Two New Species of *Doriopsilla* from the Tropical Western Atlantic with Remarks on Cariopsillidae Ortea & Espinosa, 2005

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Abstract. Four Caribbean species of *Doriopsilla* are described, including two new species to science. The first detailed anatomical examinations and illustration of living Caribbean animals of *Doriopsilla areolata* and *Doriopsilla nigrolineata* reveals that these are two distinct species. Two undescribed species are differentiated from previously known taxa by a combination of external and anatomical characteristics, including the structure of the digestive and reproductive systems, the presence or absence of black lines and white spots on the dorsum, and the morphology of the dorsal tubercles.

The genus *Cariopsilla* and the family Cariopsillidae are synonimized with *Doriopsilla* and Dendrodorididae respectively, based on the application of modern principles of systematic biology.

INTRODUCTION

Valdés and Ortea (1997) revised the species of the genus *Doriopsilla* in the Atlantic Ocean, regarding only three species as valid. *Doriopsilla areolata* Bergh, 1880, with three subspecies, is distributed through Southern Europe (*D. areolata areolata*), West Africa (*D. areolata albolineata*) and the Caribbean Sea (*D. areolata nigrolineata*). *Doriopsilla pelseneeri* d'Oliveira, 1895 is only present in the Iberian Peninsula, and *Doriopsilla pharpa* Marcus, 1961, is known from the Atlantic coast of North America and the Caribbean Sea. Since then, a third Caribbean species, *Doriopsilla espinosai* Valdés & Ortea, 1998 was described based on material collected from Cuba (Valdés & Ortea, 1998).

More recently, Ortea & Espinosa (2005) erected the new genus *Cariopsilla* Ortea & Espinosa, 2005 and the new family Cariopsillidae Ortea & Espinosa, 2005 for *Doriopsilla pharpa* based on the presence of caryophyllidia-looking tubercles in this species. Valdés et al. (2006) illustrated several additional undescribed species from the Caribbean and brought *Doriopsilla nigrolineata* back to the species level based on consistent morphological differences with *Doriopsilla areolata*.

The present paper deals with the description of two of the new species illustrated by Valdés et al. (2006) and discusses the status of Cariopsillidae based on modern concepts in systematic biology. All specimens are deposited at the Malacology Section of the Natural History Museum of Los Angeles County (LACM).

SPECIES DESCRIPTIONS

Doriopsilla elitae Valdés & Hamann, n. sp.

(Figures 1A-C, 2, 3A)

Doriopsilla sp. 1 - Valdés et al., 2006: 204-205.

Material examined: HOLOTYPE: Vieux Fort, South Point, St. Lucia, 30 m depth, 1 October 1987, 1 specimen 20 mm long, live (LACM 1930). PARATYPE: Petit Nevis, St. Vincent and the Grenadines, 18 m depth, 18 January 1987, 1 specimen 20 mm long, live (LACM 1931). Additional specimens were photographed but are not preserved.

External morphology: Living animals reach up to 20 mm in length. The general color of the living animals is variable from yellow to dark orange (Figure 1A–C). The dorsum is covered with opaque white patches, generally small, and situated on top of many dorsal tubercles. Some of the patches are much larger than the rest, also covering large tubercles situated along the edge of the visceral hump. The rhinophores and gill are the same color as the rest of the body.

The body is flat, oval (Figure 1A–C), stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of low, simple, conical tubercles stiffened with spicules. The mantle margin is wide and slightly undulate. The rhinophores are perfoliate with up to 13 lamellae. The

