or drawings available for specimen C18168 (1904), the following is a description of the specimen collected in 1990 by N. Holmes. This specimen is nearly identical to the drawing and description of *Halgerda graphica* provided by Basedow and Hedley in 1905 (Fig. 1A).

The preserved animal is 28 mm in length. The body profile is rounded, convex (Fig. 1B) and the dorsum has a low-ridged pattern. There are no small marginal tubercles. There is a low central ridge running the length of the dorsum that splits into several smaller ridges as it nears the gill pocket. The ridges have orange-yellow crests. The background color of the dorsum is gray-white. Between the ridges are black spots with some spots circled or semi-circled with the same yellow color as the ridges. The dark spots closest to the mantle edge are smaller than those on the dorsum. The mantle margin is translucent white when viewed dorsally, but when viewed ventrally, a yellow margin is apparent. On the underside of the mantle and along the side of the foot are dark spots of various sizes. The foot margin is yellow (Fig. 1C). The oral tentacles are long and tapered.

The long rhinophores have a bulging club that is tapered at the tips. The club is angled posteriorly and there is dark brown to black coloration around the top half of the club up to the tip. The base is translucent white and there is a dark line on the posterior side of the rhinophores that extends from the base to the tip.

The bipinnate gill lies flat over the dorsum and is moderately pinnate. Each of the four main gill rachae has a brown stripe on the anterior sides. The anal papilla is long and is the same color as the body.

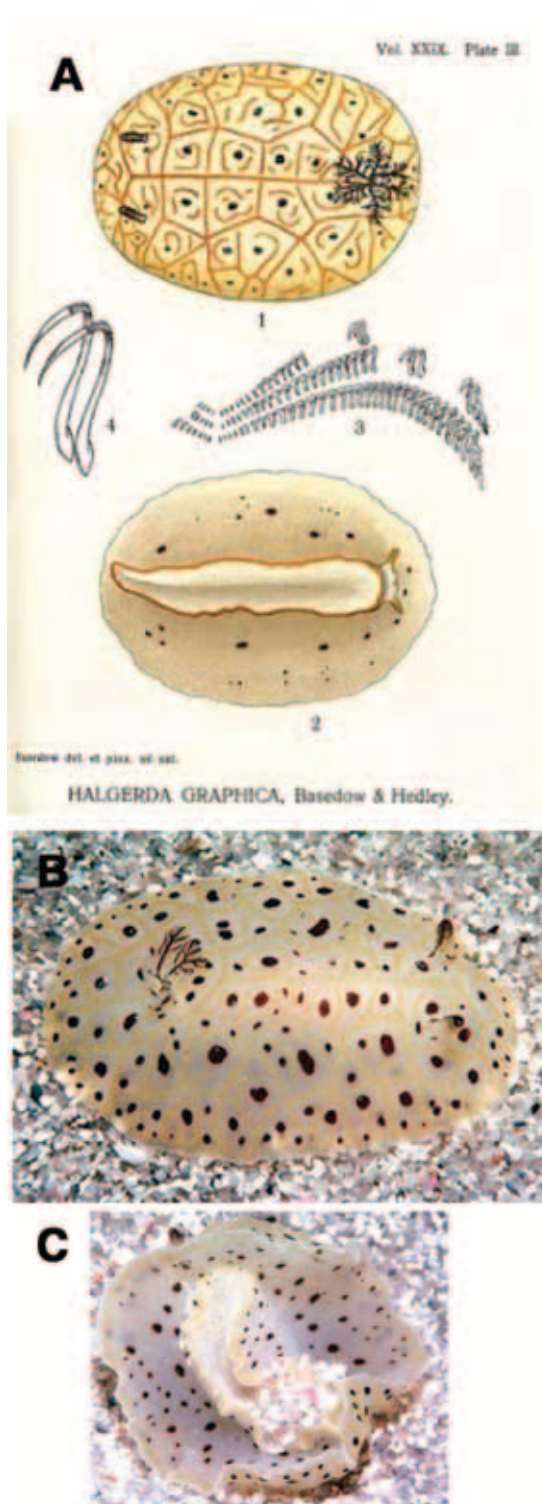


FIGURE 1. A. *Halgerda grafica* Basedow and Hedley, 1905, from the original color plate. B. *Halgerda grafica* South Australian Museum, (TD16542), photographed and collected by N. Holmes, 1990. Dorsal view. C. Ventral view.

**BUCCAL ARMATURE.**— The buccal mass has dark spots. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the specimen collected in 1990 is: 43x30.0.30 (TD16542) (Fig. 2A). The radular formula of the specimen collected in 1904 could not be determined due to poor preservation and deterioration of the radula. The three outer teeth are much smaller than the inner and middle lateral teeth and the outer two teeth have tiny denticles (Fig. 2B). The 8 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 2C) and are arranged in a shallow V-shaped pattern in the center of the radula. The middle lateral teeth are hamate (Fig. 2D) with long, pointed hooks. They have a flattened flange, which overlaps the adjacent tooth.

**REPRODUCTIVE SYSTEM.**— The reproductive system is triaulic (Fig. 3). The long ampulla is tubular, curved into a complete loop and protrudes away from the bursa and prostate. The ampulla narrows into the post-ampullary duct, which bifurcates into the vas deferens and oviduct. The long oviduct enters the female gland mass. The female gland mass is about the same size as the bursa copulatrix. The long 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 deferent duct leaves the distal prostate in a long duct that curves into one loop and multiple half-loops, then enters the wide penial bulb. The long uterine duct emerges from the female gland mass and joins the ovoid receptaculum seminis near its base. The duct con-

