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A New Nudibranch Species, Genus *Flabellina* (Opisthobranchia: Aeolidacea) from the Caribbean with Redescriptions of *F. verta* (Marcus 1970), and *F. dushia* (Marcus and Marcus, 1963)

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A new species of *Flabellina* has been discovered at Abaco, Bahamas and St. Lucia in the Caribbean Sea. This species, *Flabellina dana* sp. nov. has a translucent white body with a wide opaque white midline stripe, opaque white sides and red cerata with white cnidosacs. It has annulate rhinophores, a trait that immediately distinguishes it from all other tropical Atlantic and Caribbean species except the violet colored *Flabellina alternata* Ortea and Espinosa, 1998 from Angola. It is compared with all *Flabellina* species worldwide having annulate (ringed) rhinophores.

***Flabellina verta* (Marcus, 1970), originally described from Brazil, has been found from Venezuela to Florida (Sarasota and Miami) in a variety of color patterns. This species is redescribed to clarify its identification. *Flabellina dushia* (Marcus and Marcus, 1963), originally described from Curaçao in the Caribbean Sea, has recently been redescribed from the eastern tropical Atlantic (Canary Islands and Cabo Verde Islands) by Ortea, Caballer and Morro (2004). Both the original description and the redescription lacked any mention of the reproductive system, so this species is redescribed in this paper.**

The aeolid opisthobranch genus *Flabellina* is a large one, containing over 54 species that are found in all temperate and tropical seas. Of the almost 300 opisthobranch species described from the tropical western Atlantic (see Marcus 1977; Millen and Hamann 1992; Valdés et al. 2006), only five, possibly six, belong to the genus *Flabellina*. *Flabellina engeli* Marcus and Marcus, 1968 with lamellate rhinophores and two species, *F. marcusorum* Gosliner and Kuzirian, 1990 and *Flabellina hamanni* Gosliner, 1994 with papillate rhinophores, all have cerata elevated or inserted on pedicles. *Calmella bandeli* Marcus, 1976 possibly belongs to this group of *Flabellina* with pedunculate cerata and has smooth rhinophores. *Flabellina dushia* (Marcus and Marcus, 1963) and *F. verta* (Marcus, 1970) have smooth rhinophores and cerata without elevations or pedicles, a grouping originally placed in the genus *Coryphella*, but synonymised with *Flabellina* by Gosliner and Griffiths (1981) These latter two species are redescribed. This paper introduces a new species from the Caribbean Sea, *Flabellina dana* sp. nov., which has annulate rhinophores and bears its cerata on a notal brim.

Species Descriptions

Flabellina verta (Marcus, 1970)

Figures 1A–B, 2A, 3.

Coryphella verta Marcus, 1970:211–213, figs. 9–15.
Flabellina sp.2, Rudman (2000)
Flabellina verta Valdés et al. (2006)
Flabellina sp. 1, Valdés et al. (2006)

Material examined.— Voucher specimen, California Academy of Sciences CASIZ 110800, 1 specimen, collected by J. Hamann on Testigos Island, Venezuela, September, 29 1989, with yellow lines, 9 mm preserved, 30 m depth. Other specimens: Miami, Florida, West Atlantic, September 1, 1986, 1 specimen, 6 mm live, 2 m. depth, (photo only, J. Hamann). Sarasota, Florida, Gulf of Mexico, May 24, 1988, 2 specimens (one dissected), with white lines, 14 mm live, 1 m depth, J. Hamann. Testigos Islands, Venezuela, September 29, 1989, with yellow lines, 12 specimens (two dissected), largest 21 mm live, 30 m depth, J. Hamann. West Palm Beach, Florida, March 5 and 19, 2000, 4 m depth (photos only. A. Dupont), same locality, February 18, 2001, 1 specimen with white lines on *Eudendrium*, A. Dupont.

Distribution— Found from Cananéia, Brazil to West Palm Beach, Florida in the western Atlantic, Testigos Island, Venezuela in the Caribbean and Sarasota, Florida in the Gulf of Mexico.

External morphology.— This is an elongate, slender aeolid, wider in front and tapering gradually to a long, thin, trailing foot (Figs. 1A–B). The maximum preserved length is 10 mm, with the height exceeding the width, for example, a specimen 6.5 mm long was 1.1 mm wide and 1.3 mm high. There is a small but continuous brim giving a sharp edge to the notum. The slender rhinophores are up to 2 mm long, smooth, cylindrical and arising close together, tapering to an acute tip. The ground colour is translucent white or tinged with orange, with three opaque white or yellow lines. The three lines run the length of the body, one along each side, below the notal brim, from the oral tentacles to the posterior end of foot, sometimes extending out the sides of the oral tentacles. A dorsal line runs along each oral tentacle and meets at the anterior edge of the rhinophores where it continues as a medial line extending to the tip of the foot. None of the specimens examined had white spots on the cerata as mentioned in the original description. The rhinophores are frosted on the distal two thirds with opaque white or yellow, as are the oral tentacles on the distal one third to one half. The cylindrical cerata usually have bright red-orange cores and white cnidosacs enclosed in a translucent white sheath. The white tips taper to an abrupt point. The cores can be red, dark red-brown or orange. In some specimens, the cores darken just under the cnidosacs and fade to yellow-orange towards the cerata bases. They are attached in widely spaced clusters along the notal brim, which is expanded at the clusters. The single anterior cluster begins just behind the rhinophores and contains 13–17 cerata per side, arranged in rows with no more than four per row. There are four to six posterior clusters on each side with diminishing numbers of cerata in each cluster, up to 15 in the first, as few as 4 in the last. (Fig. 3A) The cerata are up to 2 mm long, with wide, smooth digestive diverticulae and large cnidosacs.