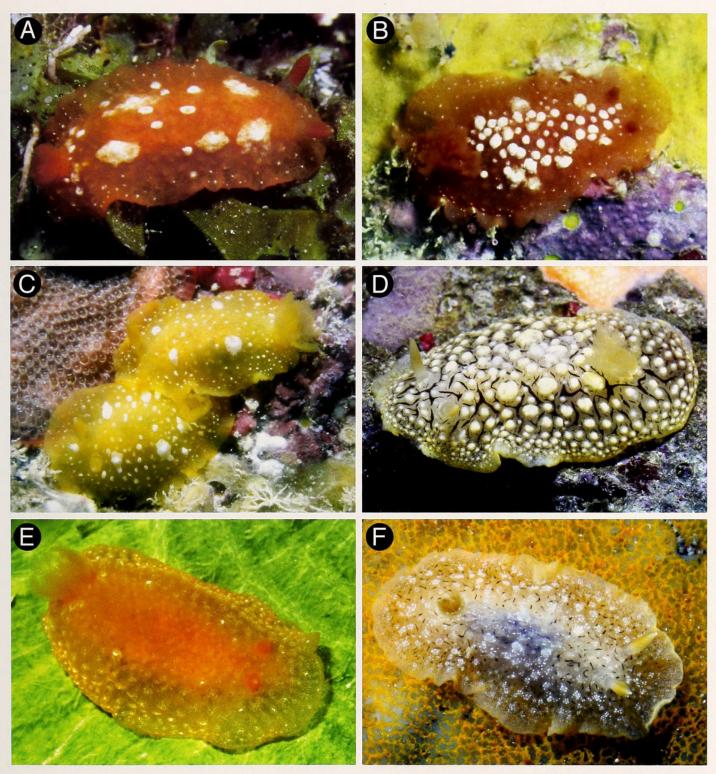


Figure 1. Living animals. A, *Doriopsilla elitae* from St. Vincent, 19 mm long (LACM 1931) – photo Jeff Hamann. B, *Doriopsilla elitae* from Martinique, size unknown – photo Greg Hamann. C, *Doriopsilla elitae* from Aruba, 25 mm long – photo Jeff Hamann. D, *Doriopsilla tishae* from Roatán, Honduras, 49 mm long (LACM 1933) – photo Jeff Hamann. E, *Doriopsilla areolata* from Martinique, 36 mm long (LACM 173780) – photo Jeff Hamann. F, *Doriopsilla nigrolineata* from Guanaja, Honduras, 25 mm long (LACM 173781) – photo photo Jeff Hamann.

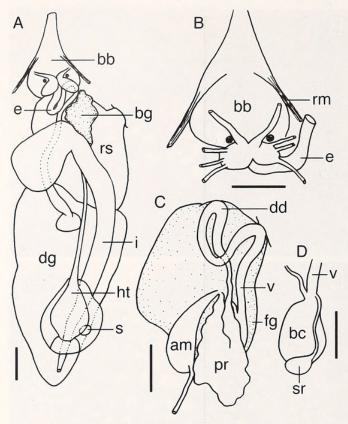


Figure 2. Drawings of the internal anatomy of the paratype of *Doriopsilla elitae* (LACM 1931). A, General view of the anatomy, scale bar = 1 mm. B, Detail of the anterior portion of the digestive system, scale bar = 1 mm. C, Reproductive system, scale bar = 1 mm. D, Connection of the bursa copulatrix and seminal receptacle, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

gill is composed of four tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused together with the mouth opening in the center. The anterior border of the foot is slightly concave but not notched.

Anatomy: The buccal bulb is oval (Figure 2A–B), covered by minute, rather undifferentiated oral glands on its proximal portion. The tubular esophagus leads from the buccal bulb. The esophagus is very long and convoluted (Figure 2A). Posteriorly, it broadens into a short muscular portion. The intestine runs posteriorly in the usual position and lacks any pyloric gland (Figure 2A).

The ampulla is short and muscular (Figure 2C). It divides into a short oviduct, which enters the female gland, and the prostate. The prostate is broad and flattened. From its distal end, the prostate leads into an elongated and convoluted deferent duct. The penis,

when everted, is very long and contains several rows of penial hooks. The penial hooks are approximately 40 μ m wide at the base and up to 55 μ m in length (Figure 3A). The vagina is long and straight. At its proximal end is a large, thin-walled, oval bursa copulatrix. The seminal receptacle is small, having a long duct that joins the vagina at the point where it connects the bursa copulatrix. From this point also emerges the uterine duct.

