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THE GENUS *PECTENODORIS* (NUDIBRANCHIA:
CHROMODORIDIDAE) FROM THE INDO-PACIFIC, WITH THE
DESCRIPTION OF A NEW SPECIES

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The genus *Pectenodoris* is reviewed. The genus contains only *Pectenodoris trilineata* and a new species, *Pectenodoris aurora*, described here. New records of *P. trilineata* from the Philippines and Papua New Guinea and more information about the variation present in *P. trilineata* are presented. The two species overlap in much of their ranges, throughout the western margins of the Pacific, and are similar in color pattern. They are part of different larger groups of similarly colored, sympatric chromodorids discussed here.

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Rudman (1984) described the monotypic genus *Pectenodoris*. He hypothesized that many unknown, small chromodorids would be found to belong to this genus. One such small species has recently been collected and is described here as *Pectenodoris aurora*.

Increased interest in colorful chromodorid nudibranchs has improved collections and knowledge of the fauna of the tropical Indo-Pacific. Traditionally, chromodorid nudibranchs have been described based on their external morphology, color pattern, radular morphology and reproductive anatomy. The arrangement and size of defensive mantle glands has previously been used to characterize genera, but not to distinguish between congeneric species (Rudman 1984, 1986). Mantle gland configuration was found to be important in separating closely related species of the chromodorid genus *Hypselodoris* (Gosliner and Johnson, in press). The variation pre-

sent in the mantle glands of the two *Pectenodoris* species is discussed here.

There are over three hundred species in the family Chromodorididae from the Indo-Pacific tropics (Gosliner and Draheim 1996). These large numbers can make it difficult to study relationships between species within large genera. One way of dealing with the enormity of the group has been the designation of color groups, groups of similarly colored species, that may or may not be closely related (Rudman 1982, 1983a, 1985, 1986). *Pectenodoris trilineata* had been included, by Rudman, in the "*Noumea purpurea* color group," based on its resemblance to *Noumea purpurea* Baba, 1949, *Noumea varians* (Pease, 1871), *Durvilledoris pusilla* (Bergh, 1874) and *Durvilledoris similis* Rudman, 1986. Once these distantly related species are placed into color groups, they can be identified, compared and discussed more easily (Rudman

1986). *Pectenodoris aurora* does not fit into this particular color group, but will be shown to be closer in color pattern to another group discussed by Rudman (1986).

SPECIES DESCRIPTIONS

Pectenodoris trilineata (Adams and Reeve, 1850)

(Figs. 1A, 2–4)

Goniodoris trilineata Adams and Reeve, 1850:68, pl. 17, fig.4.

Chromodoris virgata Bergh, 1905:160–162, pl. 4, fig. 11; pl. 14, fig. 47.

Pectenodoris trilineata (Adams and Reeve) Rudman, 1984:159–163, figs 29–31.

Pectenodoris trilineata (Adams and Reeve) Rudman, 1986:319–320, figs 1C, 5.

MATERIAL EXAMINED. — CASIZ 105638, one specimen, dissected, Bethlehem, Maricaban Island, Batangas Province, Luzon Island, Philippines, 22 m depth, 26 February 1995, T. M. Gosliner. CASIZ 083704, three specimens, one dissected, Devil's Point, SW side of Maricaban Island, Batangas Province, Luzon Island, Philippines, 8 m depth, 19 February 1992, T. M. Gosliner. CASIZ 083711, three specimens, Kirby's Rock, NW side of Maricaban Island, Batangas, Luzon Island, Philippines, 23 m depth, 18 February 1992, T. M. Gosliner. CASIZ 068813, one specimen, the Quarry, near Bunn village, 1 km south of Cape Croiselles, north of Madang, Papua New Guinea, 23 m depth, 8 August 1989, T. M. Gosliner. CASIZ 082924, one specimen, Rasch Passage, north coast near Madang Lagoon, Papua New Guinea, 9 m depth, 17 November 1990, T. M. Gosliner.

DISTRIBUTION. — *Pectenodoris trilineata* is known from the tropical western margins of the Pacific, bounded in the north by the Tropic of Cancer and the south by the Tropic of Capricorn. The northern-most limit of its distribution is the South China Sea (Adams and Reeve 1850), and the most southerly record of *P. trilineata* is from Heron Island, Capricornia Group, Great Barrier Reef, Australia (Rudman 1984, 1986). Bergh (1905) described this species as *Chromodoris virgata*, from the waters off of Sumbawa Island, Indonesia. Five new records of this species from Papua New Guinea and the Philippines are reported here. *Pectenodoris trilineata* is known from 8 to 23 m depth.

EXTERNAL MORPHOLOGY. — The variation observed in the nine newly collected specimens is consistent with that described by Rudman (1984, 1986). The animal from Devil's Point in the Philippines, CASIZ 083704, is pictured (Fig. 1A) as a comparison to *P. aurora*, the new member of the genus. All but two specimens examined here were found to have glands around the entire mantle, opening ventrally, but all animals had at least one, and up to three, enlarged posterior glands. When more than one gland was enlarged, those glands immediately adjacent and to the right of the central posterior gland were larger. The two aforementioned specimens differed only in the lack of all glands except the posterior ones (Fig. 2).