The head (Fig. 3B) is small and oval, as wide as the foot, with a T-shaped, sub-terminal mouth. It is not expanded at the sides. The oral tentacles are slender, slightly flattened ventrally, and arise from the antero-lateral corners of the head parallel to the oral surface. The oral tentacles are up to 1.5 mm long, so the rhinophores are slightly longer than the oral tentacles. The foot is narrow with a well developed flange, as wide as the notum. Anteriorly it is bilabiate and notched, and has long, recurved propodial tentacles, up to 1 mm in length. The long, slender trailing foot is up to 1 mm long and pointed, without a dorsal crest.

The genital opening is half way up the side under the anterior portion of the precardiac ceratal

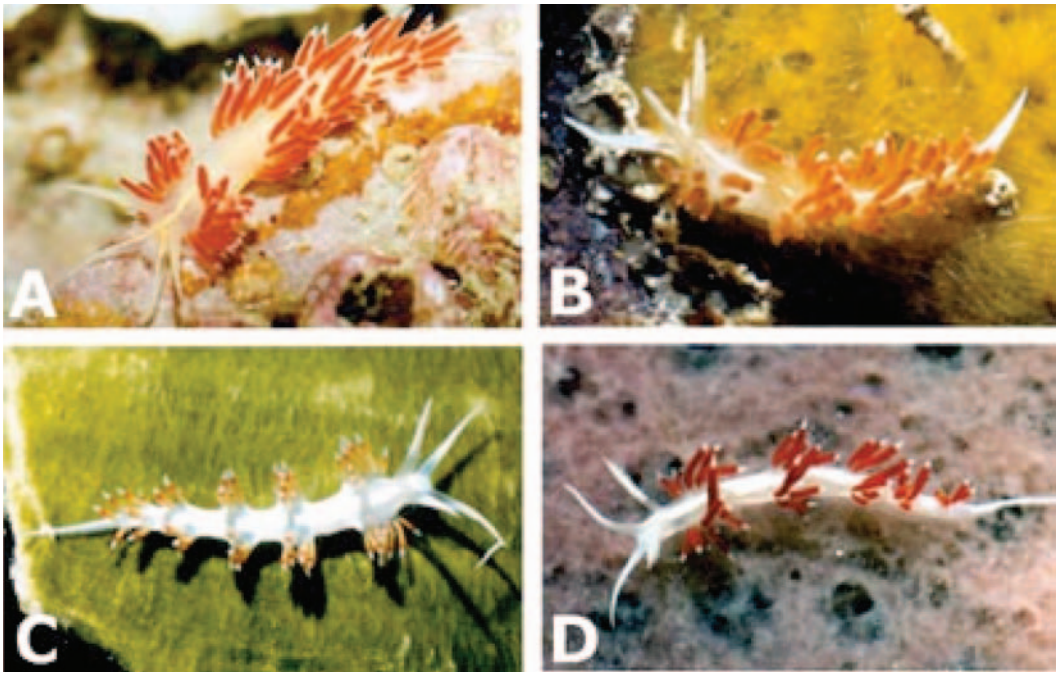

FIGURE 1. Living animals. A. *Flabellina verta* with yellow lines, Testigos, Venezuela B. *Flabellina verta* with white lines, Miami, Florida. C. *Flabellina dushia,* Martinique D. *Flabellina dana* sp. nov., St. Lucia. All photos by Jeff Hamann.

cluster. The pleuroproctic anus is on a small cone, located just under the notal brim below the 2nd and 3rd ceras of the first post-cardiac cluster, or on small specimens, below the 1st and 2nd ceratal space. The renal opening is mid interhepatic, up to 1 mm anterior to the anus.

DIGESTIVE SYSTEM.— The oval buccal mass has a small, white, muscular lip disk with a smooth cuticle surrounded by large ramified lateral oral glands that extend on each side of the anterior digestive gland ducts. Solitary pedal glands are found internally along the front edge of the foot. The elongate, triangular jaws are pale yellow and thin. They have a small dorsal flange for muscle attachment and the moderately long masticatory margin bears up to four rows of pointed denticles with over forty in the outermost row (Fig. 3A). The radula has up to 27 rows of teeth and the formula 21–27(1.1.1) (Figs 2A, 3E). The central tooth has a narrow, slightly depressed, central cusp slightly longer than the 5–9 denticles on each side. The large lateral teeth are wide, sickle shaped, with a slightly incised, broad base, projecting more on the lateral edge and 5–9 long denticles extending from ¼ of the way up from the base almost to the tip. There are two flattened, ribbon-like salivary glands with long stalks, extending from the buccal mass underneath the anterior clusters of cerata. The stomach is elongate, smooth anteriorly, striated posteriorly. The anterior diverticula lead to one cluster of cerata on each side. The posterior diverticulum travels under the ovotestis sending branches up to alternate clusters on each side, the left clusters being slightly anterior to the right. The intestine curves down and up to a small anal papilla.