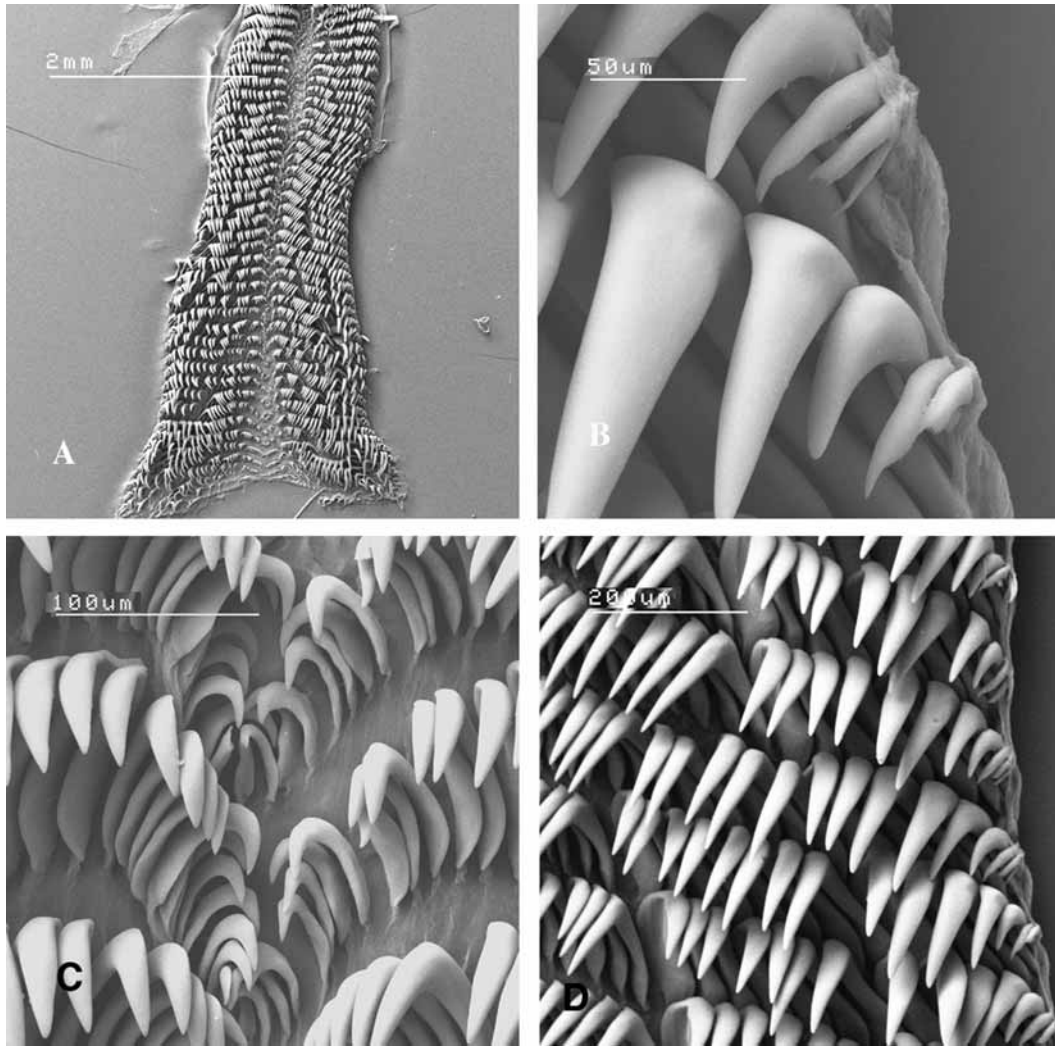


FIGURE 2. Radular morphology of *Halgerda graphica* (TD16542). A. Entire radula. Scale = 2 μm. B. Outer lateral teeth. Scale = 50 μm. C. Inner lateral teeth. Scale = 100 μm. D. Middle lateral teeth. Scale = 20 μm.

necting the receptaculum and the bursa is long and coiled. The receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. It lies under the bursa, but is not embedded in the prostate. The prostate does not completely cover the bursa copulatrix as is common in other, more highly derived species of *Halgerda*, but lies in a thin layer over two-thirds of the bursa. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit into the bulbous vagina that is adjacent to the base of the penial sheath, is a muscular sphincter. The vagina has long folds in the walls and tubercular glands on the exterior. The common genital aperture is wide, large and has long fleshy folds that extend through the body wall. The opening of the female gland mass is adjacent to the genital aperture.

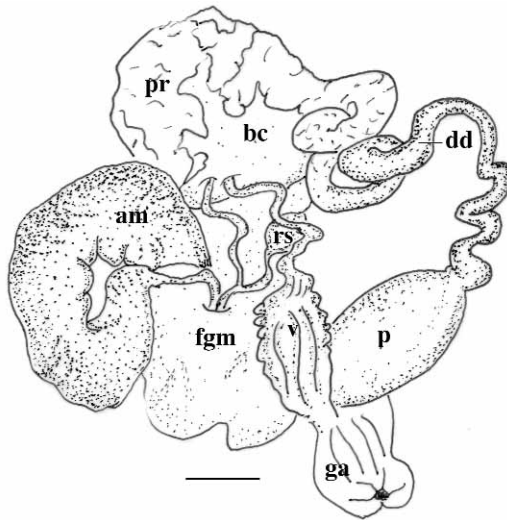


FIGURE 3. Reproductive morphology of *Halgerda grafica*. Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.25 mm.

convoluted deferent duct, a bulbous penial sheath and a wide, muscular vagina. Radular characters also have similarities to other *Halgerda* species. Those characters are hooked mid-lateral teeth, finely denticulate outer teeth that are much smaller than the remaining teeth, and small inner lateral teeth.

Because of the similarity in external coloration of *Halgerda grafica* to *H. gunnessi* Fahey and Gosliner, 2001, *H. johnsonorum* Carlson and Hoff, 2000 and *H. willeyi* Eliot, 1904, these three are herein compared and contrasted to *H. grafica*. However, because Carlson and Hoff (2000) have already compared *H. grafica* to *H. okinawa*, we will not repeat what they have already done. Neither will we repeat what Fahey and Gosliner said when they compared *H. gunnessi* to *H. johnsonorum* and to *H. formosa* Bergh, 1880, nor what Carlson and Hoff (2000) had to say when they compared *H. johnsonorum* to *H. willeyi*. Rather, we encourage reference to their respective papers. Here we concentrate on comparing the external morphology of *Halgerda grafica* to its most similar species.

All four species of greatest concern to us, *Halgerda grafica*, *H. gunnessi*, *H. johnsonorum* and *H. willeyi*, have a white or gray-white ground color with yellow to yellow-orange ridge crests. *Halgerda grafica* has low ridges without tubercles as do *H. gunnessi* and *H. johnsonorum*. Only *H. willeyi* has prominent tubercles. Although both *H. grafica* and *H. johnsonorum* have dark spots or markings in the ridge concavities, only *H. grafica* has the "hieroglyphic markings" described by Basedow and Hedley. These markings consist of a dark spot at the center of the concavity surrounded by dark circles and lines (Fig. 1). The other two species, *H. gunnessi* and *H. willeyi* may also have dark lines or markings, but both lack the associated spots.