ALIMENTARY CANAL. — In all specimens examined, the length of the two portions of the buccal mass differed only slightly, while the width of the oral tube was about three times that of the muscular portion of the buccal mass. The jaws are small and delicate and very difficult to prepare for scanning electron microscopy, owing to the extreme reduction of the rodlets. The morphology of the jaw rodlets varies, from long and undivided, to others which are short and have multiple cusps (Fig. 3A). The radulae examined here display the same comb-like teeth described by Rudman (1984). The only notable difference is the lack of a vestigial, plate-like rachidian tooth (Figs. 3B–D). The two specimens examined here had radular formulae of $22 \times 6.0.6$ and $29 \times 15.0.15$. This is similar to that reported previously by Rudman (1984) for *P. trilineata*.

REPRODUCTIVE SYSTEM. — The arrangement of organs is triaulic (Fig. 4). The ampulla is wide and curved. It divides into a very long, convoluted prostate and an extremely short oviduct, which enters the female gland mass. The prostate narrows slightly into the long ejaculatory portion, which terminates in an elongate, narrow muscular penial bulb. The vaginal duct is narrow and elongate. The large, curved, pyriform receptaculum seminis is only slightly smaller than the ovoid bursa copulatrix. A wide duct connects the receptaculum seminis directly with the bursa copulatrix. The uterine duct emerges from the middle of the vagina, is long and narrow, and enters the female gland mass below the entrance of the oviduct to the mass. The female gland mass is large and completely developed. A small,



FIGURE 1. Living animals. A. *Pectenodoris trilineata* (Adams and Reeve, 1850), from Batangas, Luzon, Philippines (CASIZ 083704), photograph by T. M. Gosliner. B. Paratype of *Pectenodoris aurora* n. sp., from Bethlehem, Maricaban Island, Batangas, Luzon, Philippines (CASIZ 110443), photograph by T. M. Gosliner.

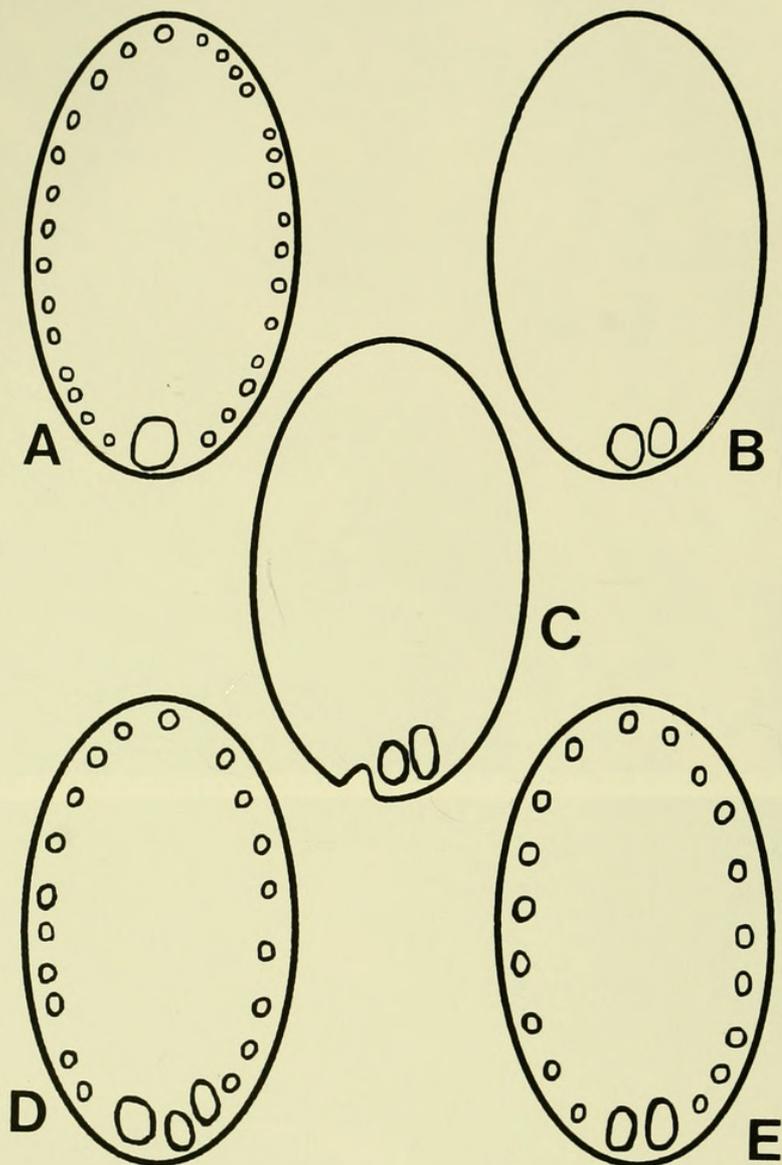


FIGURE 2. *Pectenodoris trilineata* (Adams and Reeve, 1850), distribution of mantle glands. A. CASIZ 105638, Philippines. B. CASIZ 083704, Philippines. C. CASIZ 068813, Papua New Guinea. D. CASIZ 083704, Philippines. E. CASIZ 083704, Philippines.

lobate vestibular gland is present near the distal end of the female gland mass.

DISCUSSION. — The defensive mantle glands of *Pectenodoris trilineata* are mentioned by Rudman (1984, 1986) as a series of large single mantle glands, opening ventrally. This description is consistent with present material, but some additional variation is noted (Fig. 2).

In this species, the ratio of the glandular oral tube length to the muscular portion of the buccal mass length has been described as four to one (Rudman 1984, 1986). In the specimens examined here, the length of the oral tube and the buccal mass was very similar. A difference in the width of the two portions was more apparent.