REPRODUCTIVE SYSTEM.— The ovotestis is composed of large, rounded, white clusters, which can be seen through the notum; the large male follicle is inside, several peripheral, small round female follicles are attached. Ductules unite the clusters and form a hermaphroditic duct (Fig. 3D) which leaves the left ventral edge of the ovotestis and swells into an ampulla, loops back on itself once and then extends down the outside of the female gland mass until it bifurcates into an oviduct

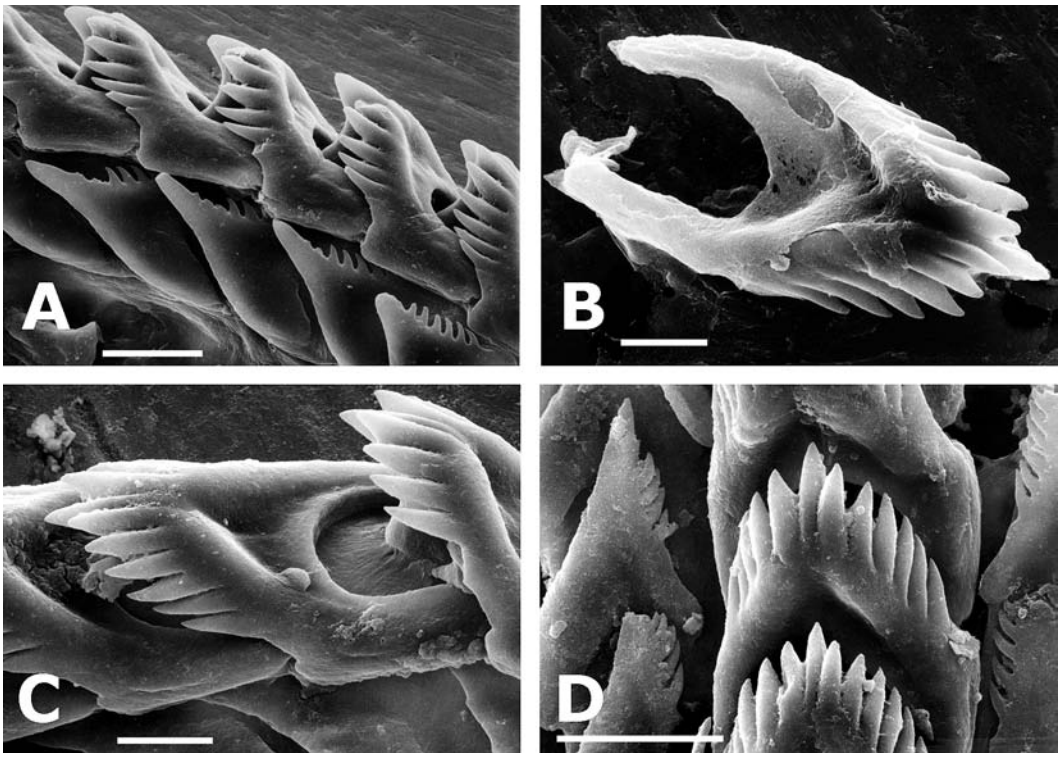

FIGURE 2. SEM view of radular teeth. A. *Flabellina verta* (Testigos, Venezuela). Scale bar = 20 µm. B. *Flabellina dushia* (Martinique). Scale bar = 10 µm. C. *Flabellina dana* sp. nov. (St. Lucia). Scale bar = 10 µm. D. *Flabellina dana* sp. nov. (St. Lucia). Scale bar = 20 µm.

and a vas deferens. The oviduct has a long stalked, semi-serially arranged, small, cylindrical, receptaculum seminis. The arrangement is androdiaulic, with the oviduct entering the female gland mass, which has a common passageway with the vagina to the female opening. There is a separate, long stalked, round, bursa copulatrix. The vas deferens is short and and thick, swelling into a large glandular, bulbous penis with a flat, discoid distal surface. The genital opening has a small knob-like preputum on the ventral side.

NATURAL HISTORY.— This species appears to feed on an orange *Eudendrium* sp. hydroid and has been found between one and thirty meters depth in February, March May, July and September. Spawn, observed in March and July is an irregular, white serpentine string laid on hydroids.

DISCUSSION OF *FLABELLINA VERTA*.— This animal is similar to the description of *Flabellina verta* (Marcus, 1970) from Cananeia, Brazil in that both have smooth rhinophores, cerata borne in clusters, a small notal brim, anus under the anterior end of the first right posterior ceratal cluster and the posterior liver duct situated under the gonads. Externally they differ in that *F. verta* from Brazil has only a small median line between the rhinophores, and opaque white spots on brown, knobby ceratal diverticulae. Our specimens had no opaque white spots on the cerata, which usually have smooth bright red orange diverticulae and there are three opaque white or yellow longitudinal lines, the medial one splitting and extending out the oral tentacles, and white frosting on the rhinophores. Photos taken by Anne DuPont in Palm Beach, Florida (Rudman, 2000) show typical specimens with three white lines and red cerata mixed in with specimens with white spotted reddish brown cerata and thicker white lines on the dorsum and head that clearly form a triangle and