The circulatory system consists of a large heart (Figure 2A), joined by the aorta with a flattened blood gland, situated behind the central nervous system.

Etymology: The species is named after Elita Hamann, middle daughter of Jeff Hamann.

Geographic range: Thus far this species has been collected or photographed in Aruba, St. Vincent and the Grenadines, Grenada, and Martinique.

Remarks: Doriopsilla elitae is clearly different from other Atlantic species of the genus. There are no other species with yellow or red background colorations and solid white spots. Species with uniform white, yellow, orange or red colorations include Doriopsilla areolata and Doriopsilla pelseneeri d'Oliveira, 1895, but the former has a complex pattern of white rings or lines and the latter lacks white pigment except for a single ring around the gill pocket. Anatomically, Doriopsilla areolata is clearly different by having a longer, thinner ampulla, a wider prostate, a proportionally larger seminal receptacle, and a much more elongate buccal bulb. Doriopsilla pelseneeri lacks any white pigment on the dorsum, except for a white line around the branchial sheath (Valdés & Ortea, 1998). Additionally, D. pelseneeri has large, irregular dorsal warts that contrast with the low, simple, conical tubercles of D. elitae. For a comparison of the external characteristics of D. elitae with other Atlantic species of Doriopsilla see Table 1.

Eastern Pacific species of *Doriopsilla* with yellowish to reddish background color and white spots include *Doriopsilla albopunctata* (Cooper, 1863) and *Doriopsilla gemela* Gosliner, Schaefer, & Miller, 1999), both characterized by having very small opaque white spots uniformly distributed over the entire dorsum (see Gosliner, Schaefer, & Miller, 1999), which never form aggregations as in *Doriopsilla elitae*.

Doriopsilla tishae Valdés & Hamann, n. sp.

(Figures 1D, 4-5, 3B)

Doriopsilla sp. 3 - Valdés et al., 2006: 204-205.

Material examined: HOLOTYPE: Coxen's Hole, Roatán, Honduras, 23 December 1991, 1 specimen 49 mm long live (LACM 1932). PARATYPES: Coxen's Hole,

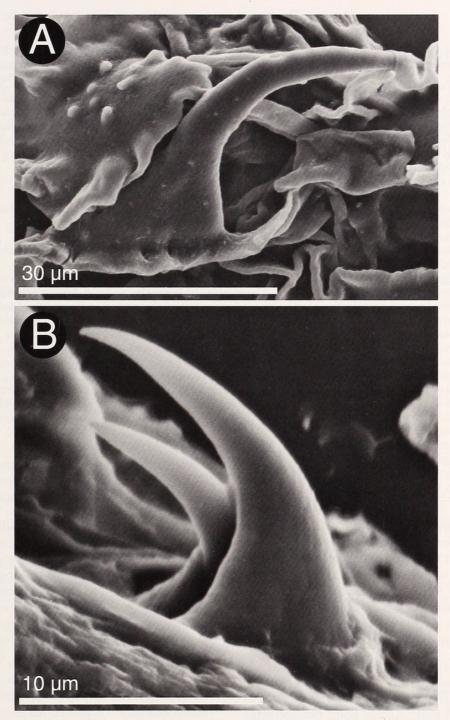


Figure 3. Scanning electron micrographs of penial spines. A, Doriopsilla elitae (LACM 1931). B, Doriopsilla tishae (LACM 1933).

Roatán, Honduras, 23 December 1991, 5 specimens 49 mm long live (LACM 1933); Soldado Channel, Guanaja, Honduras, 6 August 1991, 30 m depth, 2 specimens 25 mm long live (LACM 1975); Little French Cay, Guanaja, Honduras, 10 August 1991, 1 specimen 27 mm long live (LACM 1976).