The coloration of the mantle edge also distinguishes these four species. *Halgerda grafica* does not have perpendicular dark markings along the mantle edge, but the edge markings of *H. johnsonorum* appear as continuous lines, which extend upward and into the ridge concavities on the dorsum. The dark perpendicular lines on the mantle margin of *H. willeyi* also extend up into the

## DISCUSSION

Although Basedow and Hedley (1905) described the external and radular morphology of *Halgerda grafica*, these authors did not illustrate or describe the reproductive morphology. Despite this, based on the unique color pattern of this species, there is little doubt that the specimens examined for this study are *Halgerda grafica*. Other authors (Coleman 1975, 2001; Kay 1979; Kay and Young 1969; Wells and Bryce 1993) have erroneously attributed the name *Halgerda grafica* to other species. Wells and Bryce, mislabeled a specimen of *Halgerda gunnessi* as *H. grafica* Basedow and Hedley, 1905; Kay misidentified a specimen of *H. terramtuensis* as *H. grafica*; and Coleman (1975, 2001) misidentified a specimen of *H. willeyi* as *H. grafica*.

Examination of the reproductive morphology reveals similar characters to other *Halgerda* such as a two-part prostate, a long,

ridge cavities, but they are more numerous when compared to *H. graphica*. *Halgerda gunnessi* does not have marginal lines (see Fahey and Gosliner 2001).

The ventral surfaces of the four species are not similar in that there are irregularly scattered dark spots without lines only on *Halgerda graphica*. *Halgerda johnsonorum* and *Halgerda willeyi* have black lines; *H. gunnessi* has no markings on its ventrum.

The coloration on the rhinophores and gills differs among the species. *Halgerda graphica* has dark coloration on the tips of the rhinophores and a dark line on the posterior side. This is similar to *H. gunnessi*. The other species have either dark spots (*H. johnsonorum*, *H. willeyi*) or dark spots plus a dark stripe on the rhinophores (*H. johnsonorum*) and large gills. The gill of *H. graphica* is small and darkly colored. The gill of *H. willeyi* is sparsely pinnate with dark speckles. The gill of *H. johnsonorum* is large and has dark spots, and the gill of *H. gunnessi* is large, feathery and has dark lined branches and a dark tip.

With regard to the internal morphology, *Halgerda graphica* has radular characters similar to those of *H. gunnessi* and *H. willeyi*. All three also have three small outer teeth. *H. johnsonorum* is distinct, having six outer teeth, with the penultimate being bifid. *Halgerda graphica* has two finely denticulate outer lateral teeth; the outer three of *H. willeyi* and *H. gunnessi* are not denticulate.

The reproductive morphology of *Halgerda graphica* is most similar to *H. willeyi*. The obvious differences between the two are that the deferent duct of *H. graphica* is much longer and more convoluted than in *H. willeyi* and the vaginal duct of *H. graphica* is much wider with the vagina, being much larger with tubercular glands on the exterior. A glandular vagina is not found in any of the other three species. Both *Halgerda graphica* and *H. gunnessi* have a vaginal sphincter.

The present study confirms the combination of external and internal morphological characters that identify *Halgerda graphica* and distinguish it from the four externally most similar species. The external characters that distinguish this species in the field are: the "hieroglyphic" yellow and black markings on the dorsum, no dark lines on the mantle edge, dark-tipped rhinophores with a posterior medial line, a small, dark gill and small, dark spots on the ventral surface.

#### ***Halgerda dichromis* Fahey and Gosliner, 1999**

(Figs. 4–5)

**MATERIAL EXAMINED.**— V8234, one specimen, dissected, 42 mm, Scottburgh, Kwazulu, Natal, South Africa, 25 m deep, collected by V. Fraser, 15 January 2000; V8233, one specimen, dissected, 20 mm, Park Rynie, KwaZulu, Natal, South Africa, 25 m deep, collected by V. Fraser, 28 December 1999; V8232, one specimen, dissected, 16 mm, Park Rynie, KwaZulu, Natal, South Africa, 25 m deep, collected by V. Fraser, 21 January 2000.

**EXTERNAL MORPHOLOGY.**— The external morphology of the specimens examined for this study are as described by Fahey and Gosliner with some color variation. The variation includes the presence of dark half-lines or spots on the dorsum of some specimens, in place of a heavy, dark line. The more juvenile specimens may not have any dark markings at all. Variations in the external color within this species are shown in Figures 4A–C.

**RADULAR MORPHOLOGY.**— There were no differences noted in the radular morphology between the recent specimens examined (Figs 5A–D) and Fahey and Gosliner's (1999) original description and line drawings. Figure 5A–D are the first SEMs of the radula of this species.

**REPRODUCTIVE SYSTEM.**— There were no differences in the sexually mature specimens examined for this study (Fig. 6) and Fahey and Gosliner's (1999) original description of *Halgerda dichromis*.

**REMARKS.**— *Halgerda dichromis* was described from a single specimen collected in 1980

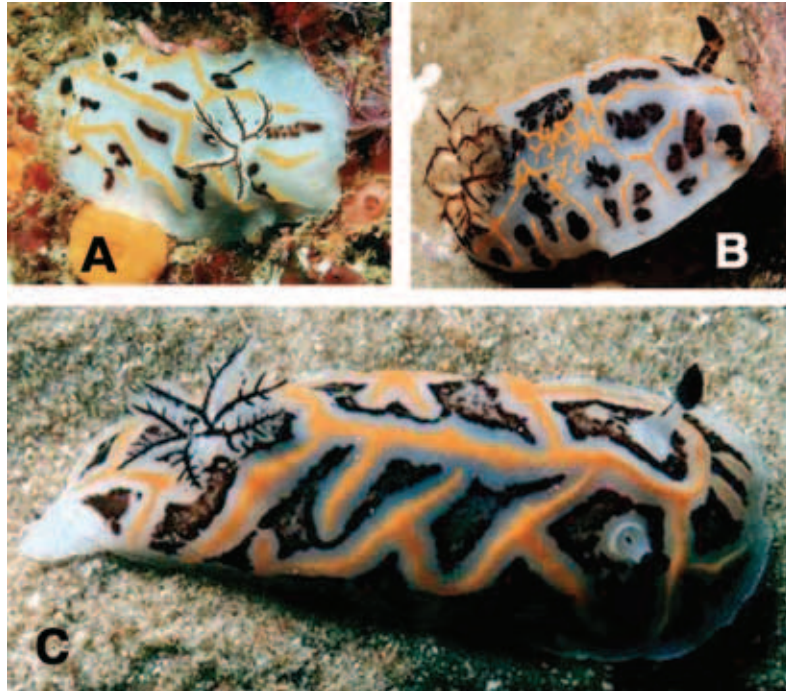


FIGURE 4. Color variation of *Halgerda dichromis*. A–C, Photographed and collected by V. Fraser, 2000.

