

The Genus *Paradoris* Bergh, 1884 (Nudibranchia: Discodorididae) in the Tropical Americas, and South Africa with the Description of a New Species

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Abstract. A new species of *Paradoris* Bergh, 1884, *P. caeruleus* sp. nov. is described based on specimens collected from South Africa. The coloration, radular morphology, and details of the reproductive system of this species differ significantly from other previously described *Paradoris* species by having a blue body with gray-blue spots and a few black spots on the dorsum, as well as an accessory gland with two stylets in each sac. A redescription of *P. mulciber* and *P. lopezi* is based on newly collected material of these species from the Caribbean coast of Costa Rica and the Galápagos Islands. The range of *P. lopezi* is extended, from Mexico to the Galápagos Islands.

INTRODUCTION

A taxonomic revision of *Paradoris* Bergh, 1884, recently published by Dayrat (2006) recognizes eight species from the Pacific, Atlantic, and Indo-Pacific oceans: *P. indecora* (Bergh, 1881); *P. dubia* (Bergh, 1904); *P. liturata*, (Bergh, 1905); *P. erythraeensis* (Vayssiére, 1912); *P. mulciber* (Marcus, 1970); *P. tsurugensis* Baba, 1986; *P. araneosa* Valdés, 2001; and *P. lopezi* Hermosillo & Valdés, 2004. According to Dayrat (2006), *Paradoris* is characterized by the following combination of characters: labial armature with three jaw plates, radula elongated and narrow, grooved outer edge of the hook of the lateral teeth, and grooved oral tentacles.

The first reference to *Paradoris* in the Western Atlantic Ocean was the description of *Paradoris mulciber* from Brazil (Marcus, 1970), originally described as the type species of the new genus *Percunas* Marcus, 1970. Later, Marcus (1976) synonymized *Percunas* with *Paradoris*. Ortea (1995) revised the species of the genus from the Canary Islands. According to this author, there were four species in this area, however Dayrat (2006) synonymized three of these species with *P. indecora*, based on individual variation. This author, as well as Ortea (1995), also concluded that *Paradoris granulata* Bergh, 1884, the type species of the genus, is a junior synonym of *Discodoris indecora* Bergh, 1881.

The first reference of this genus in the Pacific Ocean was the description of *Paradoris tsurugensis* from Japan by Baba (1986, 1989). Later, Miller (1995) described *Paradoris leuca* from New Zealand, which was

synonymized most recently with *Paradoris dubia* (Bergh, 1904) by Dayrat (2006) based on similarities of the reproductive system. Valdés (2001) described two new species from deep waters of New Caledonia: *Paradoris araneosa* and *Paradoris imperfecta*; the latter was synonymized with the former by Dayrat (2006). Finally, Hermosillo & Valdés (2004) described *Paradoris lopezi*, a new species from Mexico.

Paradoris mulciber (Marcus, 1970) is known only from the type material described from Brazil and redescribed by Dayrat (2006). This species and *Paradoris lopezi* Hermosillo & Valdés, 2004 are the only two members of the genus *Paradoris* reported from the Americas. The present paper redescribes these species on the basis of several new specimens collected from the Caribbean coast of Costa Rica and the Galápagos Islands, Ecuador, respectively. We also describe one new species from South Africa.

MATERIALS AND METHODS

The material studied is deposited at the Zoology Museum of the University of Costa Rica, the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco, USA (CASIZ), and the Natural History Museum of Los Angeles County (LACM).

Specimens were preserved in 70% ethanol. They were dissected by dorsal incision, and their reproductive systems were examined and drawn under a dissecting microscope with camera lucida. At least two specimens of each species were examined anatomically and dissected for this study. The buccal masses were

dissected and immersed in sodium hydroxide, rinsed, and then mounted on stubs for SEM examination.

The accessory gland from the reproductive system was dissected and placed in different concentrations of alcohol for at least 20 min and then transferred to a solution of xylol for 20 min. After the tissue became translucent, the gland was mounted on a cover slide. The stylets were drawn using a microscope with camera lucida.

SPECIES DESCRIPTIONS

Genus *Paradoris* Bergh, 1884

Paradoris mulciber (Marcus, 1970)

(Figures 1A, 2, 3, 4)

Type material examined: *Holotype:* Juriacu, Maranhão Province, Brazil 00°04'S, 44°33'W, 6 September 1967, 1 specimen (previously dissected), 21 mm preserved length, *leg.* Almirante Saldanha R/V (MZSP 41291).

Other material examined: Ponta de Pedra, Pernambuco Province, Brazil, 30 August 1970, 1 specimen (previously dissected), 35 mm preserved length, *leg.* Montonchet (MZSP 41292, # 1045 Marcus Coll.); Manzanillo, Área de Conservación Amistad Caribe, Sixaola, Limón, Costa Rica (9°38'42"N, 82°39'29"W), 20 October 1998, 4 specimens (3 dissected), 27–56 mm preserved length, collected under rocks by SCUBA, 9 m depth, *leg.* S. Avila (INB001501499); Silal de Cahuita, Parque Nacional Cahuita, Limón, Costa Rica (9°44'35"N, 82°48'21"W), 21 September 1999, 2 specimens (one dissected) 15–29 mm preserved length, collected under rocks by SCUBA diving, 12.5 m depth, *leg.* M. Calderón (INB001496697).

Geographic range: This species was previously known from Brazil (Marcus, 1970, 1976) and Costa Rica (Espinosa & Ortea, 2001). Some additional specimens have been collected from the Caribbean (Vinicius Padula, personal communication).

External morphology: Living animals range from 20–60 mm long. The body is oval and elevated, widest in the middle region (Figures 1A, 2A). The mantle margin is wide, undulating, and spiculate. The dorsum is covered with rounded, widely spaced tubercles of various sizes. The largest ones are generally situated in the middle region of the notum (Figure 2A), and most of them are elevated. Some specimens have one or two tubercles located anteriorly and posteriorly on the rhinophoral sheath. The rhinophores have 19–21 very thin lamellae. The rhinophoral and branchial sheaths are undulate. The gill consists of six tripinnate branchial leaves. Other specimens examined have around the same number of lamellae in the rhinophores

and branchial leaves. The oral tentacles are finger-like and have a longitudinal groove on their external side. The anterior border of the foot is grooved and notched (Figure 2B). The foot is completely covered by the notum when the animal is in motion.

The background color of the dorsum in living animals is light brown to pale cream, with numerous small dark brown spots (Figure 1A) very densely arranged on the entire dorsum and at the base of the tubercles. Each spot itself is composed of an aggregation of minute brown specks. The apices of large tubercles are yellowish. The rhinophores and branchial leaves are pale brown with small, dark brown spots arranged irregularly. The tips of the branchial leaves are yellowish, and the branchial sheath is undulate. The ventral side of the animal is cream colored. The sole of the foot has more dark spots than the hyponotum, but they are smaller (Figure 2B). The same spotting occurs on the ventral surface, foot, and mantle. The tentacles are covered with brown speckles.

Anatomy: The jaw has three distinct pieces with a number of simple, regularly arranged elements about 8 μ m in length (Figure 3A). The radular formula of an 18 mm preserved length specimen is $55 \times (18.0.18)$ (INB001501499) and a 40 mm preserved length specimen is $47 \times (16.0.16)$ (LACM ACC 4308). In general, the teeth are broad and hook-shaped. All the lateral teeth, including the outermost, are smooth. They become gradually larger from the innermost to the mid-laterals, then become smaller and less angular from the mid-laterals to the outermost. The innermost teeth are thin, pointed, and angular (Figure 3B). The mid-lateral teeth have a groove on the lower side of the cusp (Figure 3C). The outermost have a prolongation on the upper side of the teeth (Figure 3D). There is no sharp distinction between the base and the cusp in the outermost tooth.

The ampulla, which is long and tubular, is located left on top and anterior to the female glands and next to the bursa copulatrix. The deferent duct is large and thin throughout its length (Figure 4A) and leads to a granular and convoluted prostate that is folded upon itself. At the distal end, there is an unarmed penis that is wider than the rest of the duct. The long vagina connects to two accessory glands and three muscular sacs containing one stylet each (Figure 4B). Two of the sacs are located on the dorsal side and one on the ventral side of the vagina. Each stylet is about 0.6 mm in length. The whitish bursa copulatrix is semi-spherical and thin-walled. From the bursa copulatrix leads another thin duct that connects to the oval seminal receptacle and the uterine duct.