External morphology: Living animals reach up to 49 mm in length. The general color of the living animals is translucent yellowish-white (Figure 1D). The

dorsum is covered with a network of anastomosed, irregular, thick black lines running in between the dorsal tubercles. In addition, there are numerous minute opaque white spots concentrated near the edge of the mantle and on top of the dorsal tubercles, giving them the appearance of being completely white. The rhinophores and gill are pale yellow.

The body is oval, low, stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of large,

Table 1

Comparative table of the external differences among species of *Doriopsilla* in the Atlantic Ocean.

	Body color	Dorsal tubercles	Geographical range
Doriopsilla areolata	Yellow to pinkish, reddish or pale brown with white rings or lines forming a network, center of the dorsum darker	Low and rounded to conical tubercles, larger in two rows between rhinophores and gills	Eastern Atlantic: from northern Spain to the Cape Verde Islands and Mediterranean Sea. Western Atlantic: Virgin Islands, Puerto Rico, Martinique
Doriopsilla albolineata	Pearl gray with white lines most of which are transverse, brown lines in the mantle margin	Low and simply rounded tubercles, larger in two rows between rhinophores and gills	Atlantic coast of Africa, from Ghana to Angola
Doriopsilla nigrolineata	Translucent yellowish-gray with white rings around tubercles and black lines forming a network	Low and simply rounded tubercles, medial tubercles are higher and larger	Panama, Honduras
Doriopsilla pelseneeri	White, yellow, orange or red, with a white line around the gill pocket edge	Large irregular warts, larger in the center of the dorsum	Iberian Peninsula
Doriopsilla pharpa	Yellow to orange with numerous dark brown spots on the whole surface of the dorsum	Numerous and minute tubercles, all of them of a similar size	Atlantic coast of the continental USA from Maryland to Florida, and Cuba, Virgin Islands
Doriopsilla espinosai	Translucent white to yellowish with several large opaque white patches, and a number of conspicuous red spots	Numerous low, simple conical tubercles, medial tubercles larger	Cuba, Bahamas
Doriopsilla elitae sp. n.	Yellow to dark orange with opaque white patches situated on top of many dorsal tubercles	Low, simple, conical tubercles	Aruba, St. Vincent and the Grenadines, Grenada, and Martinique
Doriopsilla tishae sp. n.	Translucent yellowish-white with a network of thick black lines and numerous minute opaque white spots near the mantle edge and on the tubercles	Large, semispherical tubercles, larger in the center of the dorsum	Honduras

semispherical tubercles, stiffened with spicules. Tubercles medial on the dorsum are larger, decreasing in size toward the borders of the mantle. The mantle margin is wide and slightly undulate. The rhinophores are perfoliate with up to 15 lamellae. The gill is composed of four tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused and grooved laterally. The anterior border of the foot is notched.

Anatomy: The buccal bulb is elongate (Figures 4A, 5A), covered by minute, rather undifferentiated oral glands on its proximal portion. The tubular esophagus leads from the buccal bulb. At this point two retractor muscles insert onto the posterior of the bulb. The esophagus is very long and convoluted (Figure 5B). Posteriorly, it broadens into a large muscular portion. The intestine runs posteriorly in the usual position and lacks any pyloric gland.

The ampulla is simple, oval (Figures 4C, 5B). It divides into a short oviduct, which enters the female gland and the prostate. The prostate is broad, flattened. From its distal end, the prostate leads into an elongated deferent duct. The penis, when everted, is very long and contains several rows of penial hooks. The penial hooks are approximately $15 \, \mu m$ wide at the base and

up to 20 µm in length (Figure 3B). The vagina is very long and convoluted. At its proximal end is a large, thin-walled, spherical bursa copulatrix. The seminal receptacle is small, having a long duct that joins the vagina at the point where it connects the bursa copulatrix. From this point also emerges the uterine duct.

The circulatory system consists in a large heart (Figures 4A, 5A), joined by the aorta with a flattened blood gland, situated behind the central nervous system.