from Durban Harbor, South Africa. Since the original description, additional specimens have been collected and/or photographed from the same locality (present study) and, thus, allow a further examination of the species.

*Halgerda dichromis* has a variable external coloration (Figs. 4A–C). The coloration of the holotype includes orange and black lines that form a reticulate pattern on the notum (Fahey and Gosliner 1999). Other patterns include having only orange or yellow lines with dark lines or splotches and without dark markings at all, particularly on more juvenile specimens.

*Halgerda dichromis* externally is most similar to *H. formosa* (see Fahey and Gosliner 1999 for details).

#### ***Halgerda okinawa* Carlson and Hoff, 2000**

(Figs. 6–8)

**MATERIAL EXAMINED.**—CASIZ 144092, one specimen, 80 mm, dissected. Izu Peninsula, Japan. 22 m depth, collected by R. Nakano, April 2000; CASIZ 144093, one specimen, 46 mm, dissected. Izu Peninsula, Japan. 20 m depth, collected by R. Nakano, May 2000; CASIZ 144097, one specimen, 50 mm, dissected. Izu Peninsula, Japan. 22 m depth, collected by R. Nakano, April 2000.

**EXTERNAL MORPHOLOGY.**—The external morphology of the specimens examined from the Izu Peninsula have the same range of variation as noted in the original description of *H. okinawa* (Carlson and Hoff, 2000). Those variations include number, length and width of the dark streaks, number of lines on the inner surface of the branchia and presence of a yellow mantle margin on the specimens examined for this study. One of the specimens we examined from the Izu Peninsula has a paler shade of white on the dorsum with pale yellow tubercles (Fig. 7A). The other specimen (Fig.

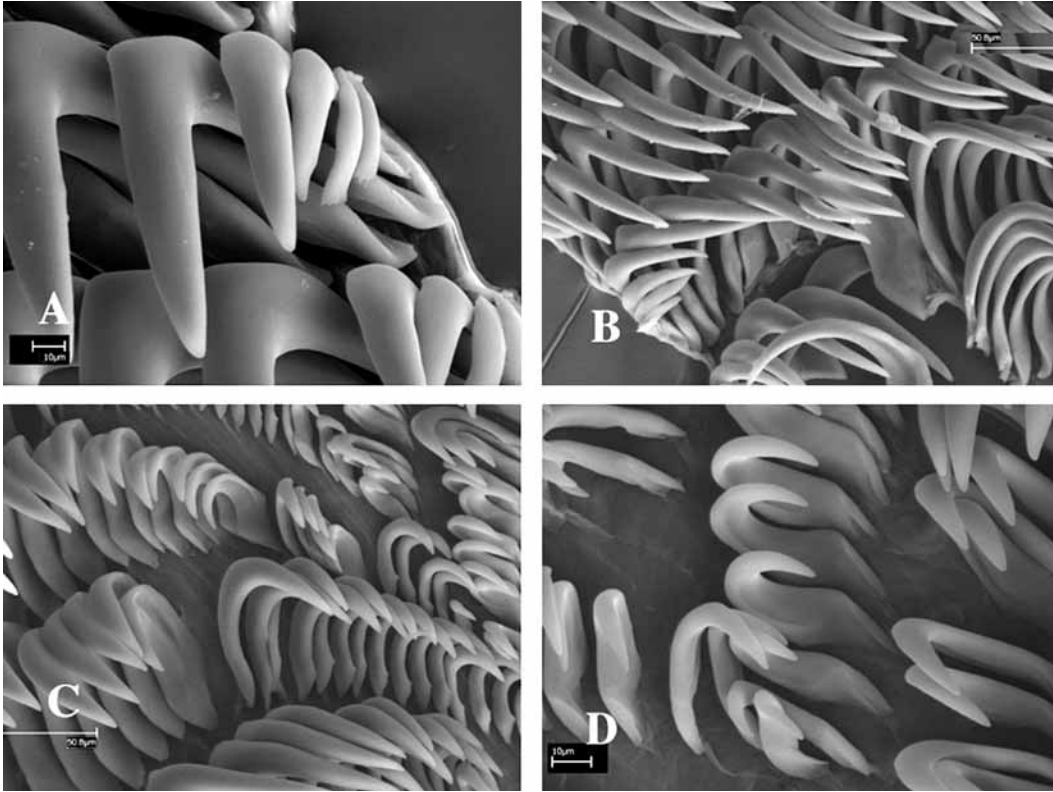


FIGURE 5. Radular morphology of *Halgerda dichromis* (V8233). A. Inner lateral teeth. Scale = 10µm. B. Middle lateral teeth. Scale = 50.8 µm. C. Middle lateral teeth. Scale = 50.8 µm. D. Outer lateral teeth. Scale = 10 µm.

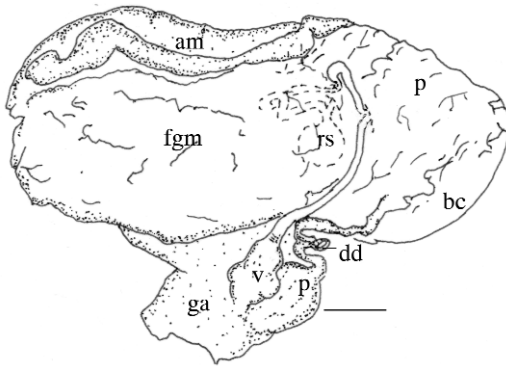


FIGURE 6. Reproductive morphology of *Halgerda dichromis* (V8234). Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.8 mm.