enough white on the rhinophores to look like lateral bands. Except for the presence of lateral and mid-dorsal white lines not mentioned in the original description, these animals fit the description by Marcus (1970) of *F. verta* from Brazil. The radulae of the animals examined, all of which lacked white ceratal spots and had three long, narrow white or yellow lines, are similar in shape to the Brazilian ones, although *F. verta* was described with fewer rows 15 vs. 21–27 and fewer denticles on both the central and lateral teeth, even though the specimen was in the same size range (7.5 mm vs 5–10 mm). The reproductive system of all specimens has a bulbiform penis and short, thick vas deferens. We found a long, stalked receptaculum seminis on the oviduct, not observed by Marcus in the original description. Despite these differences in color and parts of the reproductive system, we believe that we are dealing with the same species because of the fundamental structural differences and the unusual granular and bulbous penial structure. A similar penial structure is found in the northeastern Pacific *Flabellina trilineata* (O'Donoghue, 1921) This latter species also has similar coloration to *F. verta* including three white lines. It can be readily distinguished by the presence of annulate rather than smooth rhinophores. The only other described *Flabellina* species with smooth rhinophores from the Caribbean or tropical western Atlantic is *F. dushia*, redescribed in this paper. *Flabellina verta* can be distinguished externally from *F. dushia* because *F. dushia* has longer oral tentacles than rhinophores, more distinct clusters of shorter cerata in tight arches, a wider body and broad bands of opaque white on the notum, sides, head and distal portions of the rhinophores and oral tentacles. Internally the lateral teeth of *F. dushia* are more acute, the receptaculum is shorter stalked and larger and it has a conical penis with a pointed tip.

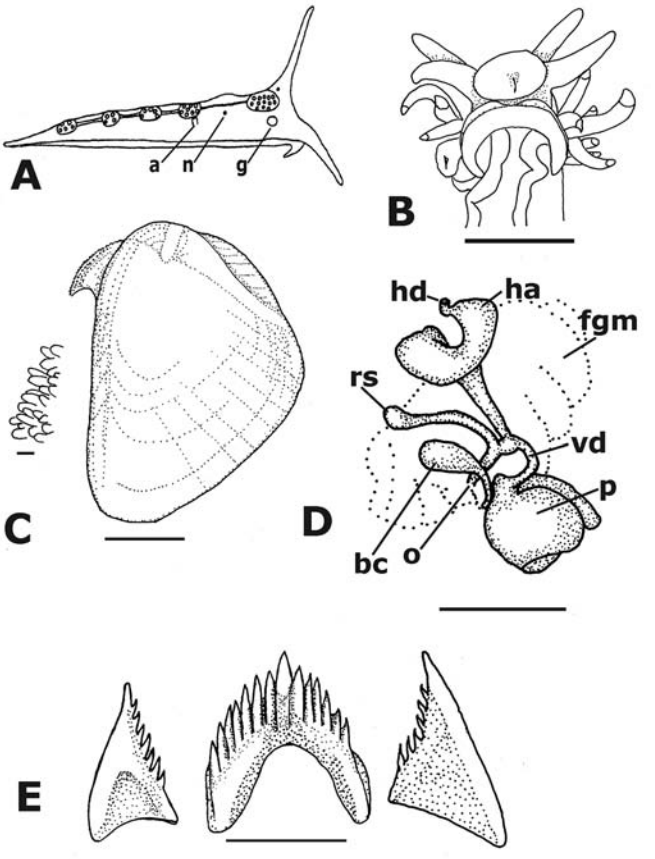

FIGURE 3. *Flabellina verta* (Sarasota, Florida). A. Right lateral view showing position of ceratal insertions. Key: a, anus; n, nephroproct; g, genital apertures. B. Ventral view of head and foot. Scale bar = 1 mm. C. One jaw plate, scale bar = 200 μm and masticatory margin enlarged to show denticles, scale bar = 10 μm. D. Reproductive system drawn using a camera lucida. Scale bar = 0.5 mm. Key: bc, bursa copulatrix; fgm, female gland mass; ha, hermaphroditic ampulla; hd, hermaphroditic duct; o, oviduct; p, penis; rs, receptaculum seminis; vd, vas deferens. E. One row of radular teeth. Scale bar =25 μm.

***Flabellina dushia* (Marcus and Marcus, 1963)**
Figures 1C, 2B, 4.

Coryphella dushia Marcus and Marcus, 1963:41–42, figs. 52–54.
Flabellina sp. B Redfern (2001)
Flabellina dushia Ortea, J., M. Caballer, and L. Moro (2004)
Flabellina dushia Rudman, W. B. (2005)
Flabellina dushia Valdés et al. (2006)

Material examined.— Voucher specimen: California Academy of Sciences CASIZ 110805, 1 specimen, 5.5 mm long. Collected by J. Hamann on 13 July 1987, at Martinique, Windward Islands, Lesser Antilles, live length 15 mm, depth 20 m on sand and rubble. Other material: One additional specimen, dissected, found with the voucher specimen. Two specimens, collected June 29, 1995, live lengths 4.5 and 4 mm, by Colin Redfern, 3m depth on floating *Sargassum* between Fish Cays and Treasure Cay, Abaco, Bahamas. Two specimens, live lengths 6 and 4 mm, collected June 28, 1996 by Colin Redfern, 2–3 m depth on floating *Sargassum* off Chub Rocks, Abaco, Bahamas. Three specimens, live lengths 6.5, 6 and 3.5 mm (one dissected), collected August 8, 1998 by Colin Redfern, 1 m depth on floating *Sargassum* off Chub Rocks, Abaco, Bahamas. Photo, 3 m on sand, West Palm Beach, Florida, photographed March 19, 2000 by Anne DuPont.