This difference in length may be an artifact of the degree of extension or contraction of the buccal mass at the time of preservation. The shape and configuration of the radular teeth was found to be the same as described by Rudman (1984), the only differences being the lack of a vestigial rachidian plate-like tooth and the presence of more lateral teeth in some specimens.

Rudman (1984) did not find a vestibular gland in his specimens, but mentioned a small glandular structure that might have been an undeveloped gland. In all of the specimens we examined a small, lobate vestibular gland was present (Fig. 4).

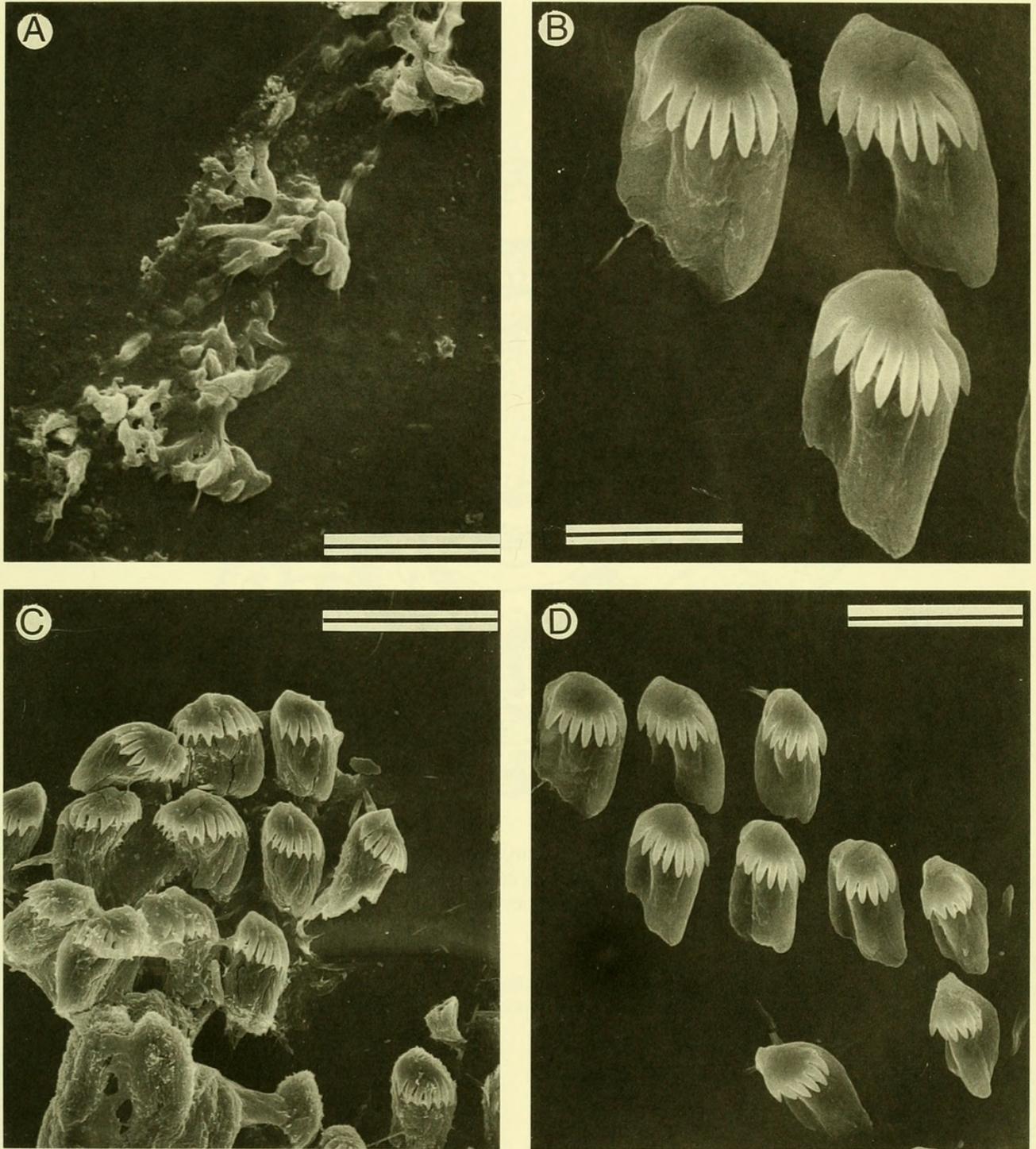


FIGURE 3. *Pectenodoris trilineata* (Adams and Reeve, 1850), scanning electron micrographs. A. Jaw rodlets, (CASIZ 105638), scale = 10 μm . B. Inner lateral teeth, (CASIZ 083704) scale = 7.5 μm . C. Lateral teeth (CASIZ 105638), scale = 20 μm . D. Lateral teeth, (CASIZ 105638), scale = 15 μm .