7B) matched the original description from Okinawa. A specimen from Lembah Strait (Fig. 7C) had few dark lines but more spots than the more commonly found specimen (Figs 7D–E).

**RADULAR MORPHOLOGY.**— There were no differences noted in the radular morphology between the recent specimens examined (Fig. 8) and Carlson and Hoff's (2000) original description.

**REPRODUCTIVE MORPHOLOGY.**— The reproductive morphology of the specimens examined for the present study (Fig. 9) were nearly identical to the original description. The exception is that the vagina is wider in the specimens we examined than was illustrated and drawn by Carlson and Hoff (2000).

**REMARKS.**— Since the original description of *H. okinawa*, additional specimens collected from the Izu Peninsula, Japan and pho-



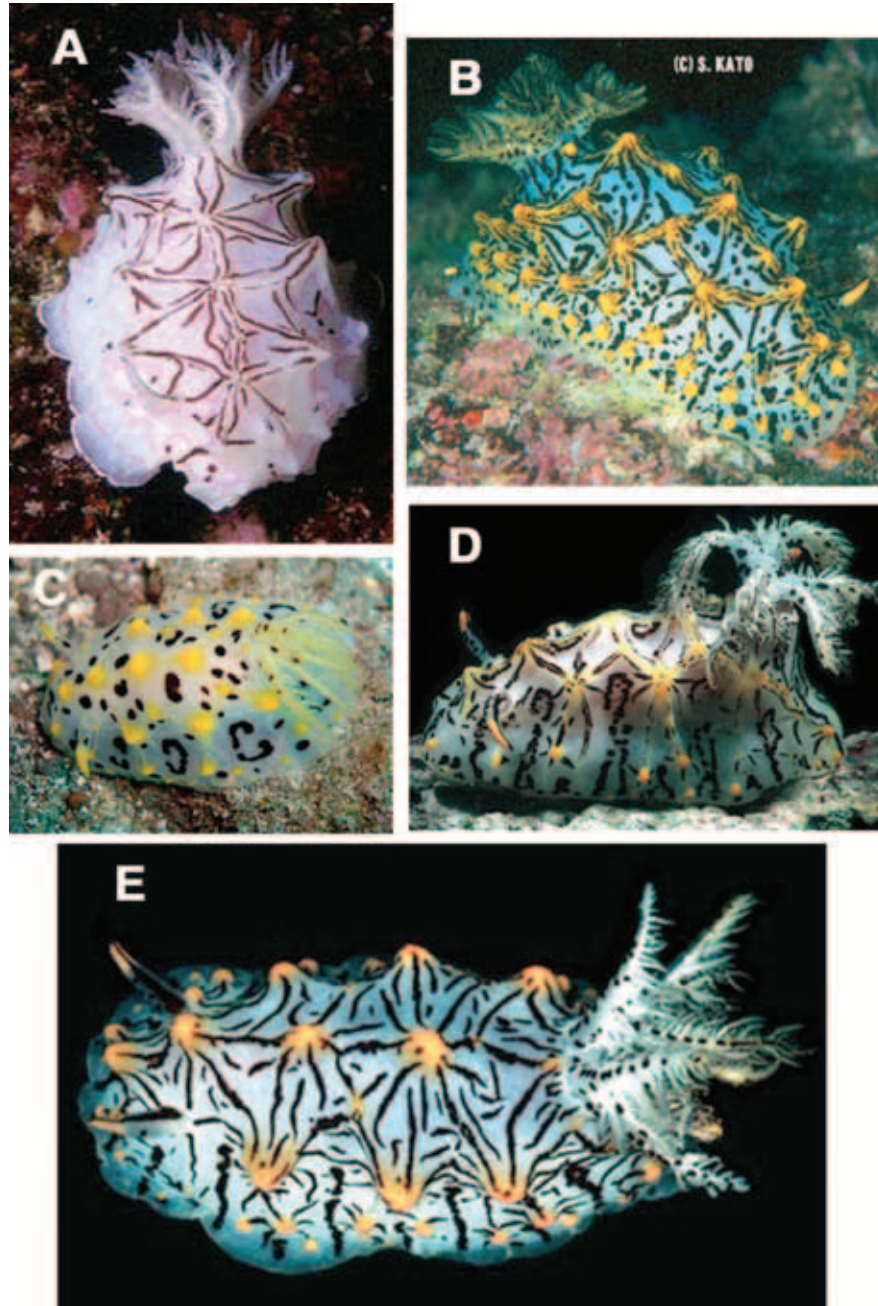


FIGURE 7. Color variation of *Halgerda okinawa*. A. Photographed by Hachijo. B. Photographed by S. Kato, 2001. C. Photographed by Carine Scheurs. D. Photographed by Carlson and Hoff. E. Photographed by R. Bolland.

tographed elsewhere show variation in the external color pattern (Fig. 7C–D). Differences between *Halgerda okinawa* and *H. graphica* were discussed thoroughly by Carlson and Hoff (2000).

