

Reviving a cold case: two northeastern Pacific dendrodorid nudibranchs reassessed (Gastropoda: Opisthobranchia)

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ABSTRACT

Ten nominal species of dendrodorid nudibranchs are known from the NE Pacific Ocean, including the Gulf of California. However, disagreement surrounds the taxonomic status of *Doriopsilla nigromaculata* (Cockerell in Cockerell and Eliot, 1905) and *Doriopsilla rowena* Marcus and Marcus, 1967, including the correct generic placement of the former. To resolve this disagreement, we examined type specimens, the original descriptions, and unpublished materials in the James Lance Collection at the California Academy of Sciences and conclude that *Doriopsilla nigromaculata* is: (1) a member of *Dendrodoris*; (2) not synonymous with the valid species *Doriopsilla rowena*; and (3) a senior synonym of *Dendrodoris behrensi* Millen and Bertsch, 2005. Like other members of the genus, *Dendrodoris nigromaculata* has a centered anus, smooth dorsum, delicate wavy mantle edge, and possesses both ptyaline and esophageal glands. It is translucent white with chocolate brown blotches, the larger of which are usually clustered into three or four groups centered mid-dorsally. In contrast, *Doriopsilla rowena* has an off-center anus, a papillate and densely spiculate dorsum with a stiff margin, and lacks both ptyaline and esophageal glands. Its scattered brown flecks and larger, round concentrations of opaque white distinguish it dorsally, and notal spicules include rods and forks. *Doriopsilla rowena* grows to 12 mm long and has been found in La Jolla, California, the Pacific coast of Baja California, and the northern Gulf of California south to Panama. *Dendrodoris nigromaculata* grows to 27 mm and is known from Monterey, California south to the San Benitos Islands, Baja California. Both species have large eggs and ametamorphic direct development, but small eggs indicating planktotrophic development have also been observed in *D. rowena* from Jalisco, Mexico, suggesting *D. rowena* may constitute a cryptic species complex or display poecilogony.

Additional Keywords: Dendrodorididae, Nudibranchia, nomenclature

INTRODUCTION

Ten nominal species of dendrodorid nudibranchs are currently recognized from the NE Pacific Ocean, includ-

ing the Gulf of California (Behrens and Hermosillo, 2005): *Dendrodoris azineae* Behrens and Valdés, 2004; *Dendrodoris behrensi* Millen and Bertsch, 2005; *Dendrodoris fumata* (Rüppell and Leuchart, 1831); *Dendrodoris stohleri* Millen and Bertsch, 2005; *Doriopsilla albopunctata* (Cooper, 1863); *Doriopsilla gemela* Gosliner, Schaefer and Millen, 1999; *Doriopsilla janaina* Marcus and Marcus, 1967; *Doriopsilla nigromaculata* (Cockerell in Cockerell and Eliot, 1905); *Doriopsilla rowena* Marcus and Marcus, 1967; and *Doriopsilla spaldingi* Valdés and Behrens, 1998. However, an important taxonomic disagreement remains in the modern literature. Camacho-García et al. (2005) considered *Doriopsilla rowena* a valid species, whereas Behrens and Hermosillo (2005) regarded it as a junior synonym of *Doriopsilla nigromaculata*. The suggested synonymy of *D. nigromaculata* and *D. rowena* was raised as a possibility by James Lance in Keen (1971: 830; cited as *Doriopsilla nigromaculata*) and again by McDonald (1983: 171; cited as *Dendrodoris nigromaculata*). However, if Camacho-García et al. (2005) were correct, and *Doriopsilla rowena* is valid, then *D. nigromaculata*, which was originally described based on a single specimen collected by Cockerell in La Jolla, California, has either remained unknown since its original description and should be regarded as a *nomen dubium*, or has since been described under another name.