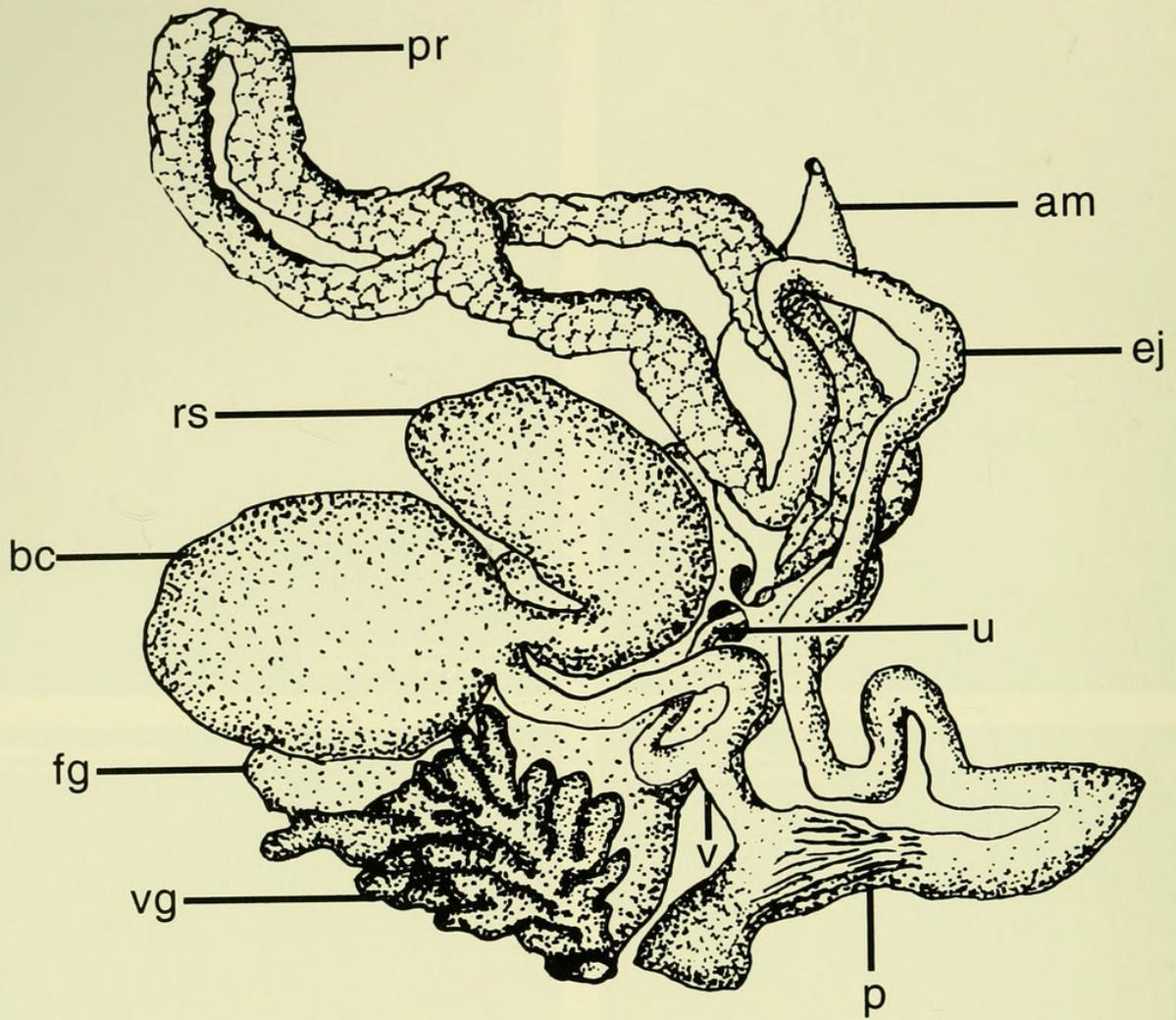


FIGURE 4. *Pectenodoris trilineata* (Adams and Reeve, 1850), reproductive system (CASIZ 083704). Abbreviations: am = ampulla, bc = bursa copulatrix, ej = ejaculatory portion of vas deferens, fg = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, u = uterine duct, v = vagina, vg = vestibular gland.

***Pectenodoris aurora* sp. nov.**
(Figs. 1B, 5–7)

TYPE MATERIAL. — Holotype: CASIZ 074702, one specimen, dissected, Seragaki Beach, ENE of Maekizaki, Ryukyu Islands, Okinawa, Japan, 58 m depth, 1 September 1989, R. F. Bolland. Paratypes: CASIZ 097631, two specimens, Batu Angus Point, Lembeh Strait, north Sulawesi, Indonesia, 28 October 1993, Pauline Fiene-Severns. CASIZ 110443, one specimen, dissected, Bethlehem, Maricaban Island, Batangas Province, Luzon Island, Philippines, 22 m depth, 21 April 1997, T. M. Gosliner. CASIZ 111059, one specimen, Horseshoe Cliffs, 1 km WNW of Onna Village, Ryukyu Islands, Okinawa, Japan, 10 m depth, 24 December 1994, R. F. Bolland.

ETYMOLOGY. — *Pectenodoris aurora* is named for Aurora, the Roman goddess of the

morning. This species is marked with all of the beautiful colors of a great sunrise.

DISTRIBUTION. — The geographical range of *P. aurora* is limited to the western edge of the Pacific. This species is known only from the Indo-Pacific tropics of the Philippines and Indonesia and sub-tropical, Okinawa, Japan. It ranges from 10 to 58 m depth.