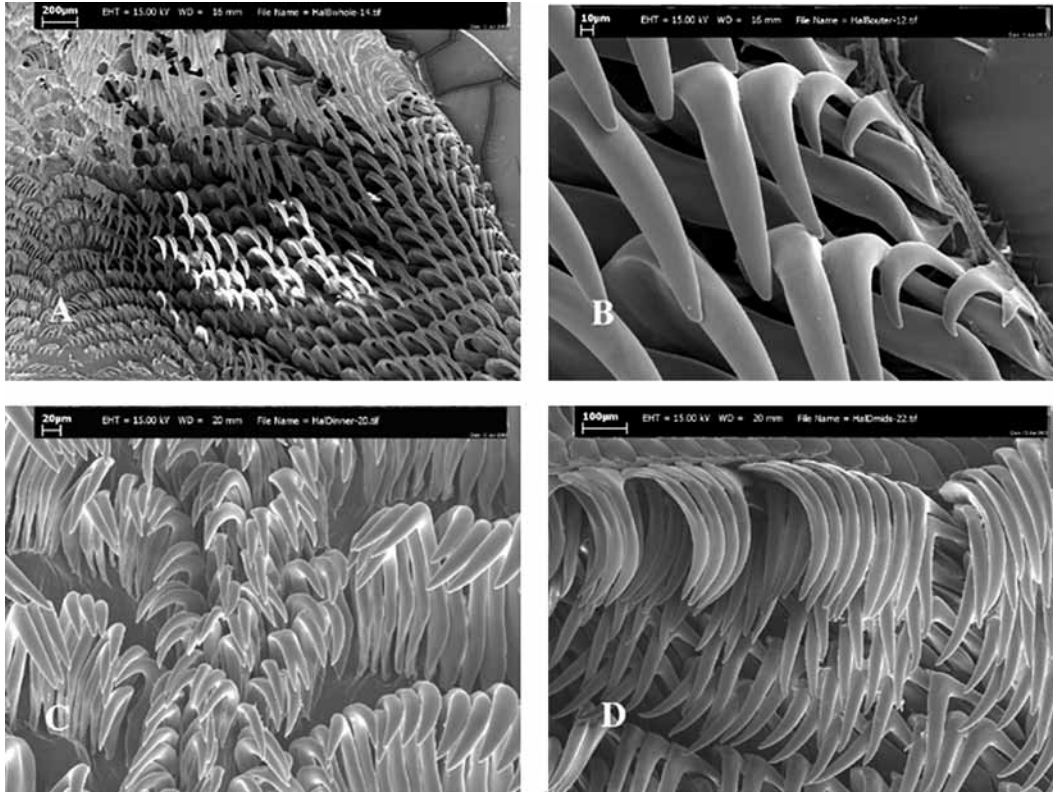


FIGURE 8. Radular morphology of *H. okinawa* (CASIZ 144093). A. Section of the radula. Scale = 200  $\mu$ m. B. Outer lateral teeth. Scale = 10  $\mu$ m. C. Inner lateral teeth. Scale = 20  $\mu$ m. D. Middle lateral teeth. Scale = 30  $\mu$ m.

### *Halgerda willeyi* Eliot, 1904

(Figs 9–11)

= *Halgerda willeyi* in Coleman, 2001, p. 58, center photo, AMPI 117; and in Coleman, 1975 p. 63, Plate 170.

**MATERIAL EXAMINED.**— CASIZ 144095, two specimens: 35 mm, 51 mm (dissected). 20 m depth, collected by R. Nakano, March 2000; CASIZ 144096, three specimens; 25mm, 28 mm, 31 mm (dissected). 21 m depth, collected by R. Nakano, April 2000; CASIZ 144121, one specimen, 40 mm, dissected. 41.5 m depth. 1.3 km ENE Maeki-zaki, Seragaki, Okinawa, Ryukyu Islands, Japan, collected by R. Bolland, January 2001; CASIZ 144123, one specimen, 30 mm. 41.5 m depth. 1.3 km ENE Maeki-zaki, Seragaki, Okinawa, Ryukyu Islands, Japan, collected by R. Bolland, 8 December 2000; CASIZ 134919, one specimen, 74 mm. 43 m depth. 1.3 km ENE Maeki-zaki, Seragaki, Okinawa, Ryukyu Islands, Japan, collected by R. Bolland, 17 August 2000; BMNH, one specimen, 60 mm. Intertidal. Bapper Bay, Aden, Yemen, leg. Sgt. Howse, RAMC. October 1966.

**EXTERNAL MORPHOLOGY.**— Both specimens examined for this study are externally similar to other specimens of *H. willeyi* published elsewhere. However, this species displays great variation in external coloration (Figs. 10A–D; also see Gosliner et al. 1996; Marshall and Willan 1999; Ono 1999; Coleman 1975, 2001; Bolland 2003; Rudman 2003).

**RADULAR MORPHOLOGY.**— There were no differences noted in the radular morphology

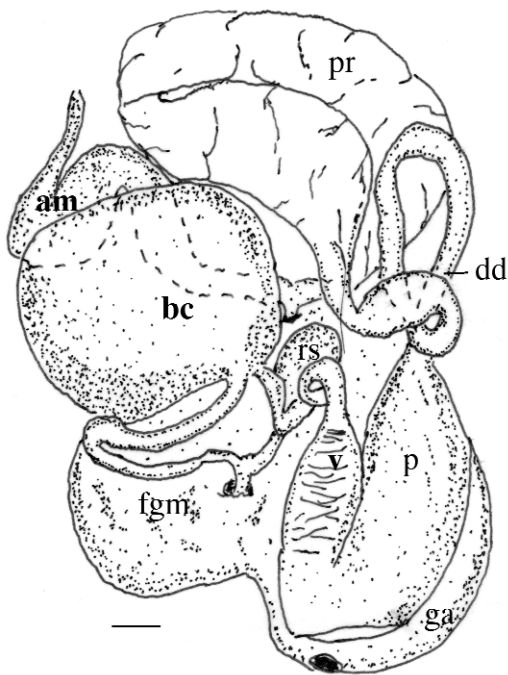


FIGURE 9. Reproductive morphology of *H. okinawa* (CASIZ 144093). Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.5 mm.

between the recent specimens examined (Figs. 11A–D) and in both the original description (Eliot, 1904) and in Rudman's (1978) description.

**REPRODUCTIVE SYSTEM.**— The reproductive morphology of the specimens examined for this study (Fig. 9) match the description provided by Rudman (1978).

**REMARKS.**— *Halgerda willeyi*, at first glance, most closely resembles *H. iota* in external morphology, at least based on the original description of *H. iota* (Yonow 1993). The phylogenetic analysis of *Halgerda* (Fahey and Gosliner 2001) supports a close, morphologically indistinguishable relationship. Regrettably, the reproductive anatomy of *H.*

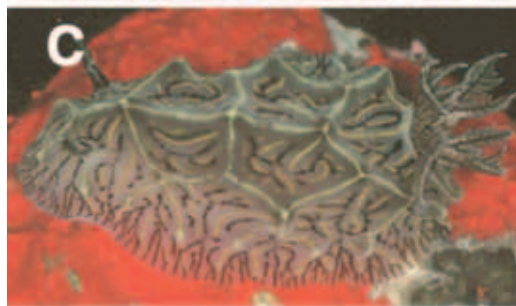
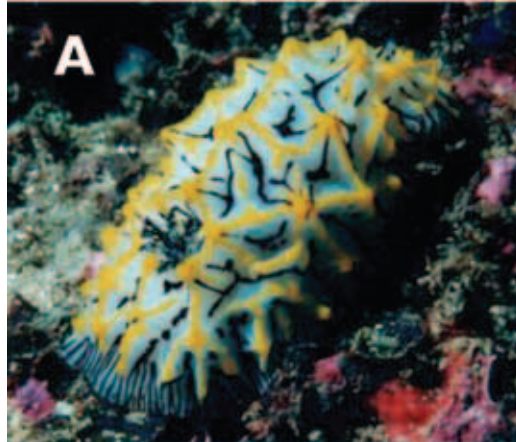


FIGURE 10. Color variation of *Halgerda willeyi*. A. Jervis Bay, NSW, Australia; photographed by L. Wiseman. B. Hachijo Island, Japan; photographed by N. Masatoshi. C. Okinawa; photographed by R. Bolland. D. Lord Howe Island; photographed by Ian Hutton.