Distribution.— This species was found in Florida, Curaçao, Jamaica, Abaco in the Bahamas and Martinique in the Caribbean and the Canary Islands and Cabo Verde Islands in the eastern Atlantic.

External morphology.— The body is elongate and slender with a long, slim trailing posterior foot.(Fig. 1C). Live length is up to 15 mm but preserved animals over 4 mm in length had mature gonads. The height exceeds the width. There is a well-developed, continuous notal brim along the sides of the body that is expanded at the cerata clusters. The smooth rhinophores are up to 1.5 mm long and taper to an acute tip. The ground color is translucent grayish white with opaque white covering most of the dorsum, sides and head except for the bases of the tentacles and rhinophores, behind the eyes and bases of the cerata. Near the ceratal clusters the white pigment narrows, sometimes disappearing dorsally, between the clusters. The rhinophores and oral tentacles are frosted with opaque white on the distal two thirds.

The elongate, cylindrical cerata usually have yellow or pale orange cores that darken to orange, then form a dark orange-red ring below the elongate white cnidosacs. The cerata tips have elongate points. The single anterior cluster of cerata begins a short distance behind the rhinophores and contains three to five rows of cerata (Fig. 4A). There are four (3–6) post-cardiac clusters per side. The first post-cardiac cluster has a total of 5–11 cerata, the second cluster is a horseshoe with 6 cerata, the third a horseshoe of 4 and the last two clusters have 2–3 cerata each. The cerata are up to 1.7 mm long with wide, smooth cores and large, elongate cnidosacs.

The head (Fig. 4B) is small and rounded with a terminal, triangular mouth. The oral tentacles are long, rounded, strong and end in an acute tip. They are up to 2 mm long, slightly longer than the rhinophores. The anterior foot is bilabiate and notched. There are well developed propodial tentacles, 0.4 mm long. The foot is narrow with a small flange. The flat trailing portion is 1 mm long and narrow, tapering to an acute tip.

The genital opening is below the anterior portion of the first cerata cluster. The pleuroproctic anus is just below the notal brim, posterior in the interhepatic space. The renal opening is mid-interhepatic, a short distance ahead of the anus.

Digestive system.— The buccal mass is short and rounded. There are ramified dorsal oral glands filling the area under the anterior hepatic diverticulae. The light yellow jaws are oval with a slight dorsal flange and a wide masticatory margin bearing up to 5 rows of denticles (Fig. 4C). Twenty-eight small rounded denticles are on the outermost row. The radula has 27 rows with the

formula 27(1.1.1). The rachidian teeth (Figs. 2B, 4E), are moderately wide with an articulation area near the base. There are 5–6 denticles on each side of a moderately long, slightly depressed, central cusp. The lateral teeth are triangular with a concave base and a straight or slightly concave inner side. The lateral edge of the base is a little longer than the inside edge. The median edge of each tooth is denticulate in the middle one third or slightly more, with a long, slender tip. There are 8–9 fine denticulations. The salivary glands are strap shaped, located medial to the oral glands and ending at the pericardium. The stomach is elongate oval, the anterior hepatic diverticula extend to one pre-hepatic cluster on each side. Posteriorly, the intestine has a slight loop down and then curves up, ending in a small cone at the anus. The posterior hepatic diverticulum is ventral to the ovotestis.