EXTERNAL MORPHOLOGY. — The living animals are small, 6–8 mm in length (Fig. 1B). The body shape is oval with a wide mantle overlap. The mantle, body and foot are all light pink in color. This color darkens to maroon on the edges of the mantle and the posterior tip of the foot. Three parallel whitish yellow, continuous or interrupted longitudinal bands run from the rhinophores to the gills. These bands are each outlined by a thin opaque white line. The central and

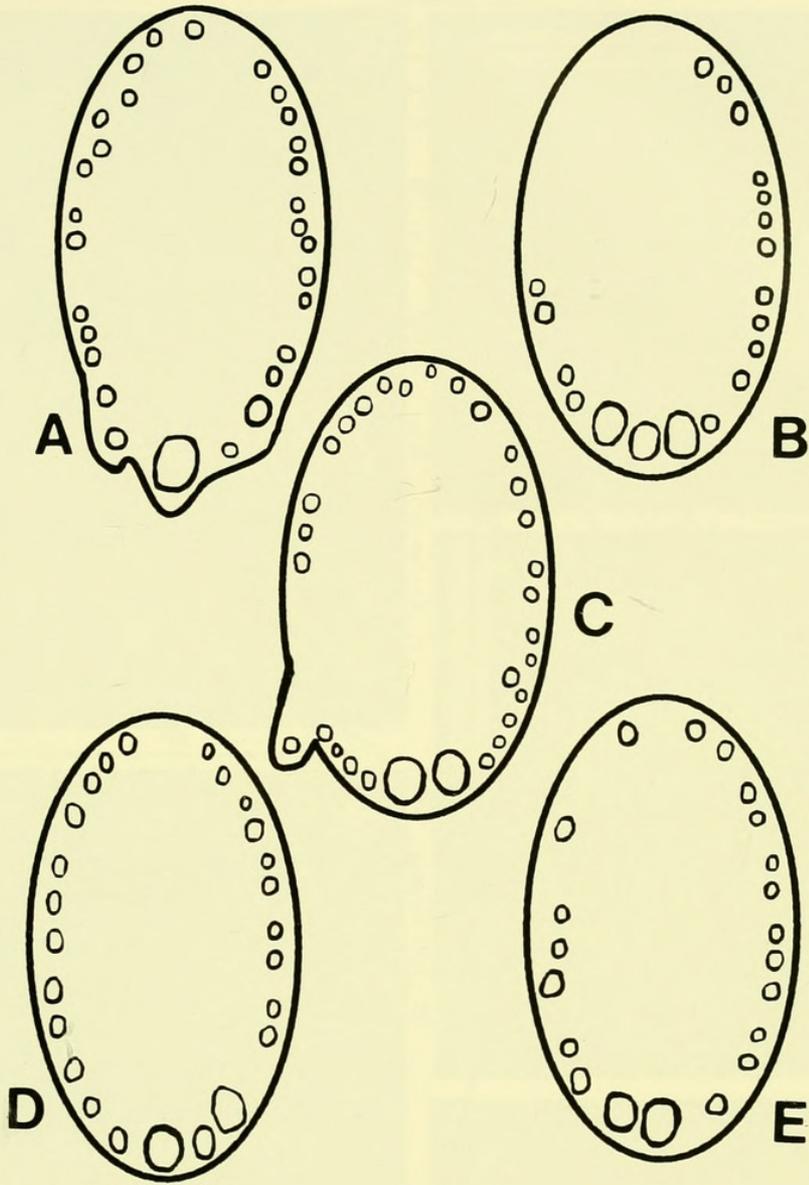


FIGURE 5. *Pectenodoris aurora* n. sp., distribution of mantle glands. A. CASIZ 097631, Indonesia. B. CASIZ 110443, Philippines. C. CASIZ 074702, Japan. D. CASIZ 097631, Indonesia. E. CASIZ 11059, Japan.

longest of these bands completely encircles the gill cavity. The lighter pink areas between the bands are dotted with 5–7 dark pink to purple spots and occasional opaque white spots. The remainder of the notum lateral to the outer bands is marked with the same dark pink to purple and opaque white spots. The short posterior end of the foot is divided by a thin, medial white line. The rhinophores each have 8–9 lamellae. They have a dark orange base and apex with a single, transverse white band through the middle. The 6–9 simply pinnate gills have the same dark orange base and apex with a central white band as do the rhinophores.

The large mantle glands all open ventrally (Fig. 5). They are visible along the mantle edge in the living animal. All of the specimens examined have 2–4 greatly enlarged posterior glands. There are 16–29 glands around the remainder of the mantle. There is some evidence that glands have been lost and regenerated in response to predation. It appears that more glands may be formed where the animal has been bitten or attacked. Areas of attack are visible in a number of specimens and these animals have more glands than their conspecifics, that lack damage along the mantle margin.