Remarks: *Paradoris mulciber* (Marcus, 1970) is the only species of the genus *Paradoris* reported from the

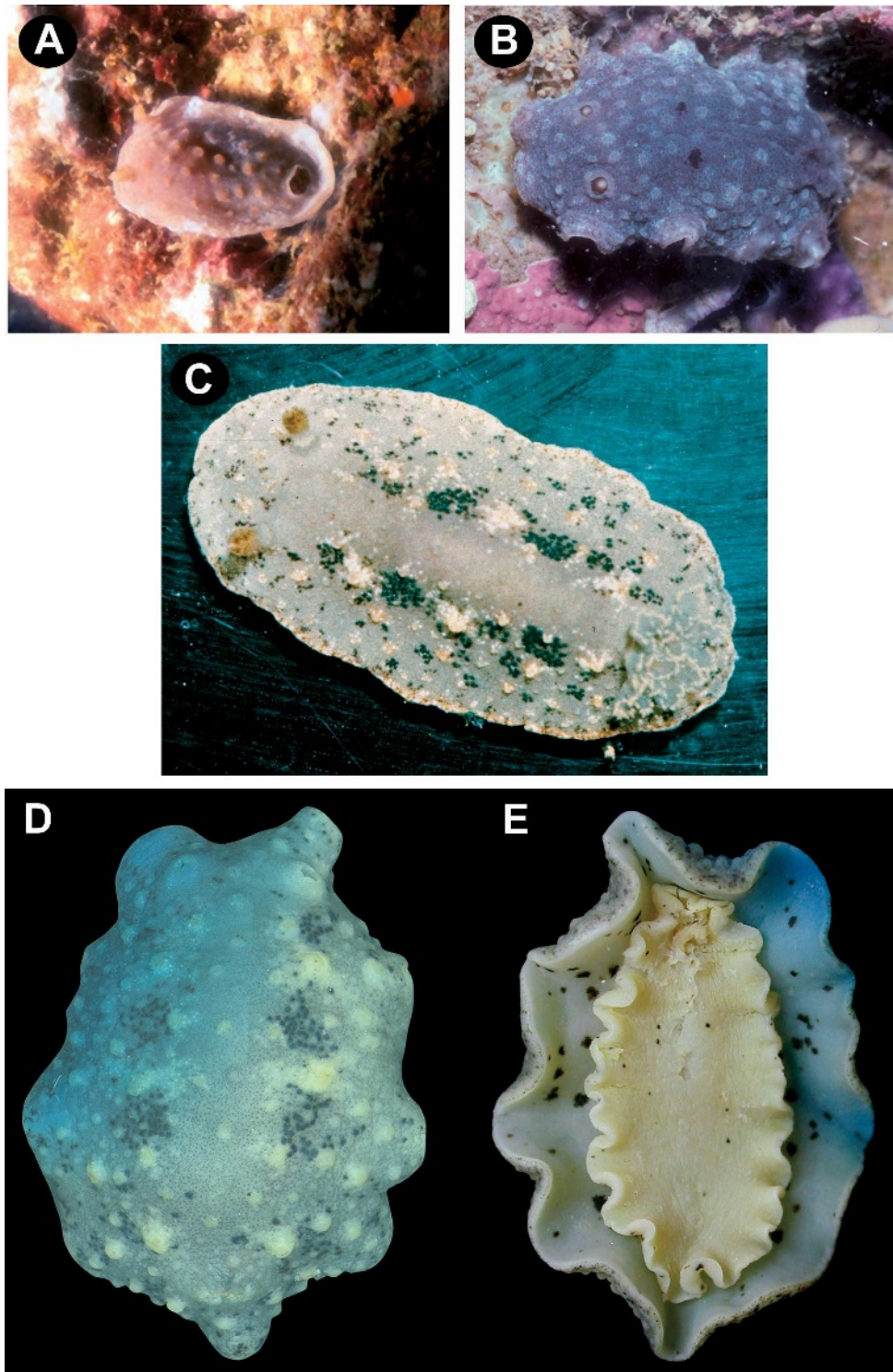


Figure 1. Living animals of *Paradoris*. A. *Paradoris multiciber*, Costa Rica (INB001501499) photo by Y. Camacho-García. B. *Paradoris caeruleus* sp. nov., South Africa (CASIZ 073954) photo by T.M. Gosliner. C. Living animal of *Paradoris lopezi*, Galápagos Islands (LACM 71-45) photograph by D.K. Mulliner. D. Dorsal view of a preserved animal of *Paradoris lopezi* (CASIZ 105978) photograph by M. Zúñiga. E. Ventral view of a preserved animal of *Paradoris lopezi* (CASIZ 105978) photograph by M. Zúñiga. Note: In fig. 1D, E, the blue color on the pictures is due to an accidental stain of the specimen with methylene blue.

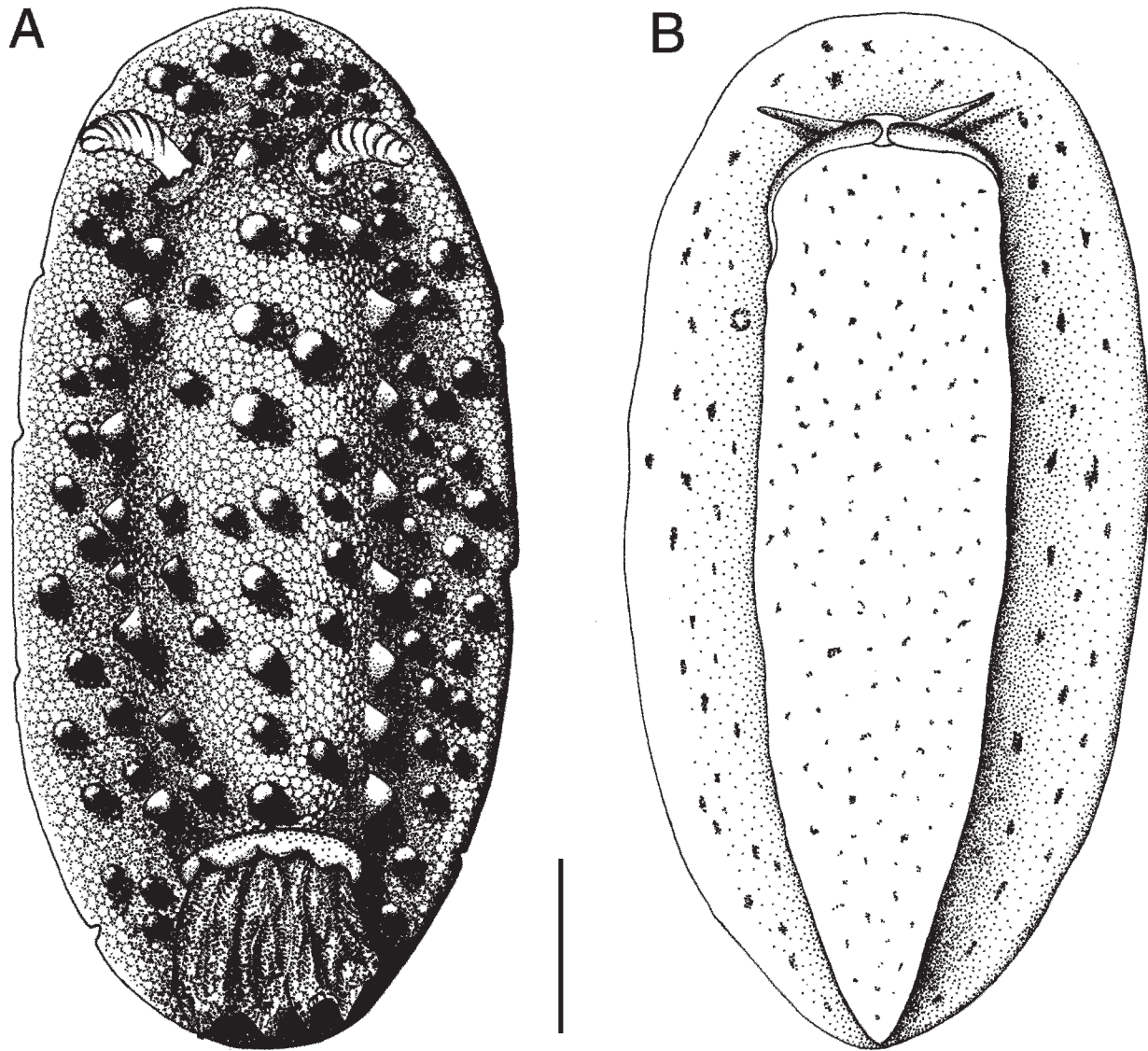


Figure 2A. Dorsal view of a preserved animal of *Paradoris multiciber* from Limón, Caribbean coast of Costa Rica (INB001501499). B. Ventral view; scale bar = 5 mm.