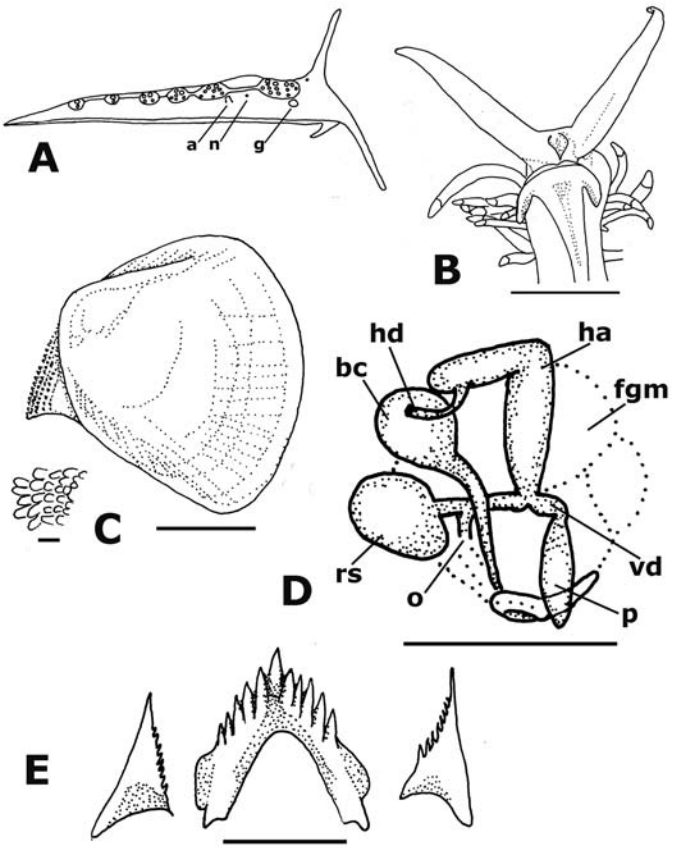

FIGURE 4. *Flabellina dushia* (Martinique). A. Right lateral view showing position of ceratal insertions. Key: a, anus; n, nephroproct; g, genital apertures. B. Ventral view of head and foot. Scale bar = 1 mm. C. One jaw plate, scale bar = 200 µm and masticatory margin enlarged to show denticles, scale bar = 10 µm. D. Reproductive system drawn using a camera lucida. Scale bar = 0.5 mm. Key: bc, bursa copulatrix; fgm, female gland mass; ha, hermaphroditic ampulla; hd, hermaphroditic duct; o, oviduct; p. penis; rs, receptaculum seminis; vd, vas deferens. E. One row of radula teeth. Scale bar = 25 µm.

REPRODUCTIVE SYSTEM.— The ovotestis consists of clusters with several large female follicles peripheral to each smaller, central male follicle. Small ducts unite the clusters and join to form the hermaphroditic duct. The hermaphroditic duct (Fig. 4D) expands into a curved, C-shaped ampulla that extends down the outer surface of the female gland mass. It narrows and divides into an oviduct and vas deferens. The vas deferens is short and prostatic, still wide where it enters the penial bulb. The penis is muscular and conical with an unarmed tip. The oviduct has a large, round, short-stalked receptaculum seminis arranged semi-serially. The oviduct then enters the albumen gland. There is no separate vagina; the arrangement is diaulic. There is a separate, long stalked, rounded, bursa copulatrix located between the ampulla and the receptaculum seminis.

NATURAL HISTORY.— This species has been found on *Thallassia, Sargassum* and hydrozoans at depths of from 1 to 20 m. during the months of February, March, April, June, July and August.

DISCUSSION OF *FLABELLINA DUSHIA*.— This species has smooth rhinophores and a continuous notal brim as does *F. verta*. It differs in external coloration, radula shape and in the reproductive system. (see discussion of *F. verta*). *Flabellina dushia* was reported from the Canary Islands and Cabo Verde Islands by Ortea, Caballer and Moro (2004) and they indicated that their animal was

the same as animals photographed from the Caribbean. On the basis of radula, color, thin trailing portion of the foot, and ceratal distribution, they united the eastern Atlantic specimens with *F. dushia* from Curaçao. The original description of *Flabellina dushia* by Marcus and Marcus (1963) did not describe the reproductive system, but the genital openings are far forward under the first cluster and the anus is low and posterior in the interhepatic space as in the present material. Ortea, Caballer, and Moro illustrated a slightly different pattern. In both descriptions, animals have a similar radula, although the lateral teeth are larger and more incised at their bases and bear fewer denticles in the original description. Other differences are that *Flabellina dushia* in the original description, lacks notal brims, has longer rhinophores than oral tentacles, and there are no white patches on the notum although the animal is described as white. Ortea, Caballer and Moro (2004) have specimens from the eastern Atlantic that appear to lack a notal brim, their rhinophores are equal to the oral tentacles in length and the colour is translucent white with white patches. All of the animals we examined had a notal brim and large white patches. Since the descriptions agree on major points, our redescription has been made to fill in and clarify information on this species as found in the Caribbean area.

Flabellina dana Millen and Hamann, sp. nov.

Figures 1D, 2C–D, 5.

Flabellina sp. A Redfern (2001)
Flabellina sp. 3 Valdés et al. (2006)

Etymology.— This species is named for Jeff Hamann's daughter Dana, using a noun in apposition.

Material examined.— Holoype: California Academy of Sciences CASIZ 110795, collected by J. Hamann on 23 July 1987 at Pigeon Is., St. Lucia Island, Windward Islands, Caribbean Sea, on sand and rubble at a depth of 20 m. Other material: One specimen collected with the type (dissected). Two specimens (one dissected), live length 12 and 2.5 mm, collected by Colin Redfern, June 30, 1995, on *Sargassum* attached to substrate in 0.6m. Guana Cay, Abaco, Bahamas. One specimen, live length 8 mm, collected by Colin Redfern, August 8, 1998, on *Sargassum* attached to substrate in 0.6 m. Guana Cay, Abaco, Bahamas.

Distribution.— This species has been found only near the Caribbean island of St. Lucia and Abaco in the Bahamas.

External morphology.— This aeolid is extremely slender with an elongate trailing posterior foot (Fig. 1D). The largest living specimen was 12 mm long. The height is greater than the width, the type specimen measures $5.5 \times 0.7 \times 1$ mm (l × w × h). There is a notal brim on each side, wide at the cerata and almost imperceptible in-between cerata clusters. The rhinophores are annulate with 9–10 complete rings and a pointed tip. The rhinophores are slightly longer than the oral tentacles (1.3:1.1 mm).