A contributing factor to this disagreement is that historically the distinctions between *Dendrodoris* and *Doriopsilla* have been confusing, including for species from the northeast Pacific Ocean (reviewed by Steinberg 1961; Valdés and Ortea 1997; Gosliner et al. 1999). However, Valdés et al. (1996) and Valdés and Ortea (1997) provided clear anatomical and morphological criteria separating the two genera, and recent phylogenetic analyses support this separation (Valdés and Gosliner 1999, Valdés 2003). Here, we use these criteria and the examination of type specimens to first establish the correct generic placement of *D. rowena* and *D. nigromaculata*, ruling out the synonymy of these two species. Then we compare their original descriptions with those of other species of dendrodoridids known from the region to

show that (1) *Doriopsilla rowena* is valid, and (2) that one species described recently from the region is in fact a junior synonym of *Dendrodoris nigromaculata*. In both steps we also draw from extensive materials in the James R. Lance Collection at the California Academy of Sciences in San Francisco (hereafter, Lance Collection). These constitute new evidence not available prior to Lance's death in 2006 and shed light on what had effectively become a taxonomic cold case.

MATERIALS AND METHODS

To establish the generic placement of *Doriopsilla nigromaculata* and *Doriopsilla rowena*, we extracted from their original descriptions information on four morphological and two anatomical characters which taken together can be used to separate *Dendrodoris* from *Doriopsilla* (Table 1). We corroborated this information by examining the type specimens of both species, which were obtained, respectively, from The Natural History Museum, London (NHMUK) and the U.S. National Museum of Natural History (USMNH). We also examined Lance's specimens of *D. rowena* in the Invertebrate Zoology and Geology collection at the California Academy of Sciences (CASIZ) and used his description of *D. rowena* in Keen (1971), as well as his unpublished notes, 35mm photographic slides, and illustrations in the Lance Collection. Lance kept many of these materials organized by species in folders, which contain information on the morphology, color, anatomy, egg masses, and development of living specimens of most of the dendrodoridids known from the northeast Pacific Ocean. The folder for *D. rowena* in particular supplements Marcus and Marcus's original (1967) description of *D. rowena*, which was based on preserved material. Where appropriate, we refer to species folders in the Lance Collection by their names; field accounts by number, date, and locality; and 35mm slides by date and locality when possible. To compare *D. nigromaculata* with other species of *Dendrodoris* from the northeast Pacific Ocean, we used information from our examination of the type specimen, as well as from the Lance Collection, Behrens and Hermosillo (2005), Millen and Bertsch (2005), and Goddard (2005). Finally, we used the online searchable database of the California Academy of Sciences Invertebrate Zoology collection ([http://](http://research.calacademy.org/research/izg/iz_coll_db/index.asp)

research.calacademy.org/research/izg/iz_coll_db/index.asp) to obtain additional and otherwise unpublished locality information to further document the known geographic distribution of these species. Here, we used information for specimens identified by established authorities familiar with the nudibranch fauna of the region. These are referenced below by CASIZ and the corresponding catalog numbers.