Atlantic coast of the Americas. The original description of this species (in the genus *Percunas*) was a brief description, later expanded by Marcus (1976). The specimens examined here are identical to those described by Marcus (1970, 1976), and there is no detectable variation among the specimens. The only differences between Marcus's descriptions and ours (also pointed out by Dayrat, 2006) are that the prostate is larger in the original description than that found in the present material, the branchial sheath of our specimens has several undulations rather than being smooth as in Marcus's description, and the rhinophoral sheaths in some specimens examined here have one or two tubercles on each side.

A drawing of the reproductive system of a specimen from the Caribbean made by Vinicius Padula (unpublished data) consistently shows the presence of two accessory glands and three stylets. Also, the ampulla has a U-shaped form and a long and convoluted prostate folded upon itself that is also present in the three specimens we dissected from Costa Rica. The only difference found in the reproductive system of the specimen from the Caribbean that differs from ours and that of Marcus (1976) is that the duct that leads from the seminal receptacle joins the duct from the vagina before it enters into the bursa copulatrix.

Ortea (1995) stated that *P. indecora* is possibly an amphiatlantic species and that *P. multiciber* is a junior

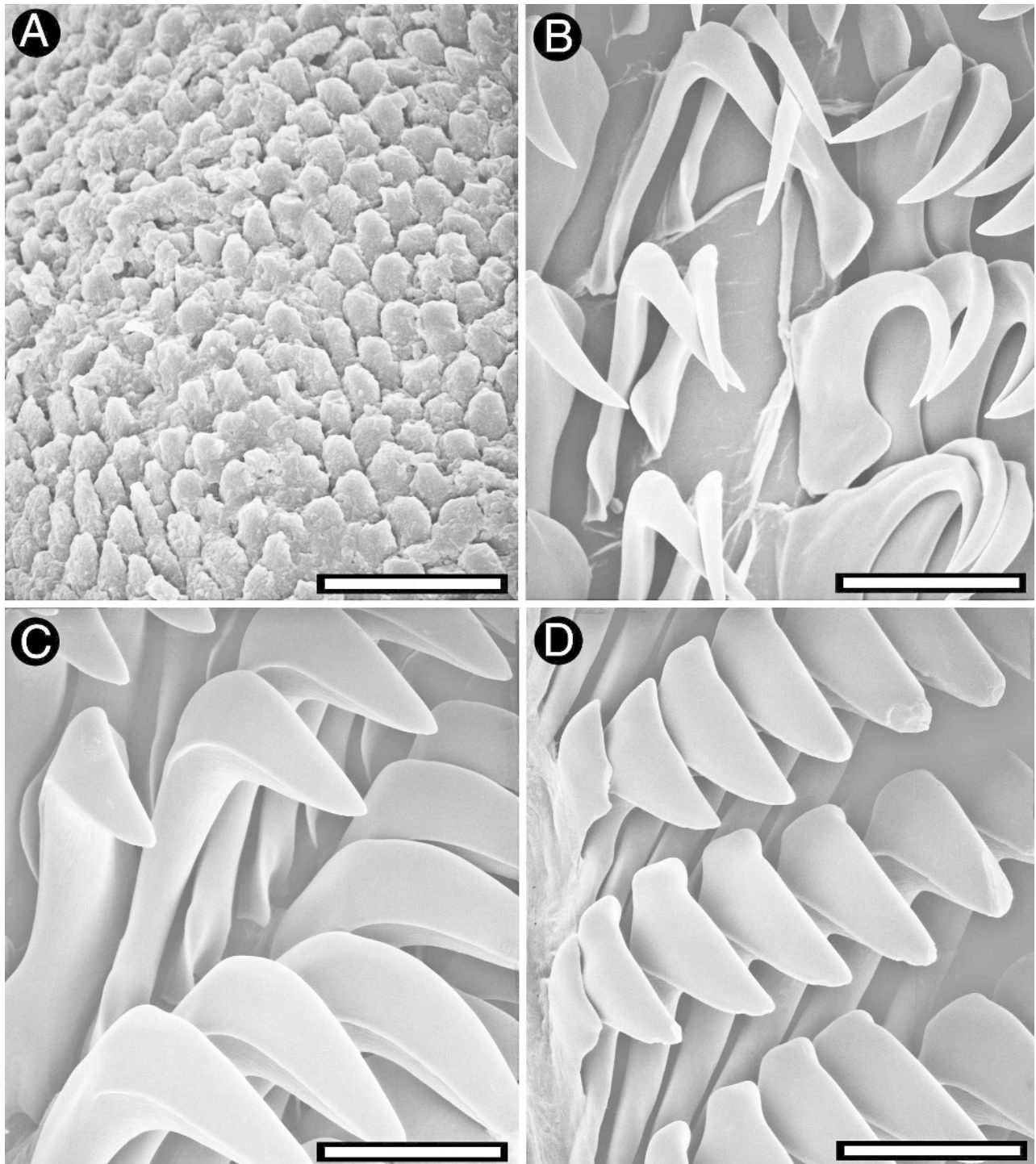


Figure 3. Scanning electron micrographs of *Paradoris multiciber* (INB001501499). A. Jaw elements, scale bar = 25 μ m. B. Innermost radular teeth, scale bar = 75 μ m; C. Mid-lateral radular teeth; scale bar = 75 μ m. D. Outermost radular teeth scale bar = 75 μ m.

synonym of *P. indecora*. Dayrat (2006) concluded that “the differences between *multiciber* and *indecora* are slight” and that *multiciber* and *indecora* cannot be distinguished from each other. Despite these slight

differences, and considering the geographical range of the species, Dayrat agreed to keep these species as two valid species. Based on the new specimens we examined from Costa Rica, we conclude that these two species

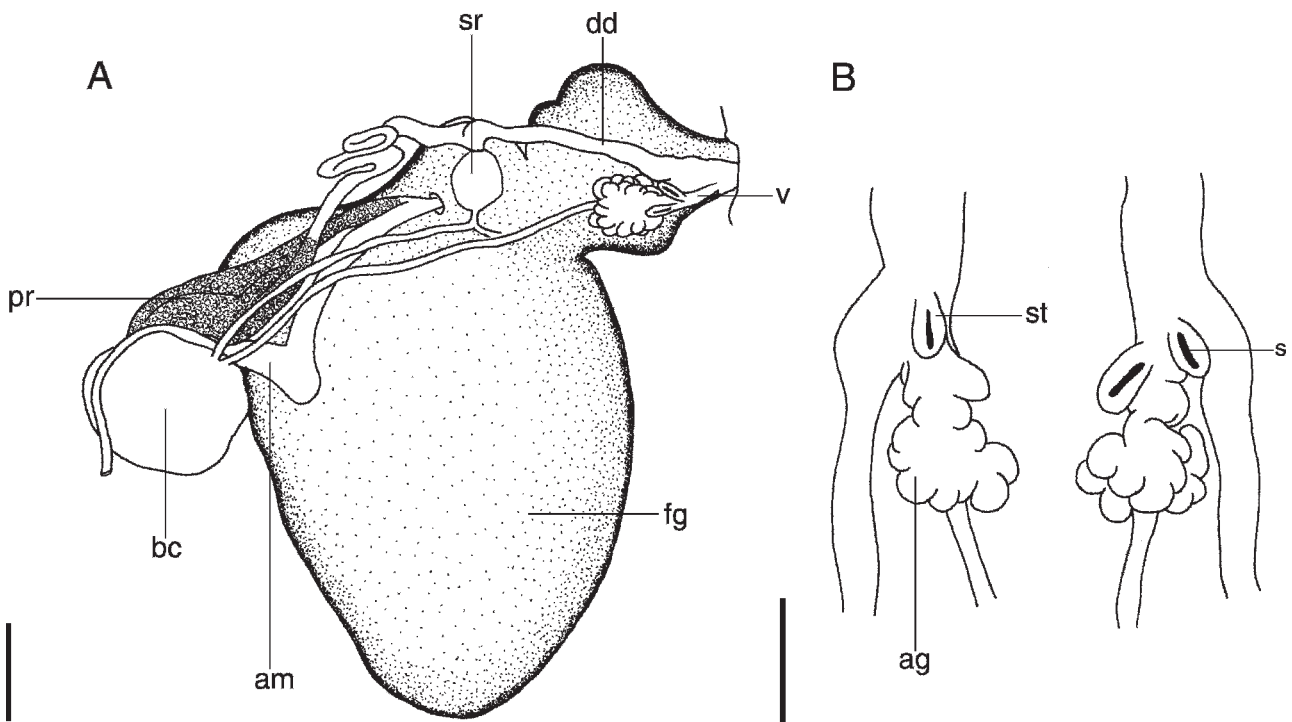


Figure 4A. Reproductive system of *Paradoris multicber* (INB001501499), scale bar = 18 mm. B. Detail of the reproductive system (INB001501499), scale bar = 23 mm; Abbreviations: ag = accessory gland, am = ampulla, bc = bursa copulatrix, dd = deferent duct, fg = female gland, pr = prostate, s = stylet, sr = seminal receptacle, st = stylet sac, v = vagina.