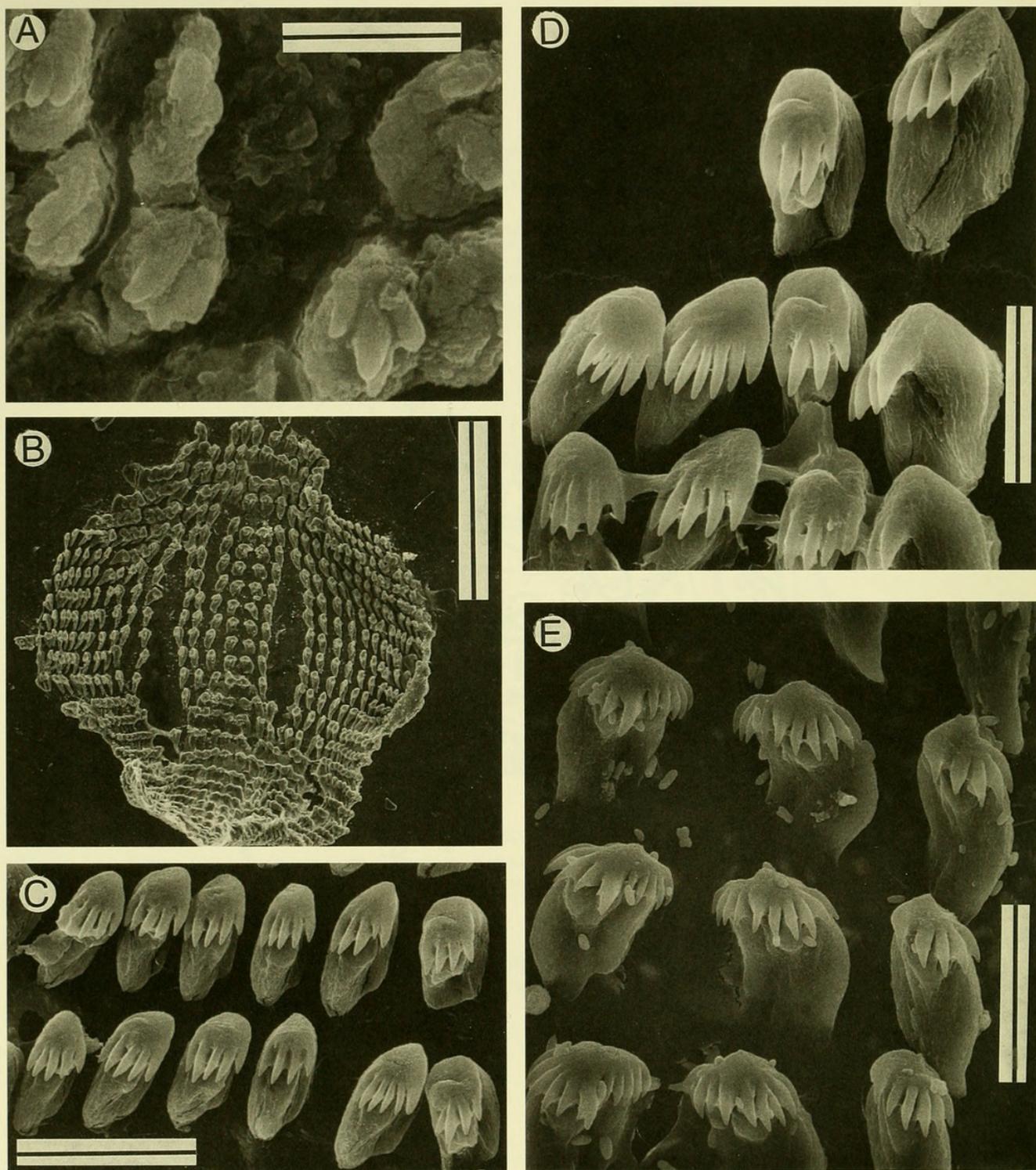


FIGURE 6. *Pectenodoris aurora* n. sp., scanning electron micrographs. A. Jaw rodlets (CASIZ 074702), scale = 7.5 μ m. B. Entire radula (CASIZ 074702), scale = 150 μ m. C. Lateral teeth (CASIZ 097631), scale = 15 μ m. D. Lateral teeth (CASIZ 097631), scale = 10 μ m. E. Lateral teeth (CASIZ 074702), scale = 15 μ m.

ALIMENTARY CANAL.—The oral tube is about three times the width of the muscular portion of the buccal mass. The jaws of this species are small, fragile and difficult to prepare for microscopy. The jaw rodlets are very small, fairly wide and appear to have multiple cusps

(Fig. 6A). The radular formula of a specimen from Okinawa is $28 \times 16.0.16$ (Fig. 6B). It was not possible to determine the number of rows in the specimen from Indonesia, but there are thirteen teeth per row. There is some variation in the number of denticles per tooth in the specimens