The ground color is translucent white or pinkish white, with opaque white on the head and continuing as a wide opaque white stripe down the center of the back that enlarges between the ceratal clusters. The clavus of the rhinophores is opaque white or pinkish white, or yellowish, the bases hyaline. The oral tentacles are opaque white and the white meets up with the white on the head and mid-dorsal white line that continues down the elongate, 1.4 mm trailing posterior foot. The sides are entirely opaque white from under the notal brim to the foot. The cerata are up to 1.6 mm long and are bright red or reddish-orange and may darken before the elongate, white cnidosacs. The cerata are in clusters on an expanded area of the notal brim (Fig. 5A). The single pre-cardiac cluster has four rows of 3–5 cerata each with 8–10 cerata. The first post cardiac cluster has 5–8 cerata, the next three pairs have 3–6 each. The last three post cardiac cerata clusters are well spaced and all

arranged in a single horseshoe shape.

The head (Fig. 5B) is oval, as wide as the foot. The mouth is vertical and sub-terminal. The tentacles arise slightly dorsal to the oral surface and are flat near the head. They are quite long and thin, tapering to a slender point. The foot is bilabiate and notched with long propodial tentacles, their length being one half the width of the foot. The posterior end is long, narrow, and tapers to a blunt point.

The genital aperture is situated under the anterior one half of the pre-cardiac cluster. The pleuroproctic anus is posterior in the inter-hepatic space and the renal opening is in front of it, in the middle of the inter-hepatic space.

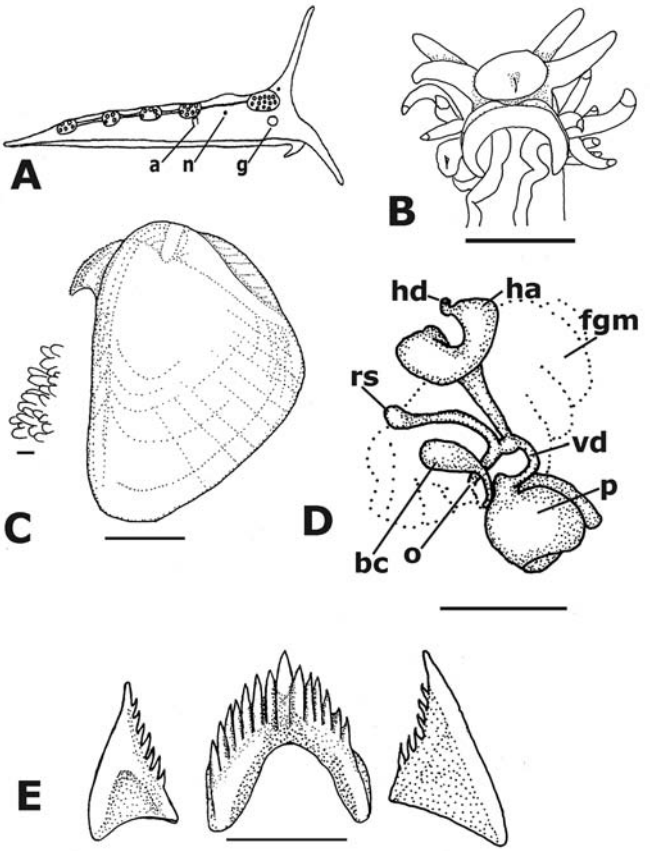

FIGURE 5. *Flabellina dana* sp. nov. (St. Lucia). A. Right lateral view showing position of ceratal insertions. Key: a, anus; n, nephroproct; g, genital apertures. B. Ventral view of head and foot. Scale bar = 1 mm. C. One jaw plate, scale bar = 200 µm and masticatory margin enlarged to show denticles, scale bar = 10 µm. D. Reproductive system drawn using a camera lucida. Scale bar = 0.5 mm. Key: bc, bursa copulatrix; fgm, female gland mass; ha, hermaphroditic ampulla; hd, hermaphroditic duct; o, oviduct; p, penis; rs, receptaculum seminis; vd, vas deferens. E. One row of radular teeth. Scale bar =25 µm.

DIGESTIVE SYSTEM.— The mouth has solitary buccal glands on either side of the smooth lip disk. There are short, highly ramified white oral glands located in the head region, not extending posterior to the rhinophores. The jaws are bright yellow and round in shape (Fig. 5C) with a well developed masticatory margin containing up to 8 rows of denticles with thirty seven denticles in the outermost row. The radular sac protrudes from the buccal mass. It has the formula 19–21(1.1.1) (Figs. 2C–D, 5E). The central teeth are moderately wide with a short, slightly depressed, central cusp and 5–9 well developed denticles on each side. The lateral teeth are broad triangles with a slightly curved base and a slightly longer lateral edge. There are 6–9 well developed denticles on the upper two thirds of the medial side and a short tip distal to the denticles.

The salivary glands are broad and long, located on the right above the reproductive system and on the left in the anterior one half of the first cerata cluster, ending before the cardiac region. The short esophagus leads into an elongate oval stomach. There is one anterior hepatic diverticulum on each side leading to a single cerata cluster on each side. The intestine loops down on the right then up to an anal cone just under the notal brim. The posterior hepatic diverticulum runs centrally between clusters of the ovotestis, with branches upwards to the cerata clusters.

REPRODUCTIVE SYSTEM.— The ovotestis has peripheral clusters of large female follicles

around each central male follicle. Small interconnecting collecting ducts unite to form the hermaphroditic duct. The hermaphroditic duct (Fig. 5D) leads into a sausage-shaped ampulla with one curve, which then descends down the female gland mass. It subdivides into an oviduct that bears a small, short stalked, semi-serially arranged, receptaculum seminis mid way along its length before it enters the female gland mass at the albumen gland. There is a long-stalked, rounded bursa copulatrix opening separately at the base of the female gland mass. The prostatic vas deferens is short and almost immediately enters a large penial sac. The bulbous penis is unarmed, tapering to a small, smooth, rounded tip with a central opening.