Etymology: The species is named after Tisha Thiessen, oldest daughter of Jeff Hamann.

Geographic range: Thus far this species is only known from the Bay Islands, Honduras.

Remarks: Doriopsilla tishae is most similar to Doriopsilla nigrolineata (Figure 1F), originally described from the Caribbean of Panama, due to the presence of dorsal black lines in both species. Differences between these two species include the external coloration and the anatomy. Externally, both species have a pattern of black lines on the dorsum, however, in D. tishae the lines are more conspicuous, thicker, longer and consistently anastomosed, whereas in D. nigrolineata

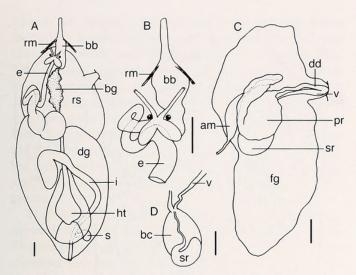


Figure 4. Drawings of the internal anatomy of the paratype of *Doriopsilla tishae* (LACM 1933). A, General view of the anatomy, scale bar = 1 mm. B, Detail of the anterior portion of the digestive system, scale bar = 1 mm. C, Reproductive system, scale bar = 1 mm. D, Connection of the bursa copulatrix and seminal receptacle, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

they are generally shorter, thinner and rarely contact each other (Figure 1F). Additionally, the tubercles of *D. tishae* are much larger than those of *D. nigrolineata*, and are completely covered with opaque white spots, whereas in *D. nigrolineata* the white spots surround smaller and more elongate tubercles. For a comparison of the external characteristics of *D. tishae* with other Atlantic species of *Doriopsilla* see Table 1.

Internally, the structure of the reproductive and digestive system is different. In *D. nigrolineata* the proximal region of the intestine is more inflated and the proximal region of the esophagus is proportionally smaller than those of *D. tishae* (see Figure 6). The buccal bulb of *D. tishae* is elongate, whereas that of *D. nigrolineata* is shorter. The seminal receptacle of *D. nigrolineata* is proportionally larger and joined to the bursa copulatrix by a much shorter duct than in *D. tishae*. No other Atlantic species of *Doriopsilla* have a network of dorsal black lines.

There are no eastern Pacific species of *Doriopsilla* with a color pattern similar to that of *Doriopsilla tishae*.

Doriopsilla areolata Bergh, 1880

(Figures 1E, 7)

Material examined: Anse Noire, North Point, Martinique, 15 July 1987, 30 m depth, 1 specimen 36 mm long

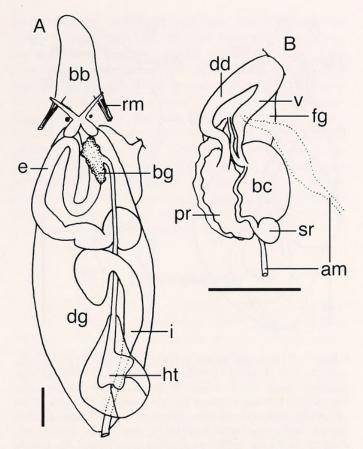


Figure 5. Drawings of the internal anatomy of a paratype of *Doriopsilla tishae* (LACM 1975). A, General view of the anatomy, scale bar = 1 mm. B, Reproductive system, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; sr, seminal receptacle; v, vagina.

live (LACM 173780). Additional specimens were photographed but are not preserved.

External morphology: Living Caribbean animals of this species reach 36 mm in length. The general color of the Caribbean animals varies from yellowish to pinkish or reddish (Figure 1E; Valdés et al., 2006). The dorsum is completely covered with numerous minute opaque bluish-white dots. The largest tubercles, situated on the outer side of the dorsum and inner mantle margin as well as on the branchial sheath, are surrounded by conspicuous white rings composed of accumulations of opaque white dots. The rhinophores and gill are the same color as the dorsum.