are distinct (Table 1) based on several anatomical differences. For example, in these specimens, and that which V. Padula examined from the Caribbean, there are consistently two accessory glands with three stylets. *Paradoris indecora* has only one accessory gland and a maximum of three stylets (Dayrat, 2006). Also, *P. indecora* has fewer, smaller tubercles arranged in two mid-dorsal lines (see description by Valdés, 2002, and Ortea, 1995:fig. 2) while those of *P. multicber* are larger, more numerous, and more evenly distributed over the entire dorsum (Figure 2).

Paradoris lopezi Hermosillo & Valdés, 2004

(Figures 1C–E, 5A, B, 6A–D, 7A, B)

Type material examined: Holotype: Punta de Pichilingue, Baja California Sur, La Paz, Mexico. (24°21'25"N, 105°33'88"W), 31 October 2004, 1 specimen (previously dissected), 32 mm preserved length, collected under coral rubble at 1 m depth, *leg.* A. Hermosillo (CASIZ 171661).

Other material examined: Punta Espinosa, Isla Fernandina, Galápagos Islands, Ecuador, 16 September 1974, 1 specimen, 71 mm preserved length, collected in the intertidal rocky shore under rocks, *leg.* G. H. Wellington (CASIZ 117625); Punta Espinosa, Isla

Fernandina, Galápagos Islands, Ecuador, 16 September 1974, 3 specimens (dissected for this study) 26–61 mm preserved length, collected in the intertidal rocky shore under rocks, *leg.* G. H. Wellington (CASIZ 105978); Darwin Research Station, Academy Bay, Santa Cruz Island, Galápagos Islands, Ecuador (0°45'06"S, 90°15'38"W), March 1971, 1 specimen, 25 mm preserved length, collected between 1–3.3 m depth, *leg.* Ameripagos Expedition (LACM 71-45).

Geographic range: This species is known only from Baja California Sur and Bahía Banderas, México, and the Galápagos Islands (present study).

External morphology: The dorsum is covered with numerous, semispherical tubercles of different sizes arranged regularly (Figures 1C, 5A). Generally, the largest tubercles are located near the center. There are no tubercles located on the rhinophoral or branchial sheaths in any of the specimens. The gill is composed of six tripinnate branchial leaves, and the rhinophores have 18–20 lamellae in a 36 mm preserved length specimen (CASIZ 105978). An SEM of the notum (not included here) clearly shows the presence of mantle holes. The margin of the mantle is wide and undulating. The anterior border of the foot is grooved and notched (Figure 5B). The oral tentacles are conical and grooved.

The background color of the living animals is gray

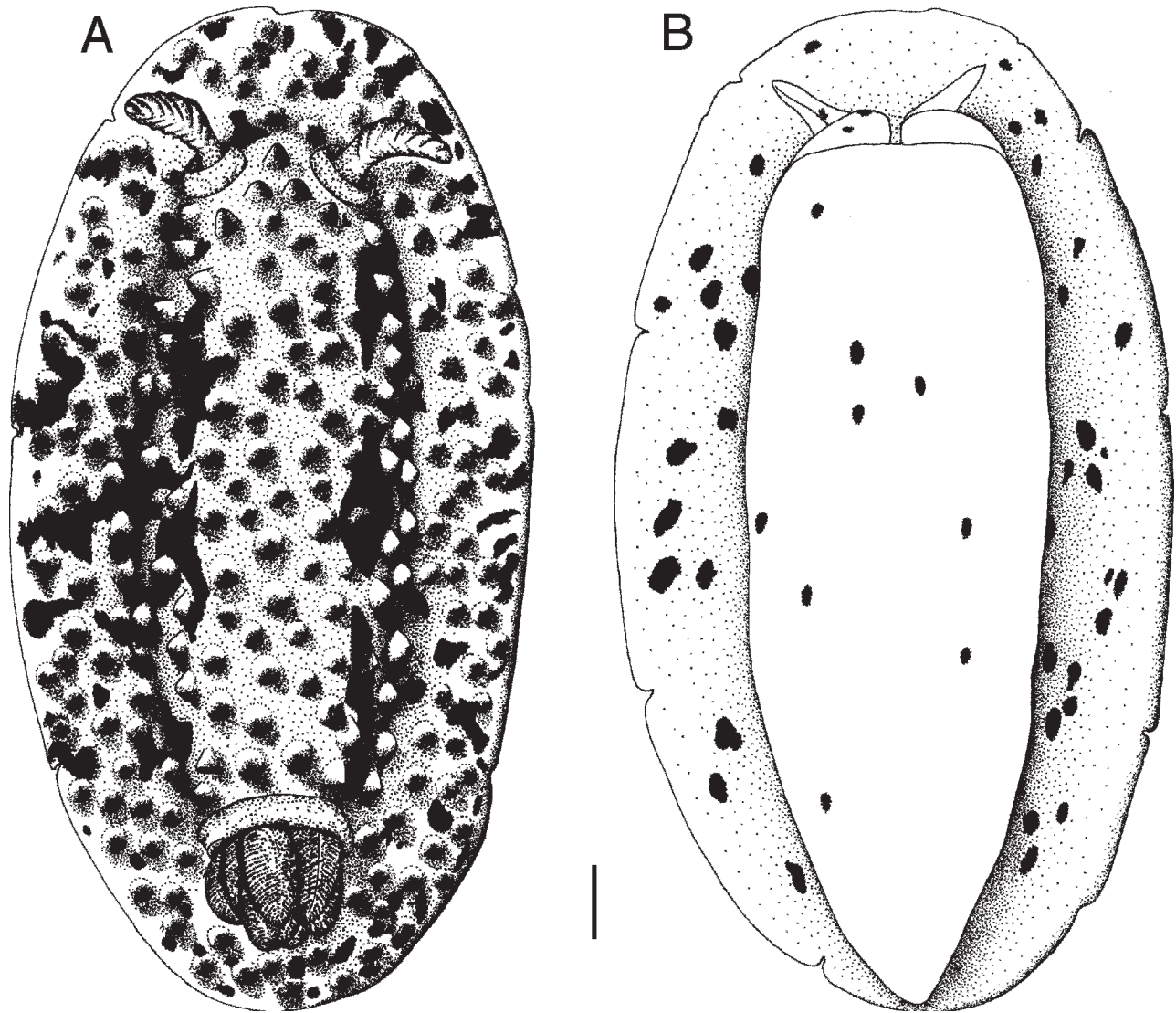


Figure 5A. Dorsal view of a preserved animal of *Paradoris lopezi* (CASIZ 117625) from Punta Espinosa, Galápagos Islands, Ecuador. B. Ventral view, scale bar = 5 mm.

with numerous small brownish orange spots arranged very densely on the entire dorsum (Figure 1C). The gray color is darker towards the middle of the dorsum. The tubercles have a pale gray base and an orange tip. There are several large black patches (one specimen has eight) composed of an aggregate of small black specks. There are simple black and brown spots near the margin of the mantle as well. Opaque white spots are also present all over the dorsum. The rachises of the branchial leaves are dark gray with small brown spots, the tips being yellowish. The foot is pale gray spotted with brown. The color of the ventral side of the mantle is pale gray with some dark brown spots. These spots are larger than those on the

foot and are arranged irregularly (Figures 1E, 5B). The rhinophores are light brown with small darker brown spots.