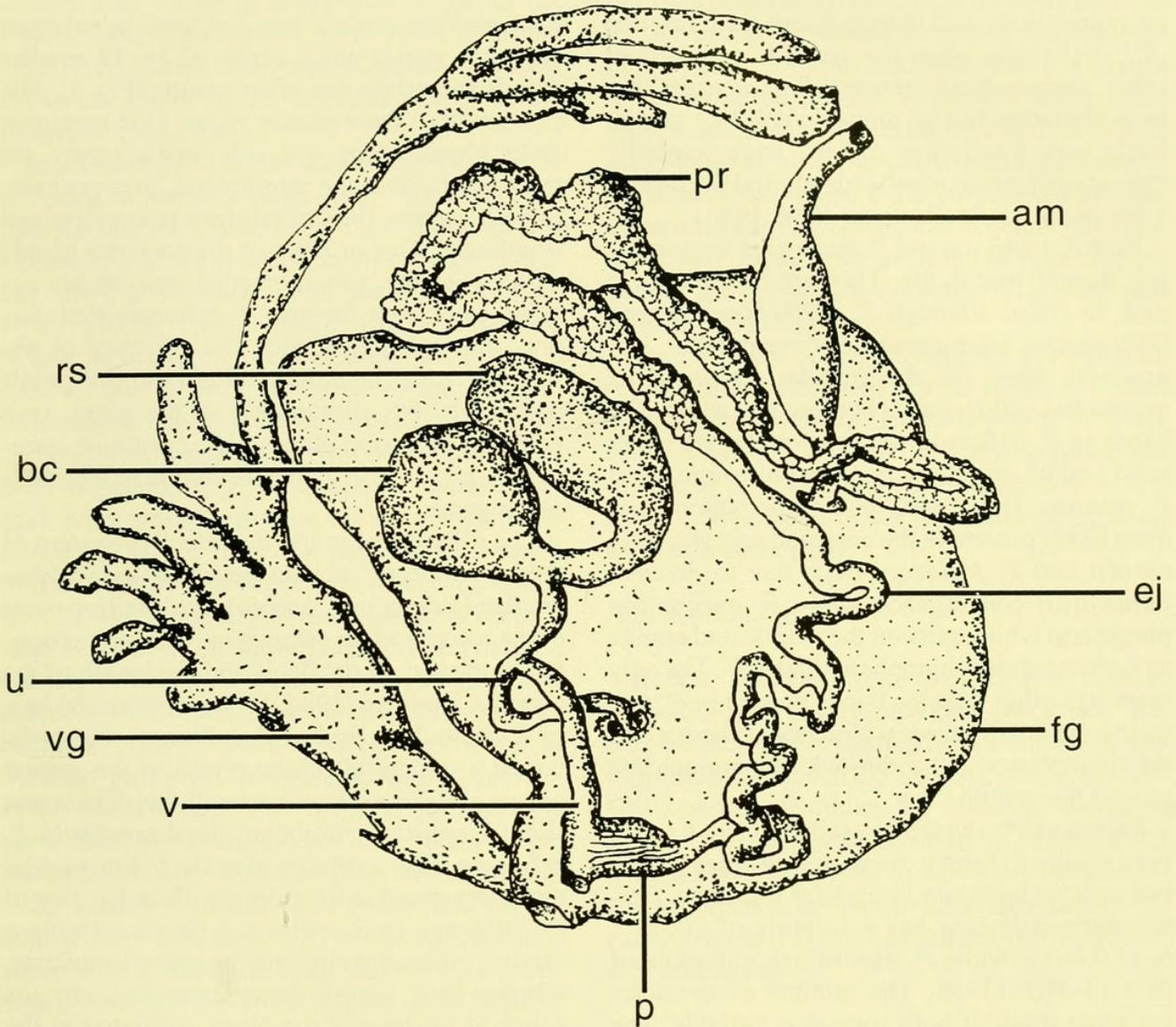


FIGURE 7. *Pectenodoris aurora* n. sp., reproductive system (CASIZ 110443). Abbreviations: am = ampulla, bc = bursa copulatrix, ej = ejaculatory portion of vas deferens, fg = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, u = uterine duct, v = vagina, vg = vestibular gland.

examined here. One specimen from Okinawa, Japan has ten denticles on the inner lateral teeth and five to six denticles on the middle lateral teeth (Fig. 6E), whereas the specimen from the Philippines has only five to six denticles per tooth, in all teeth observed (Figs. 6C, D).

REPRODUCTIVE SYSTEM. — The arrangement of organs is triaulic (Fig. 7). The ampulla is long and straight. It divides into a short, simply looped prostate and an extremely short, wide oviduct, which enters the female gland mass. The prostate narrows slightly into the very long, convoluted ejaculatory portion, which terminates in a short, bulbous, muscular penial bulb. The vaginal duct is narrow and elongate. The large, curved, pyriform

receptaculum seminis is longer than the ovoid bursa copulatrix. A wide duct connects the receptaculum and the bursa copulatrix at the top of the vaginal duct. The uterine duct emerges from the proximal third of the vagina, is long and narrow, and enters the female gland mass below the entrance of the oviduct to the mass. The female gland mass is large and completely developed. A large, highly ramified vestibular gland is present near the distal end of the gland mass.

DISCUSSION

Rudman (1984) created the genus *Pectenodoris* based on the differences found in the radu-

lar morphology and mantle gland configuration of *P. trilineata*, when compared to members of other chromodorid genera. *Pectenodoris* has been characterized by unique comb-like radular teeth; very fragile jaw rodlets; large, ventrally opening defensive mantle glands and the lack of a vestibular gland (Rudman 1984, 1986).

Both *P. trilineata* and *P. aurora* are very small, less than 10 mm in life. They are both purple to pink in color, although *P. trilineata* is darker. Both species have a series of three parallel, longitudinal lines on the mantle. *Pectenodoris aurora* has yellow bands bordered by white. The bands in *P. trilineata* are smaller and are either solid yellow or yellow bordered by white, as in *P. aurora*. This three-lined color pattern was most likely present in the common ancestor of *P. aurora* and *P. trilineata*. It is due to descent, rather than convergence. Only *P. aurora* has purple and white spots on the mantle and orange and white banded rhinophores and gills. The only markings other than the bands present in *P. trilineata* are small maroon blotches at the base of the rhinophores and a thin white marginal line around the mantle.

Pectenodoris aurora has radular teeth that are very similar in form to those of *P. trilineata*. The two species have similar radular formulae. *Pectenodoris trilineata* has a formula of $20-29 \times 6-15.0.6-15$, while *P. aurora* has a formula of $28 \times 13-16.0.13-16$. The number of denticles per inner tooth of both species is variable. The inner teeth have either 5-6 or 10-11 denticles, while the middle teeth have 5-6 denticles. Rudman (1984) mentioned the presence of a rachidian plate in some specimens of *P. trilineata*. This type of tooth was not seen in any of the specimens of *P. aurora* or any specimens of *P. trilineata* examined here.