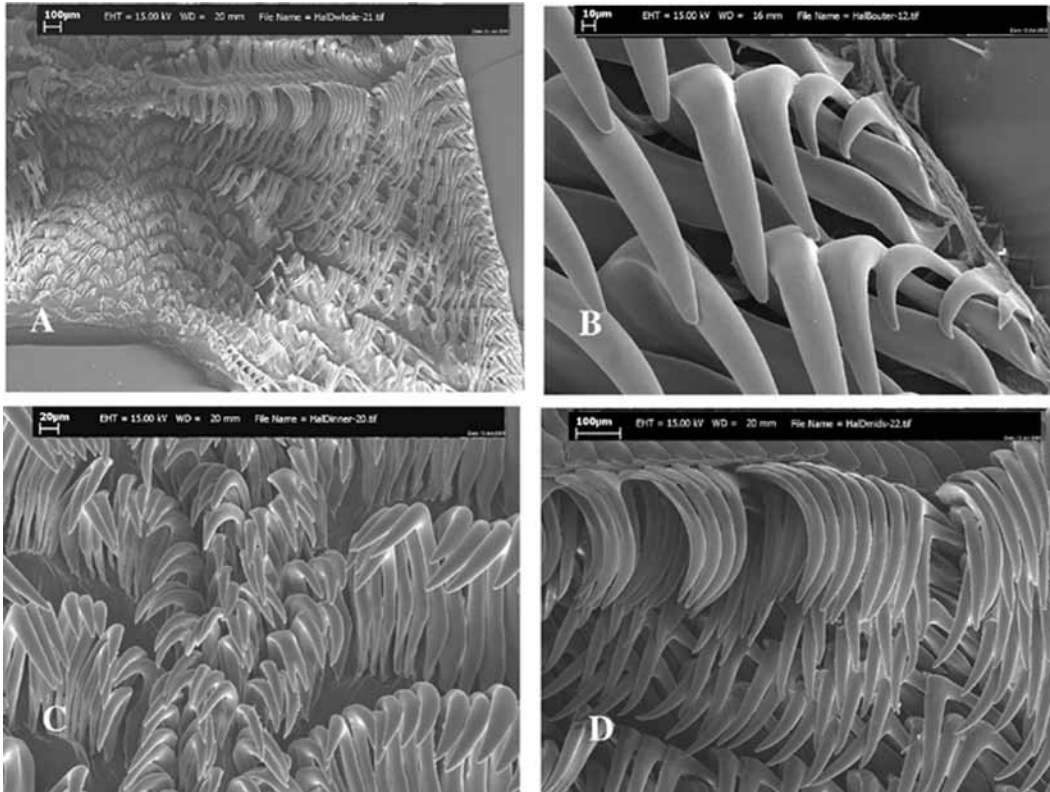


FIGURE 11. Radular morphology of *H. willeyi* (CASIZ 134919). A. Section of the radula. Scale = 200  $\mu\text{m}$ . B. Outer lateral teeth. Scale = 10  $\mu\text{m}$ . C. Inner lateral teeth. Scale = 20  $\mu\text{m}$ . D. Middle lateral teeth. Scale = 30  $\mu\text{m}$ .

*iota* is unknown, and until additional specimens of *H. iota* are collected and the internal anatomy examined, no further comparison of *H. iota* to other species is possible.

*Halgerda willeyi* also is externally similar to other *Halgerda* species. For instance, Carlson and Hoff compared *H. willeyi* to *H. okinawa* and to *H. johnsonorum* (see Carlson and Hoff 2000). There are also some external similarities between *H. willeyi* and *H. elegans* (see Fig. 7C [from Okinawa SlugSite and SeaSlug Forum; photo by B. Picton, SeaSlug Forum, March 8, 2000]); both species have dark lines perpendicular to the mantle edge and yellow-orange lines along the ridge crests. However, the dark marginal lines of *H. elegans* do not extend to as large a degree from the mantle edge throughout the dorsum and into the ridge concavities as they do with *H. willeyi*. The dark lines on specimens of *H. willeyi* are much more numerous, with complex patterns that merge and interweave with the yellow or orange lines all over the dorsum. The yellow ridge crests are the most notable feature of *H. elegans* whereas it is the dark lines with the orange or yellow ridges that are most notable on specimens of *H. willeyi*.

The gill in these two species is quite different as well. In *H. elegans*, it is sparse, irregularly pinnate and has dark coloration encircling the top half of each of the leaves; in *H. willeyi*, is quite bushy, feathered and has a dark line extending the length of each of the leaves.

The rhinophores of the two species also differ in coloration. Those of *H. willeyi* have dark stripes, those of *H. elegans* have black subapical coloration.

The reproductive morphology is vastly different between *Halgerda willeyi* and *H. elegans*. The

most obvious differences are that *H. willeyi* has a large, bulbous penial sheath and a muscularized vagina, whereas *H. elegans* has a tubular penis and a glandular vagina.

Other conspicuous internal differences are noted with the radular morphology of the two species. *Halgerda elegans* has fimbriate outer lateral teeth, with some specimens having multifid teeth with or without pronounced flanges (Bergh 1905; Gosliner and Fahey 1998). The teeth of *H. willeyi* are simple, hamate and the outer two or three are flattened plates (Rudman 1978; Carlson and Hoff 2000).

Although color patterns can vary enormously within *Halgerda* species, as apparent from recently published photographs cited herein, field identifications can be assisted by consideration of not just one or two characters, taken by themselves, but by the combination of characters observed. Examination of the internal morphology will probably be necessary to confirm the more difficult-to-identify specimens.