Anatomy: The radular formula is $42 \times (22.0.22)$ in a 35 mm preserved length specimen and $55 \times (26.0.26)$ in a 61 mm preserved length specimen. The radula is very elongated and the labial cuticle has three pieces. Jaw elements are arranged regularly (Figure 6A) (CASIZ 105978). The innermost teeth are larger, more angular, and more pointed than the rest (Figure 6B). The midlateral teeth are hook-shaped and pointed (Figure 6C). Generally, the teeth have a prolongation on the upper side that is strongest in the outer teeth.

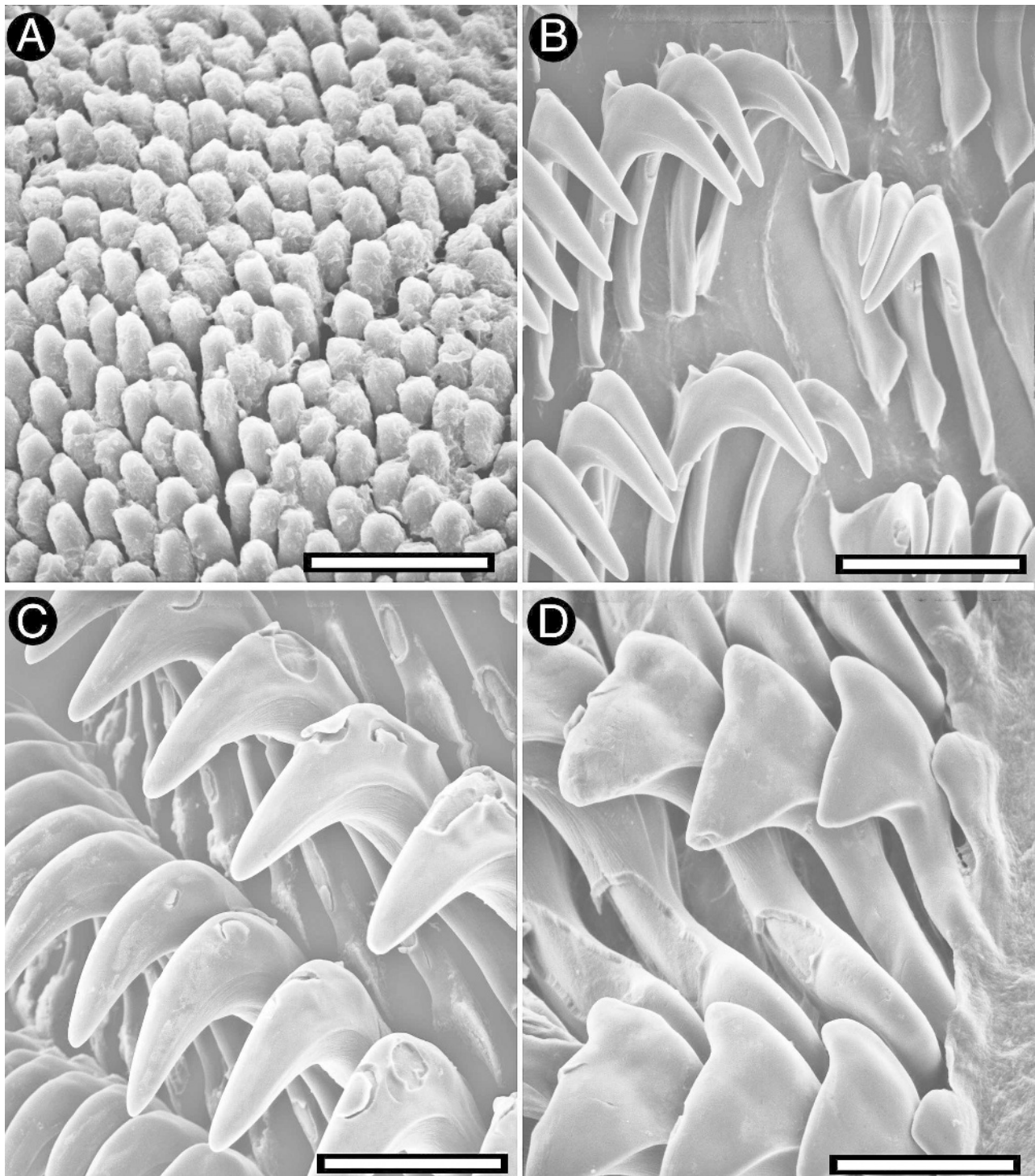


Figure 6. Scanning electron micrographs of *Paradoris lopezi* (CASIZ 117625). A. Jaw elements, scale bar = 25 μ m. B. Innermost radular teeth, scale bar = 75 μ m; C. Mid-lateral radular teeth, scale bar = 75 μ m. D. Outermost radular teeth, scale bar = 75 μ m.

There is not a sharp distinction between the base and the cusp in the outermost teeth (Figure 6D).

The ampulla is long, wider in the middle, and folded upon itself. It has a long duct located distally, prior to

its bifurcation into the oviduct and deferent duct. There is a large and convoluted prostate (Figure 7A). The deferent duct gradually narrows before ending in a short, unarmed penial section. The vagina is long

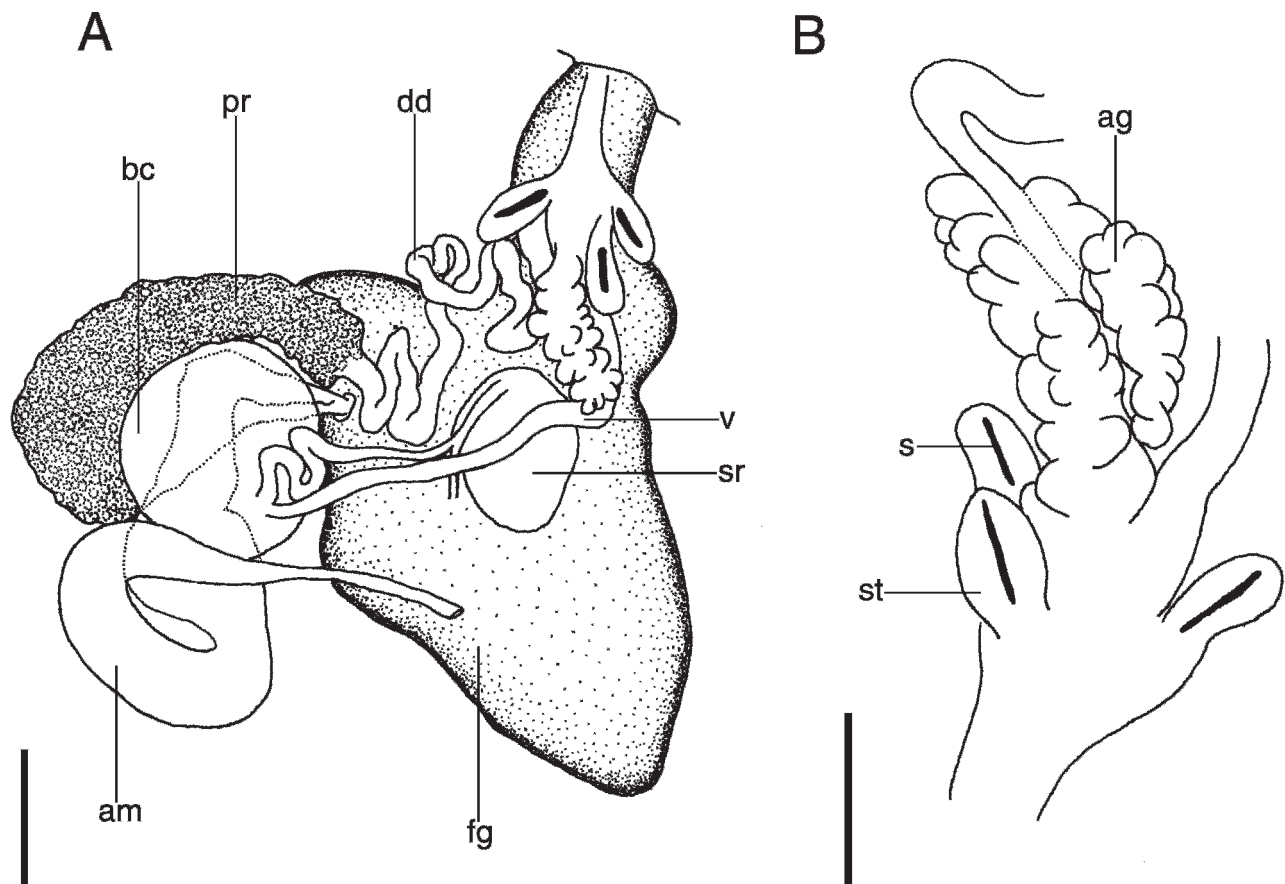


Figure 7A. Reproductive system of *Paradoris lopezi* (CASIZ 117625), scale bar = 18 mm. B. Detail of the reproductive system (CASIZ 117625), scale bar = 23 mm. Abbreviations: ag = accessory glands, am = ampulla, bc = bursa copulatrix, dd = deferent duct, fg = female gland, pr = prostate, s = stylets, sr = seminal receptacle, st = stylet sac, v = vagina.

and connects with two accessory glands and three muscular sacs, each containing a single stylet about 0.9 mm in length. The glands and the sacs are both located on the dorsal side (Figure 7B). The bursa copulatrix is pale cream, semispherical, and twice the size of the seminal receptacle. There is a convoluted duct that leads from the bursa copulatrix to the oval seminal receptacle and to the uterine duct.