The body is oval, low, stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of round to conical tubercles, stiffened with spicules. Tubercles on the sides of the dorsum are larger, decreasing in size toward the borders of the mantle and the center of the dorsum. The mantle margin is wide and slightly undulate. The

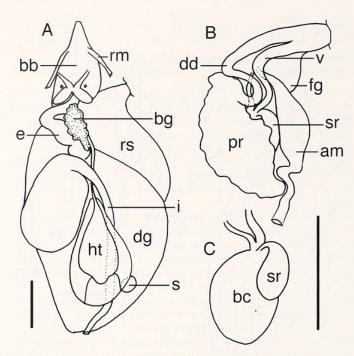


Figure 6. Drawings of the internal anatomy of *Doriopsilla nigrolineata* (LACM 173781). A, General view of the anatomy, scale bar = 1 mm. B, Reproductive system, scale bar as in C. C, Connection of the bursa copulatrix and seminal receptacle, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

rhinophores are perfoliate with up to 12 lamellae. The gill is composed of five tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused and grooved laterally. The anterior border of the foot is notched.

Anatomy: The buccal bulb is very elongate (Figure 7A–B), covered by minute, rather undifferentiated oral glands on its proximal portion. The tubular esophagus leads from the buccal bulb. The esophagus is very long and convoluted (Figure 7B). Posteriorly, it broadens into a small muscular portion. The intestine runs posteriorly in the usual position and lacks any pyloric gland.

The ampulla is simple, very elongate (Figure 7D). It divides into a short oviduct, which enters the female gland and the prostate. The prostate is broad, flattened (Figure 7C). From its distal end, the prostate leads into a short deferent duct. The penis, when everted, is very long and contains several rows of penial hooks. The vagina is very long and convoluted particularly at its proximal end where it connects to the thin-walled, spherical bursa copulatrix. The seminal receptacle is small, having a long duct that joins the vagina at the point where it connects to the bursa copulatrix. The uterine duct also emerges from this point.

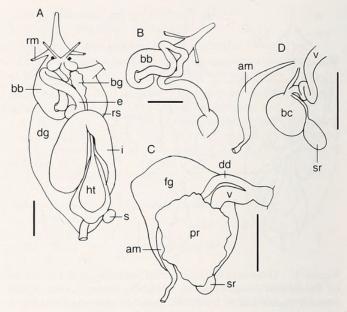


Figure 7. Drawings of the internal anatomy of *Doriopsilla areolata* (LACM 173780). A, General view of the anatomy, scale bar = 1 mm. B, Detail of the anterior portion of the digestive system, scale bar = 1 mm. C, Reproductive system, scale bar = 1 mm. D, Connection of the bursa copulatrix, seminal receptacle, and ampulla, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

Remarks: Eastern Atlantic specimens of this species have been described in detail by Valdés & Ortea (1997). Caribbean specimens are anatomically identical to those from the eastern Atlantic, but they lack the pattern of irregular white lines on the dorsum. Instead they only display the white rings present in juvenile specimens from the eastern Atlantic.

Marcus & Marcus (1962) cited *Doriopsilla areolata* for the Caribbean (St. John, Virgin Islands) based on a single specimen that was preserved before study, therefore the color of living Caribbean animals remained unknown. The anatomical descriptions by Marcus & Marcus (1962) match our observations and the descriptions for eastern Atlantic animals, confirming that they are all members of the same species.

Doriopsilla nigrolineata Meyer, 1977 (Figures 1F, 6)

Material examined: Michael Rock Channel, Guanaja, Honduras, 5 August 1991, 2–3 m depth, 1 specimen 25 mm long, live (LACM 173781). Punta Hospital, Bocas del Toro, Panama, 23 August 2006, 10 m depth, 1 specimen 25 mm long live (LACM 173782).