The distribution of defensive glands around the mantle of these species is similar and exhibits a similar degree of variability. Rudman (1984, 1986) described a general pattern for the genus as a series of single, large mantle glands opening ventrally, as he described for *P. trilineata*. In the five specimens of *P. trilineata* examined here, two distinct patterns were observed (Fig. 2). In both cases there are 1-3 greatly enlarged posterior glands, but two of the specimens have no other glands besides those in the posterior. The other three specimens have a series of equally spaced glands around the rest of the mantle.

Pectenodoris aurora has 2-4 greatly enlarged posterior glands and a series of 16-19 smaller glands around the rest of the mantle (Fig. 5). The placement of these glands varies. One specimen lacks glands along one side, while others are missing glands at the anterior end. In every case, in both species, the central-most posterior gland is enlarged. One or more of the posterior glands adjacent to the postereomedial one are always enlarged, except for one *P. trilineata* that has only one enlarged gland. The presence or absence of lateral, antero-lateral and anterior glands is variable, but all members of the genus have enlarged posterior glands. The ventrally openings of all of these glands is unique to members of the genus.

The differences in the reproductive system of these two species include the size of the vestibular gland (larger in *P. aurora*), the insertion point of the receptaculum seminis into the bursa copulatrix, the size of the penis and the length of the prostate. Rudman (1984, 1986) reported the lack of a vestibular gland in *P. trilineata*, but mentioned a minute glandular pouch at the genital opening. Here we found a small, but lobate and slightly ramified vestibular gland present in *P. trilineata*. The vestibular gland in *P. aurora* was much larger and much more ramified than that of *P. trilineata*. In *P. trilineata*, the receptaculum seminis enters directly into the bursa copulatrix, whereas in *P. aurora* the receptaculum seminis enters at the base of the bursa copulatrix at the vaginal duct. The penis in *P. aurora* is wide, muscular and short. In *P. trilineata* it is elongate, narrow and only slightly muscular. In addition, *P. aurora* has a long, highly-convoluted muscular portion, while *P. trilineata* has a shorter simple loop. Reproductive characteristics, like those mentioned above, have been shown to be important in distinguishing closely related species in other chromodorid genera, such as *Hypselodoris* (Gosliner and Johnson, in press).

Pectenodoris trilineata has been reported from the western margins of the Pacific, from the South China Sea to the Great Barrier Reef. *Pectenodoris aurora* is also found along the western margins of the Pacific, but only as far north as Okinawa, Japan and as far south as the Lembeh Strait, Indonesia. The range of *P. aurora* is completely circumscribed by that of *P. trilineata*. These species overlap within the bathymetric range, 8-23 m, although one specimen of *P.*

aurora was found at a depth of 58 m. In the Philippines, both species have been collected from Bethlehem, Maricaban Island, Batangas Province, Luzon at 22 m depth, within a few meters of each other.

In an attempt to better understand the species included in the very large family Chromodorididae, the members have been divided into groups of species that are not necessarily closely related, but share a common color pattern (Rudman, 1982, 1983a, 1985, 1986). This method has helped us to more closely examine the different species and to bring attention to the possible importance of these color patterns in studying the evolution and biogeography of the family. It has been suggested that the sympatric members of each color group represent a case of Müllerian mimicry, that similar color patterns are a result of convergence and not common ancestry (Rudman, 1991). Sympatry of these similarly colored species supports the idea of mimicry as a defense against predation. *Pectenodoris trilineata* was placed in the "*Noumea purpurea* color group" by Rudman (1986) based on its resemblance to *Noumea purpurea*, *Noumea varians*, *Durville-doris similis* and *Durville-doris pusilla*. The basic pattern of these species is a pinkish purple background color with a median white line. All of the members of this color group have ranges that overlap with that of *P. trilineata*. *Pectenodoris aurora* shares its color pattern with members of the "*Chromodoris decora* color group." This group consists of *Chromodoris decora* (Pease, 1860), *Thorunna australis* (Risbec, 1928), *Hypselodoris maculosa* (Pease, 1871), *Noumea alboannulata* Rudman, 1986, and the juvenile stage of a *Hexabranhus sanguineus* (Rüppell and Leuckart, 1830–31) (this species is not in the family Chromodorididae). All of these species are pinkish or yellowish pink with longitudinal white lines, purple and white spots and often orange and white banded rhinophores. *Noumea alboannulata* is the only member of this color group that has not been recorded in at least part of the range of *P. aurora*. However, a specimen has recently been collected from Batangas, Philippines, within the range of *P. aurora* (M. Miller, pers. comm.)

As mentioned above, color groups represent potential mimicry complexes (Rudman 1991). These groups are based only on the biological reality of perception of visual predators. The

more variation that is present in the color patterns in each group the weaker the selective advantage of a mimicry complex becomes. There is quite a bit of variation present in each of these color groups, and potential overlap between the groups depending on which set of patterns are chosen to separate these groups. Different portions of color patterns in another chromodorid genus *Hypselodoris* were found to be the result of both convergence and common ancestry (Gosliner and Johnson, in press).

Further work in determining the phylogenetic relationships of all genera in the family Chromodorididae is necessary. The only way to properly address questions of mimicry, convergence and evolution of color patterns by descent is with a testable hypothesis of the relationships between species, a phylogeny.

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