Remarks: Dayrat (2006) found some differences in the original description of the species when reexamining the type material. For example, the oral tentacles were grooved (Dayrat, 2006) instead of not grooved (Hermosillo & Valdés, 2004), and there were two accessory glands and three stylet sacs (Dayrat, 2006) instead of just one stylet sac and two accessory glands (Hermosillo & Valdés, 2004). The three specimens we examined from the Galápagos Islands are in complete agreement with the description provided by Dayrat (2006). However, we also observed some morphological differences between the holotype from Mexico and the

three specimens from Isla Fernandina, Galápagos. The specimen designated as the holotype has higher tubercles (about 1.3 mm), and smaller and lighter spots on the hyponotum and notum. On the other hand, the specimens from Isla Fernandina have lower tubercles and bigger and darker spots on the hyponotum and notum.

There are several morphological differences between *P. lopezi* and *P. mulciber*. In *P. lopezi*, there are long black patches clearly visible all over the dorsum, and single black and brown-orange spots close to the margin of the mantle (Figure 1C), whereas no dark pigmentation is present on the dorsum or mantle in *P. mulciber* (Figure 1A). Also, while the foot of *Paradoris mulciber* has more but smaller dark spots than the hyponotum (Figure 2B), *P. lopezi* has fewer but larger dark spots on both the foot and hyponotum (Figure 1E). The tubercles present on each side of the rhinophoral sheaths in *P. mulciber* are not present in any of the specimens examined of *P. lopezi*. *Paradoris indecora* (Bergh, 1881) from the Mediterranean differs from *P. lopezi* by the external coloration and the mid-dorsal position of the tubercles.

Paradoris dubia, described by Bergh (1904), is also easily distinguished from *P. lopezi* by the white color of the body with dark brown spots, the translucent color of the foot, the smooth dorsum, and the lack of accessory glands and stylets. *Paradoris tsurugensis* (Baba, 1986, 1989) from Japan differs slightly from *P. lopezi* in external morphology and coloration (see Hermosillo & Valdés, 2004); for example, *P. lopezi* has more stylet sacs (Table 1) but fewer teeth ($[42 \times [22.0.22]]$) than *P. tsurugensis* ($90 \times [20-25.0.20-25]$) in specimens of comparable size.

We agree with Dayrat (2006) that the presence of dark red tubercles on the dorsal notum is probably a good character to distinguish *P. lopezi* from the rest of the species of the genus *Paradoris*, such as *P. araneosa*, *P. liturata*, and *P. erythraeensis*.

Paradoris caeruleus, new species

(Figures 1B, 8, 9)

Type material: *Holotype*: Phillips Reef, Algoa Bay, Indian Ocean coast, Cape Province, South Africa, February 1984, 1 specimen (dissected for this study) 25 mm preserved length, collected at 10–15 meters depth by SCUBA diving, *leg.* WR. Liltved (SAM A36019); *Paratype*: Phillips Reef, Algoa Bay, Indian Ocean coast, Cape Province, South Africa, May 18, 1984, 1 specimen (dissected for this study) 24 mm preserved length, *leg.* WR. Liltved (CASIZ 073954), with two microslides.

Geographic range: This species is known only from South Africa (present study).

External morphology: The body is oval and elongated, higher in the middle portion. The dorsum is covered with numerous low tubercles of various sizes closely arranged and densely distributed. Wider tubercles are surrounded by smaller ones. There are no larger tubercles located on the rhinophoral sheaths as in *P. multiciber*. There are numerous large holes covering the surface of the notum. The gill is composed of seven tripinnate branchial leaves, and the rhinophores have 10 lamellae in a 24 mm preserved length specimen (SAM A36019). The number of lamellae and branchial leaves in the other specimen available are not provided since these structures were retracted in their sheaths. The mantle is wide and undulating. The anterior border of the foot is grooved and notched (Figure 9A). The oral tentacles are finger-like in shape and grooved. The foot is completely covered by the notum when the animal is in motion.

The background color of living animals is a uniform gray blue with two black spots (Figure 1B) located almost halfway between the rhinophores and the branchial leaves; however, there are also some small

spots present around the margins of the notum. Around the larger and smaller tubercles, there is an aggregation of minute white spots that are also present along the mantle margins. The branchial leaves and the base of the rhinophores are brownish black in color, while the tips of the rhinophores are white.

The ventral side of preserved specimens is cream. The foot has several brown spots along the external margin that are also present on the hyponotum. However, there are no spots present on the sole of the foot. The oral tentacles are lightly speckled with brown.

Anatomy: The radular formula of a 25 mm long specimen is $50 \times (21.0.21)$ (SAM A36019) and a 23 mm long specimen is $38 \times (21.0.21)$ (CASIZ073954). The jaw elements are arranged regularly in three discrete pieces (Figure 8A). The teeth are strong, smooth, and slender. The innermost teeth are less angular and pointed than in the other species (Figure 8B). The midlateral teeth are hook-shaped and pointed (Figure 8C). The outermost teeth do not have the prolongation on the upper side or cusp sometimes present in other species of *Paradoris* (Figure 8D).

The ampulla is short, tubular, and convoluted in the middle section, and it branches into a short oviduct and the prostate. The oviduct enters the female gland mass distally. The thick and convoluted deferent duct leads to a short and granular prostate (Figure 9B). The deferent duct opens into a common atrium with the vagina. The penis is unarmed. There is a pair of highly ramified accessory glands and two muscular sacs containing two stylets each. The glands and the sacs are located on the dorsal side (Figure 9C). Each stylet is about 0.2 mm in length. The short vagina connects to a large and oval bursa copulatrix. From the bursa copulatrix leads another short duct that connects to the seminal receptacle and the short uterine duct. The bursa copulatrix is about five times larger than the seminal receptacle.

Etymology: From the Latin “*caeruleus*” in reference to the blue color of the species.

Remarks: Dayrat (2006) described specimens from the Cape Province of South Africa that he attributed to *Paradoris erythraeensis* (Vayssiére, 1912). These animals differ from the holotype of *P. erythraeensis* in several important aspects of their anatomy. The holotype of *P. erythraeensis* has a series of conical tubercles on the back. Gohar & Abu-Ela (1959) also noted these tubercles in another specimen they examined from the Red Sea. They also described the color of the living animal as “light gray with scattered roundish or irregularly shaped blackish brown patches. It is finely tuberculated, large tubercles occurring in the centre of the black patches and surrounded by more