External morphology: Living animals reach up to

25 mm in length. The general color of the living animals is translucent yellowish-gray (Figure 1F). The viscera is visible through the skin as a dark gray area. The dorsum is covered with a series of thin, irregular black lines running in between the dorsal tubercles and almost never contacting each other. In some specimens the lines may be longer than in others. In addition, there are numerous minute opaque white spots all over the dorsum, forming rings around the dorsal tubercles but never on the tubercles themselves. The rhinophores and gill are pale yellow. The rhinophores have white apices.

The body is oval, low, stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of round tubercles, stiffened with spicules. Medial tubercles on the dorsum are higher and larger, decreasing in length and size toward the borders of the mantle. The mantle margin is wide and slightly undulate. The rhinophores are perfoliate with up to 12 lamellae. The gill is composed of four tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused and grooved laterally. The anterior border of the foot is notched.

Anatomy: The buccal bulb is short and wide (Figure 6A), covered by minute, rather undifferentiated oral glands. The tubular esophagus leads from the buccal bulb. The esophagus is short and convoluted. Posteriorly, it broadens into a muscular portion. The intestine is greatly expanded proximally, runs posteriorly in the usual position and lacks any pyloric gland.

The ampulla is simple, elongate (Figure 6B) and enters the female gland near the opening of the prostate. The prostate is broad and flattened. From its distal end, the prostate leads into a relatively short deferent duct. The penis, when everted, is very long and contains several rows of penial hooks. The vagina is short and convoluted. At its proximal end is an oval, thin-walled bursa copulatrix. The seminal receptacle is small, having a very short duct that joins the vagina at the point where it connects the bursa copulatrix (Figure 6C). From this point also emerges the uterine duct.

The circulatory system consists in a large heart (Figure 6A), joined by the aorta with a flattened blood gland, situated behind the central nervous system.

Geographic range: Originally described from Panama, this species has been subsequently collected and photographed from Honduras.

Remarks: The original description of this species (Meyer, 1977) was based on external characteristics but did not include anatomical examinations. The redescription by Valdés & Ortea (1997) was a reexamination of the external morphology of the

holotype and produced no new information. The present paper provides the first anatomical examination of this species, which clearly differs from *Doriopsilla areolata* in several regards. Differences include the length of the buccal bulb, which is several times longer in *D. areolata* than in *Doriopsilla nigrolineata*. Also the structure of the reproductive system is different in these two species, with a larger seminal receptacle in *D. nigrolineata* connected to the bursa copulatrix by a much shorter duct. Finally, the ampulla is proportionally longer in *D. areolata*. Externally these two species are readily distinguishable by the presence of irregular black lines in *D. nigrolineata* that are absent in *D. areolata*.

DISCUSSION

Cariopsillidae Ortea & Espinosa, 2005, type genus *Cariopsilla* Ortea & Espinosa, 2005, was described based on the species *Doriopsilla pharpa* Marcus, 1961, which has dorsal tubercles superficially similar to the caryophyllidia present in other dorid nudibranchs. Ortea & Espinosa (2005) indicated that this new taxon is proposed to rationalize the systematics of radula-less dorids, independently from phylogenetic studies that produce erroneous results due to the incorrect use of characters. More specifically, Ortea & Espinosa (2005) criticized the phylogenetic analysis conducted by Valdés & Gosliner (1999) because of the exclusion of characters referring to the caryophyllidia-like tubercles of *D. pharpa*.

According to the only available phylogenetic hypothesis including *D. pharpa* (Valdés & Gosliner, 1999), this species is nested in the *Doriopsilla* clade, so the introduction of a new genus and a new family for this species would render both *Doriopsilla* and Dendrodorididae as paraphyletic. Ortea & Espinosa (2005) did not provide arguments to support the evolutionary distinctiveness of *D. pharpa* or a phylogenetic hypothesis to support their alternative grouping. For all these reasons, and until new evidence becomes available, we regard Cariopsillidae as a junior synonym of Dendrodorididae and *Cariopsilla* as a junior synonym of *Doriopsilla*.

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