Natural history.— This species has been found on *Sargassum* near the surface and on sand and rubble to a depth of 20 m during June, July, and August.

Discussion of *Flabellina dana*.— None of the *Flabellina* species known from the tropical western Atlantic have annulate rhinophores. The general discussion will compare *Flabellina dana* with all other known species worldwide that have annulate rhinophores and discuss the position of *Flabellina dana* compared with other Western Atlantic tropical species.

Discussion

Annulate, or ringed rhinophores can be distinguished from perfoliate ones, in that the latter have many thin leaves that slope from an anterior longitudinal rib and meet at a small posterior rib. Annulate rhinophores have thick, parallel rings that do not have an anterior or posterior rib, although some rings may be incomplete. All seven of the described annulate species can be clearly distinguished from *Flabellina dana*. Several species with annulate rhinophores have compound peduncles (*F. affinis* [Gmelin, 1971]*, F. funeka* Gosliner and Griffiths, 1981, *F. ischitana* Hirano and Thompson, 1990) or simple peduncles (*F. pricei* [MacFarland, 1966], *F. alternata*). All of these species, except *F. pricei* can also be distinguished by their mauve body coloration. Two species, *F. trilineata* and *F. triophina* (*fusca*) (Bergh, 1894) do not have peduncles. *Flabellina triophina* can be distinguished by the presence of continuous cerata on the notal brim and very weak annulations that may not be true annulations as they are fine and irregular. *Flabellina trilineata* is the closest species to *F. dana*. Its smaller notal brim is discontinuous, and the clustered cerata are in rows, not horseshoes, the penis is glandular with a flat disk (not tapering) and there is a small projecting preputum, absent in *F. dana*. Living *Flabellina trilineata* can also be distinguished by the presence of three narrow longitudinal white lines while wide bands of white pigment covers most of the body in *F. dana*.

A cladogram of most of the described species in the genus *Flabellina* was produced by Gosliner and Kuzirian (1990). In a subsequent paper, Gosliner and Willan (1991) presented a cladistic analysis of the two clades containing the most highly derived taxa, those with elevated cerata on peduncles and densely annulate or perfoliate rhinophores, and those with a bilobed receptaculum seminis, usually having papillate rhinophores. Of the species known from the tropical western Atlantic, *Flabellina engeli* belongs to the former clade and *F. marcusorum* and *F. hamanni* to the latter. These clades have apomorphies that show they are well separated from each other and several synapomorphies that separate them from the rest of the tropical western Atlantic Flabellinidae.

None of the *Flabellina* species found in tropical western Atlantic waters are basal within the context of the trees presented. Basal *Flabellina* species appear to be restricted to colder waters both in the north (*F. islandica* [Odhner, 1937]*, F. salmonacea* [Couthouy, 1838] *F. nobilis* [Verrill, 1880]), and in the south (*F. falklandica* [Eliot, 1907]). Derived characters shared by all species found in the tropical western Atlantic are the restriction of cerata into groups, forward position of the anus, presence of oral glands, small or depressed central tooth cusp, presence of long propodi-

al tentacles and the presence of a distinct penis. *Flabellina verta* appears to be the most basal of the tropical western Atlantic flabellinids because the anus is behind the interhepatic space and a preputum is present on the margin of the reproductive opening. *Flabellina dana* and *F. dushia* are slightly more derived and close to each other. It is interesting to note that although elaboration of the rhinophores is a derived characteristic, the presence of annulate rhinophores, in contrast to perfoliate and papillate rhinophores, is scattered among groups that do not seem to be closely related. It appears that annulate rhinophores are found in a highly derived group, *F. affinis, F. ischitana, F. alternata* and *F. funeka,* which are geographically close in longitude, mauve or violet in colour and found in tropical and subtropical waters. There is also a moderately derived group (*F. pricei, F. trilineata*) from the cold temperate east Pacific.

The tropical western Atlantic *Flabellina dana* appears to be allied with this moderately derived group, from which it has been separated by the Isthmus of Panama since the Pliocene. The most basal, with weakly annulate rhinophores, is the northeastern Pacific species *Flabellina triophina*. It is sympatric over part of its range with *F. pricei* and *F. trilineata*, but extends further north in the Pacific and across into the Russian western Pacific. This northern distribution is consistent with more basal members of the genus (Gosliner and Kuzirian 1990). As found with species with perfoliate rhinophores by Gosliner and Willan (1991), subsequent dispersal has created sympatry that masks the allopatric events causing speciation. However, a possible scenario is that dispersal from a center of origin in the Mediterranean (Tethys Sea) spread into the Atlantic and thence across the Atlantic from Africa to the Caribbean on the equatorial current. From the Caribbean, species could spread through to the Pacific before the closing of the Panamic isthmus and thence north and south in the Pacific. The northernmost species, *Flabellina triophina*, would be considered a relict species from the original Tethys Sea distribution. It does not appear to have synapomorphies with other annulate species from the Pacific and the weak rhinophoral annulations may not be an homologous feature.

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