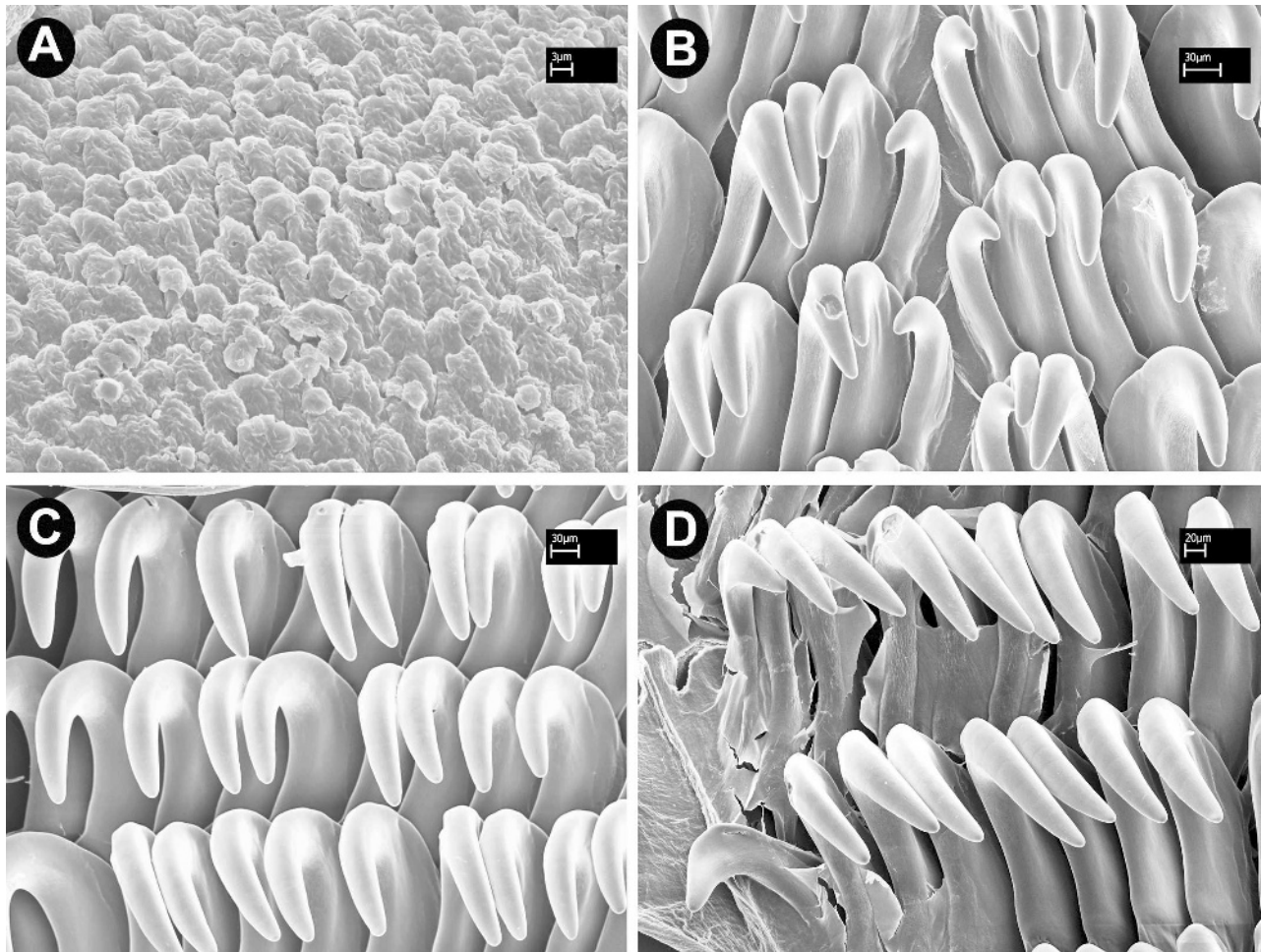


Figure 8. Scanning electron micrographs of *Paradoris caeruleus* sp. nov. (SAM A36019). A. Jaw elements. B. Innermost radular teeth. C. Mid-lateral radular teeth. D. Outermost radular teeth.

numerous smaller ones.” In contrast, the specimens from South Africa that Dayrat examined are white with black spots and have a granular notum without any tubercles. Dayrat noted that the radular teeth of specimens of *P. erythraeensis* have a hook-shaped spur on the base of the outermost teeth, and that the shape of the outer radular teeth of the specimens from South Africa could not be determined, because the slides containing the radulae had dried out. We remounted these two radulae, and the outermost teeth lack a basal spur on the outer tooth in both specimens. Dayrat noted that the holotype of *P. erythraeensis* has two simple accessory glands and a single elongate stylet sac, and that no glands or stylet sacs could be found in one of the South African specimens (A32370). He did not mention the second South African specimen (A35586). This specimen does have the vestibular glands and stylet sacs present with other portions of the reproductive system in the previously dissected animal.

There are two ramified accessory glands and two stylet sacs, although no stylets were visible with the sacs.

Based on his examination of specimens of *Paradoris* from the Indian and Pacific Oceans, he concluded that all of these specimens should be considered as *P. erythraeensis*, although he did state that these may actually represent a species complex. His criterion for uniting these specimens was the presence of an elongate duct of the receptaculum seminis, and he concluded that all other features, including the texture of the notum, body color, radular tooth shape, and number and shape of accessory glands and stylets, represented intraspecific variation. Another interpretation of this variation can be made. For example, the three specimens attributed to *P. erythraeensis* from Tanzania all have a smooth notum, a pinkish tan color with mottled darker areas, and two ramified accessory glands with one or two stylet sacs. In other words, combining species solely on the basis of having a long receptacu-

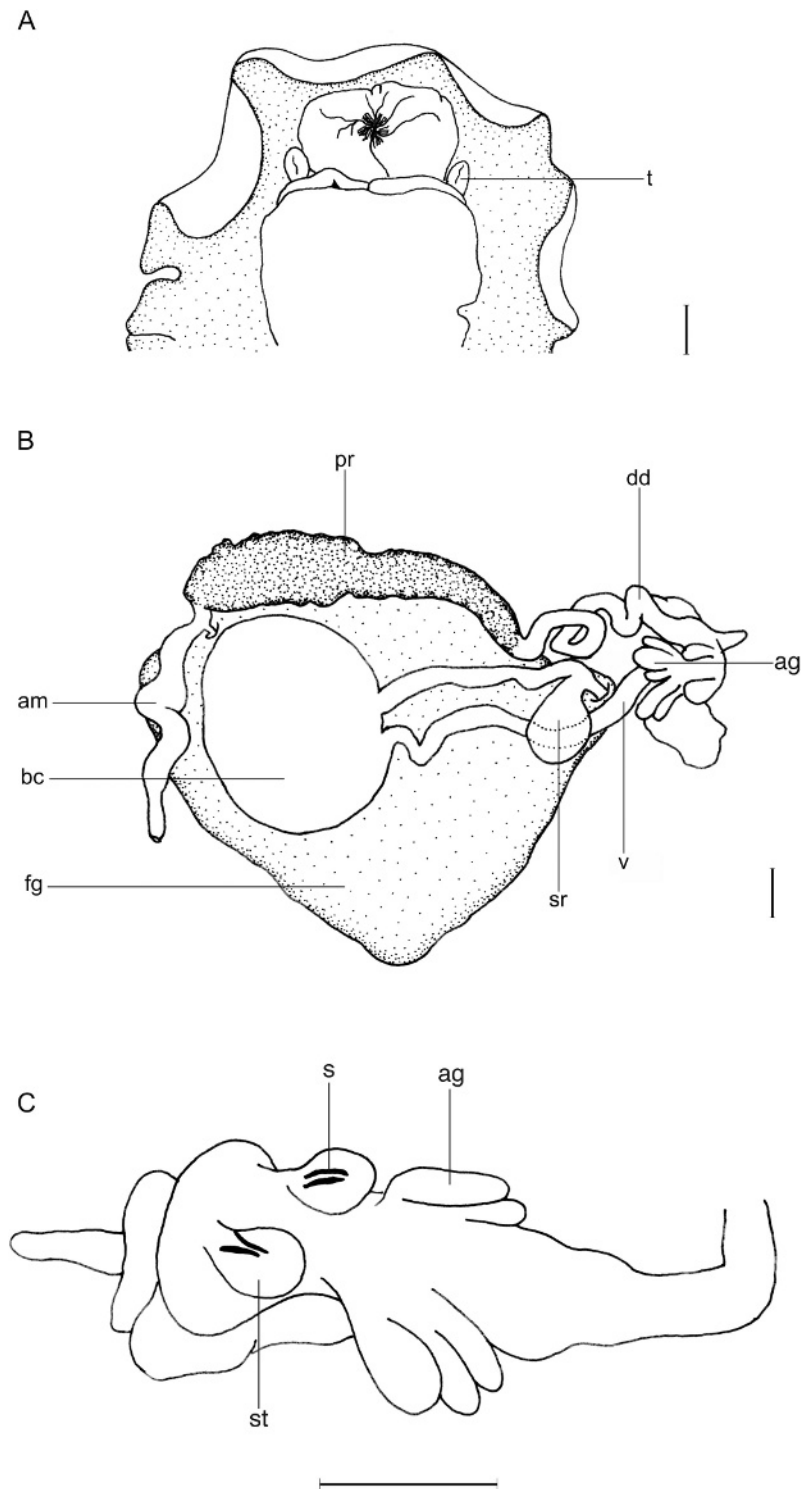


Figure 9A. Ventral view of the mouth area, scale bar = 1 mm. B. Reproductive system of *Paradoris caeruleus* sp. nov. (SAM A36019), scale bar = 1 mm. C. Detail of the reproductive system (CASIZ 117625), scale bar = 1 mm. Abbreviations: ag = accessory glands, am = ampulla, bc = bursa copulatrix, dd = deferent duct, fg = female gland, pr = prostate, s = stylets, sr = seminal receptacle, st = stylet sac, t = tentacle, v = vagina.