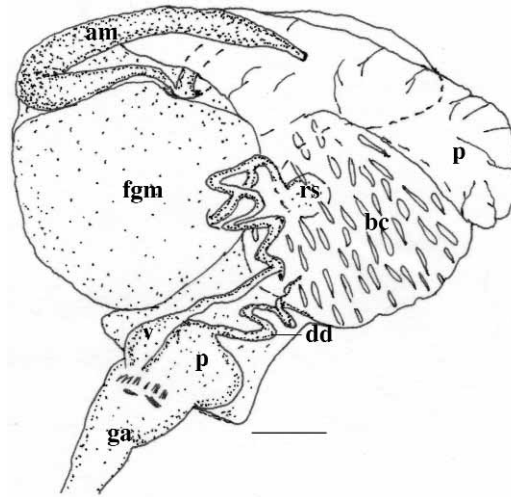


FIGURE 12. Reproductive morphology of *H. willeyi* (CASIZ 144095). Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.8 mm.

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#### LITERATURE CITED

- BASEDOW, H., AND C. HEDLEY. 1905. South Australian Nudibranchs, and an enumeration of the known Australian species. *Transactions of the Royal Society of South Australia* 20:34–60.
- BERGH, R. 1880. Beitrage zur Kenntniss der japanischen nudibranchien. I. *Verhandlungen der koniglich-kaiserlichen Zoologisch-botanischen Gesellschaft in Wien* 30:155–200.
- BERGH, R. 1905. *Die Opisthobranchiata der Siboga-Expedition*. Monographie. 1–248, pls. 1–20 pp.
- BOLLAND, R. 2003. *Okinawa SlugSite*, vol. 2003. <http://rfbolland.com/okislugs/index.html>.
- CARLSON, C., AND P.J. HOFF. 1973. Three new *Halgerda* species. (Doridoidea: Nudibranchia: Opisthobranchia) from Guam. *The Veliger* 36(1):16–26.
- CARLSON, C., AND P.J. HOFF. 2000. Three new Pacific species of *Halgerda* (Opisthobranchia: Nudibranchia: Doridoidea). *The Veliger* 43(2):154–163.
- COLEMAN, N. 1975. *What shell is that?* Paul Hamlyn Pty. Limited, Sydney, Australia. 308 pp.
- COLEMAN, N. 2001. *1001 Nudibranchs*. Neville Coleman's Underwater Geographic Pty. Limited, Springwood. 144 pp.

- DEBELIUS, H. 1998. *Nudibranchs and Sea Snails: Indo-Pacific Field Guide*, 2 edition. IKAN-Unterwasserarchiv, Frankfurt, Germany. 321 pp.
- ELIOT, C. 1904. On some nudibranchs from East Africa and Zanzibar. Part III. *Proceedings of the Zoological Society of London* 1903(2):354–385.
- FAHEY, S.J., AND T.M. GOSLINER. 1999a. Description of three new species of *Halgerda* from the Western Indian Ocean with a redescription of *Halgerda formosa*, Bergh, 1880. *Proceedings of the California Academy of Sciences* 51(8):365–383.
- FAHEY, S.J., AND T.M. GOSLINER. 1999b. Preliminary phylogeny of *Halgerda* (Nudibranchia: Halgerdidae) from the tropical Indo-Pacific with descriptions of three new species. *Proceedings of the California Academy of Sciences* 51(11):425–448.
- FAHEY, S.J., AND T.M. GOSLINER. 2000. New records of *Halgerda* Bergh, 1880 (Opisthobranchia: Nudibranchia) from the deep Western Pacific Ocean, with descriptions of four new species. *Zoosystema* 22(3):471–498.
- FAHEY, S.J., AND T.M. GOSLINER. 2001a. On the genus *Halgerda* (Nudibranchia: Halgerdidae) from Western Australia with descriptions of four new species. *Bollettino Malacologico* 37(5–8):55–76.
- FAHEY, S.J., AND T.M. GOSLINER. 2001b. The phylogeny of *Halgerda* (Opisthobranchia, Nudibranchia) with the description of a new species from Okinawa. *Zoologica Scripta* 30(3):199–213.
- GOSLINER, T.M., D.W. BEHRENS AND G.C. WILLIAMS. 1996. *Coral Reef Animals of the Indo-Pacific: Animal Life from Africa to Hawaii, Exclusive of the Vertebrates*. Sea Challengers, Monterey, California. 314 pp.
- GOSLINER, T.M., AND S.J. FAHEY. 1998. Description of a new species of *Halgerda* from the Indo-Pacific with a redescription of *Halgerda elegans* Bergh, 1905. *Proceedings of the California Academy of Sciences* 50(15):347–359.
- KAY, E.A. 1979. *Hawaiian Marine Shells*. Special Publication edition. Bernice P. Bishop Museum, Honolulu. 653 pp.
- KAY, E.A., AND D.K. YOUNG. 1969. The Doridacea (Opisthobranchia: Mollusca) of the Hawaiian Islands. *Pacific Science* 23:172–231.
- MARSHALL, J.G. AND R.C. WILLAN. 1999. *Nudibranchs of Heron Island, Great Barrier Reef*. Backhuys, Leiden. 257 pp.
- ONO, A. 1999. *Opisthobranchs of Kerama Islands*. TBS-Britannica Co., Ltd., Tokyo. 183 pp.
- RUDMAN, W.B. 1978. The dorid opisthobranch genera *Halgerda* Bergh and *Sclerodoris* Eliot from the Indo-West Pacific. *Zoological Journal of the Linnean Society, London* 68:59–87.
- RUDMAN, W.B. 2003. *SeaSlug Forum*, vol. 2003. <http://www.seaslugforum.net>.
- WELLS, F.E., AND C.W. BRYCE. 1993. *Sea Slugs of Western Australia*. Western Australian Museum, Perth. 184 pp.
- WILLAN, R.C., AND G.D. BRODIE. 1989. The nudibranch *Halgerda aurantiomaculata* (Allan, 1932) (Dorid-idea: Dorididae) in Fijian waters. *The Veliger* 32(1):69–80.
- YONOW, N. 1993. Opisthobranchs from the Maldive Islands, including descriptions of seven new species (Mollusca: Gastropoda). *Revue Française d'Aquariologie* 20(4):97–130.