Table 1
Comparative morphology of the valid species of the genus *Paradoris*.

Species	Description source	Distribution	Dorsal color	Ventral color in preserved animals	Middle part of the notum	Rhinophoral sheaths	Branchial leaves	Prostate	Accessory Glands	Stylets	Radula
<i>Paradoris inaequalis</i> (Bergh, 1881)	Valdés, 2002 and Dayrat, 2006	Mediterranean and eastern Atlantic ocean	light gray to light cream or whitish with a pale brown tinge in the center. Several small brown spots on tips of tubercles and small opaque white dots	whitish with or without dark dots	covered with small, rounded tubercles. The largest ones occur in two lines	with tubercles	8 tripinnate leaves	tubular, divided into two portions	1 (Valdés, 2002); 2 (a maximum of 2 (Dayrat, 2006))	2 (0.4 mm) (Valdés, 2002); a maximum of 3 (Dayrat, 2006)	56 × (23/24) 24-0.23(24) 34 mm long specimen
<i>Paradoris abia</i> (Bergh, 1904)	Miller, 1995 and Dayrat, 2006	South-western Pacific Ocean (from New Zealand to South Australia) and south-eastern Indian Ocean (Western Australia)	white body with dark reddish brown spots and light gray spots on tips of tubercles	creamish with or without brown spots	with tubercles all over	smooth or with crenulate edge	up to 8 tripinnate leaves	tubular in U-shaped or convoluted	lacks accessory gland	absent	37 × (16.0.16) 15 mm long specimen
<i>Paradoris liturata</i> (Bergh, 1905)	Dayrat, 2006	Papua New Guinea and Indonesia	light greyish to whitish with a network of black longitudinal and/or transversal lines	—	with tubercles of various sizes surrounded by a network of black lines	smooth	up to 8 tripinnate leaves	flattened, divided into two portions	up to 4 accessory glands	2 (0.56-0.82 mm)	45 × (17.0.13) 16 mm long specimen
<i>Paradoris erythraensis</i> (Vayssiére, 1912)	Dayrat, 2006	Djibouti, Suez Canal, Red Sea, Tanzania, South Africa, Thailand, Indonesia and the Philippines	white or yellowish to pink-tan with brown spots	whitish sometimes with brown dots	smooth or with tubercles	smooth	6 tripinnate leaves	flattened, divided into two portions	2	2 (0.32-0.42 mm)	37 × (15.0.15) 14 mm long specimen
<i>Paradoris multicirrus</i> (Marcus, 1970)	present study	Brazil and Costa Rica	light brown to pale cream scattered with numerous small dark brown spots composed of an aggregate of brown points	white with dark spots arranged separately	the largest tubercles located in the middle	some specimens with 1-2 tubercles at each side	6 tripinnate leaves	very large, and folded into itself	2	3 (0.5 mm)	55 × (18.0.18) 18 mm long preserved specimen; 47 × (16.0.16) 40 mm long preserved specimen
<i>Paradoris isurigenis</i> (Baba, 1989 and Dayrat, 1986)	Baba, 1986; Baba, 1989 and Dayrat, 2006	Japan	faintly grayish yellow or grayish brown scattered with blackish brown flecks	covered with chocolate spots	with tubercles speckled with chocolate brown at the base	smooth	6 tri or quadripinnate leaves	very large, discrete and massive	2	2 (1 mm)	90 × (20-25.0.20-25) 50 mm long specimen
<i>Paradoris arancosa</i> (Valdés, 2001)	Valdés, 2001 and Dayrat, 2006	New Caledonia (deep-sea)	pale brown with dark brown spots and numerous small darker dots. Larger tubercles opaque white	—	covered with rounded tubercles except in those areas with a number of small depressions	—	6 tripinnate leaves	flattened and granular, divided into two portions	1 or 2	2 (0.3 mm)	68 × (16.0.16) 32 mm long preserved specimen
<i>Paradorislopezi</i> (Hermosillo & Valdés, 2004)	present study	Mexico and Galapagos Islands	gray with small dark brown-orange spots. Several big black spots composed of an aggregate of small black points	pale gray with brown spots larger than those in the foot	the largest tubercles located in the middle	smooth	6-7 tripinnate leaves	granular and convoluted	2	3 (0.9 mm)	42 × (22.0.22) 35 mm long preserved specimen; 55 × (26.0.26) 61 mm long preserved specimen
<i>Paradoris caeruleus</i> sp. nov.	present study	South Africa	gray blue with some black spots. Tubercles surrounded by an aggregate of minute white spots	cream	covered with low tubercles of different sizes. Wider tubercles surrounded by small ones	smooth	7 tripinnate leaves	short and granular	4	4 (2 stylets in each sac)	50 × (21.0.21) 25 mm long specimen; 38 × (21.0.21) 23 mm long preserved specimen

— No information available

lum duct may not be the most precise way to determine distinct taxa. Rather, looking for correlations of characters appears to have produced a better estimation of species boundaries and diagnostic characters. When these practices are employed, it appears that the South African specimens share several characters not found in other specimens attributed to *P. erythraeensis* by Dayrat. Namely, the two specimens from South Africa both have a smooth body, white body color with black spots, outer radular teeth without a basal spur, and are distinct from all other material examined. We consider these specimens to represent a distinct, undescribed species. This conclusion is further reinforced by the fact that the South African specimens are found in both warm and cold waters of the Cape Peninsula, a region with an extremely high level of endemism and relatively few Indo-Pacific species (Gosliner, 1987). The rest of the specimens considered *P. erythraeensis* by Dayrat are from strictly tropical regions of the Indo-Pacific.

Paradoris caeruleus differs from the rest of the species of the genus *Paradoris* by its gray blue dorsal color with black spots. Also, the radular teeth are much finer than those found in other species. In most species of the genus *Paradoris* (with the probable exceptions of *P. dubia* and the specimens from South Africa that Dayrat attributed to *P. erythraeensis*), the outer teeth are smaller and have a short triangular cusp, and the outermost tooth is sometimes reduced to a simple plate (see Dayrat (2006) for comparison). In *P. caeruleus*, there is a prolongation of the outer teeth that is not present in most of the species of the genus. It also differs in its reproductive anatomy in that it is the only species known to have two stylets in each of two stylet sacs.

Paradoris caeruleus will be compared in detail to the South African specimens that Dayrat included in *P. erythraeensis* and that we consider as representing a distinct, undescribed species (see above). *Paradoris caeruleus* has a notum that bears regular rounded tubercles evenly distributed over most of the surface of the notum, while the notum of *P. sp.* is granular in texture and devoid of tubercles. The body color of *P. caeruleus* is blue with two black spots on the notum, situated between the rhinophores and gill. Minute opaque white spots are found at the base, covering the tubercles and surrounding their base. In contrast, *P. sp.* is white with a few small scattered black spots and evenly scattered smaller opaque white spots. The number of radular teeth per half-row differs consistently, based on examination of the two specimens of each species. In *P. caeruleus*, there are 21 teeth per half-row, while in *P. sp.* there are 15 and 16 teeth per half row. Perhaps even more importantly, all of the teeth of *P. caeruleus* have rounded apices, while those of *P. sp.* are more acutely pointed. This is not an artifact of

wear, as all teeth in the radula, whether old or newly formed have these distinctive shapes. Both species have two ramified accessory glands, but there are more ramifications in the glands of *P. caeruleus* than in *P. sp.* Both species have a pair of stylet sacs, but each sac of *P. caeruleus* had two stylets, while no stylets were found in the sacs of *P. sp.* Finally, the receptaculum duct of *P. caeruleus* is relatively short, while that of *P. sp.* is elongate. While the sample size for both species is relatively small, with only two individuals each, the number and degree of difference warrants separating them as distinct species. The description of *P. sp.* will be published in a separate paper that reviews it together with several other species that were considered *P. erythraeensis* by Dayrat.

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