RESULTS

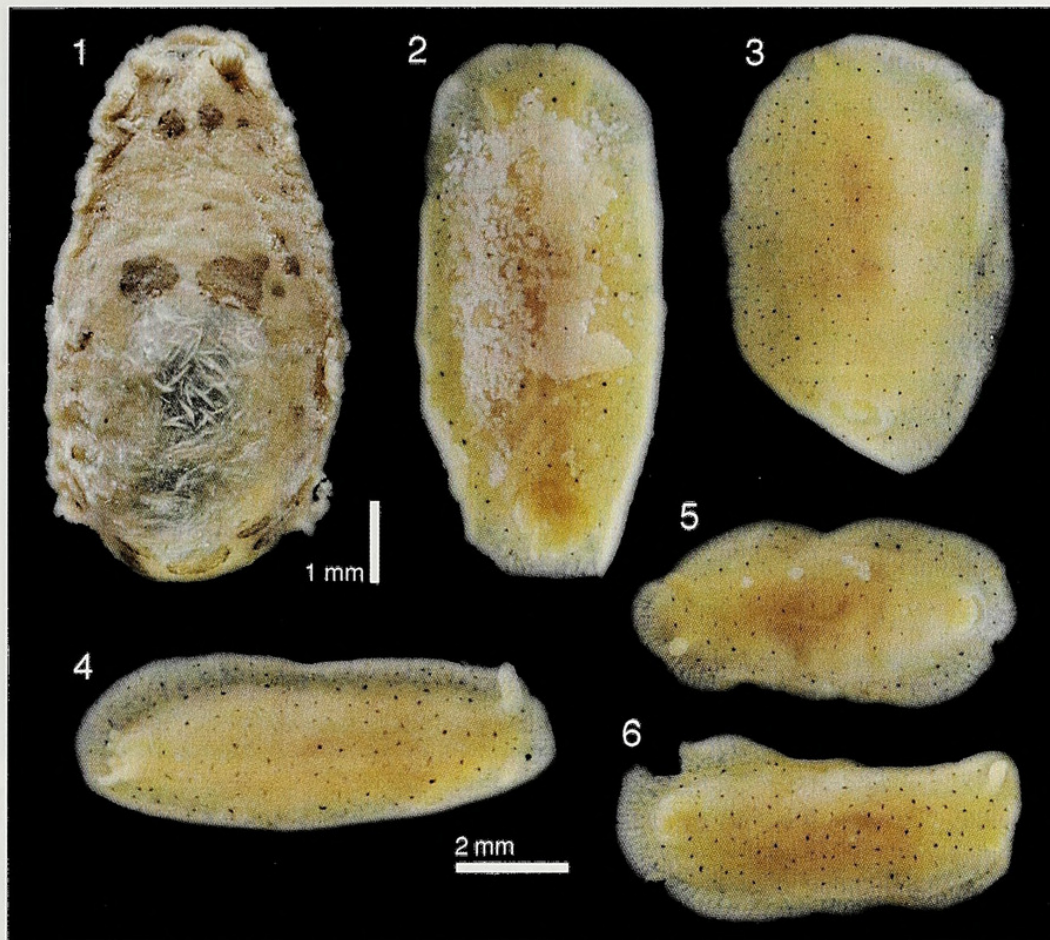
DESCRIPTION OF RELEVANT MATERIALS IN THE LANCE COLLECTION

1. Species Folder: *Doriopsilla rowena* contains: (1) A hand-written description, accompanied by pencil sketches, of this species with the manuscript name "*Doriopsilla puertecitensis*" (later, Lance wrote the name *D. rowena* in red ink on this description). The pencil sketches are based on living specimens (CASIZ 182606) collected 20 March 1965 from 4.4 mi south of Puertecito, Baja California, and include dorsal and ventral views of an adult, details of the notum and notal spicules, and penis. The description also includes a sketch and brief description of an egg mass laid by a 12 mm adult. (2) Six separate pen and ink illustrations, all labeled as *Doriopsilla rowena* and clearly based on the above pencil sketches. (3) A sheet labeled "*Doriopsilla rowena* – Field Account Data" for sites in the Gulf of California. The dates listed include years from 1954 to 1979, and out of 10 sites listed record *D. rowena* only from Puerto Peñasco. (4) One clear plastic sheet holding 35 mm slides from 1966 and 1969, the earliest labeled first as "*Dendrodoris* sp." and later as "*Doriopsilla rowena* or *D. nigromaculata*?"

2. Species Folder: *Doriopsilla nigromaculata* contains: (1) A list of specimens found at South Casa Reef and Windansea Reef, both in La Jolla, California. (2) A lined sheet with dorsal and ventral sketches of an adult from La Jolla. The notation "F.A. 181" on this sheet refers to Field Account 181, which was for 25 June 1967 at South Casa Reef, La Jolla. This sheet is first labelled as "Brown spotted *Doriopsilla*," with "? *D. nigromaculata*" later added in red ink. (3) A note stating "*D. nigromaculata* Published sketch in Opis. News. 14(8): 29 of hatching." (4) A three page typed description of this species with the

Table 1. Select diagnostic characters distinguishing *Dendrodoris* from *Doriopsilla*. Based on Valdés et al. (1996) and Valdés and Ortea (1997).

Character	<i>Dendrodoris</i>	<i>Doriopsilla</i>
Mantle	Smooth and soft, rarely with large tubercles	Hard and tuberculate
Mantle spicules	Absent or isolated	Strong network, including in tubercles
Mantle margin	Delicate, wavy	Stiff
Position of anus relative to midline of body	Centered	Off-center
Ptyaline glands	Present	Absent
Esophageal glands	Present	Absent



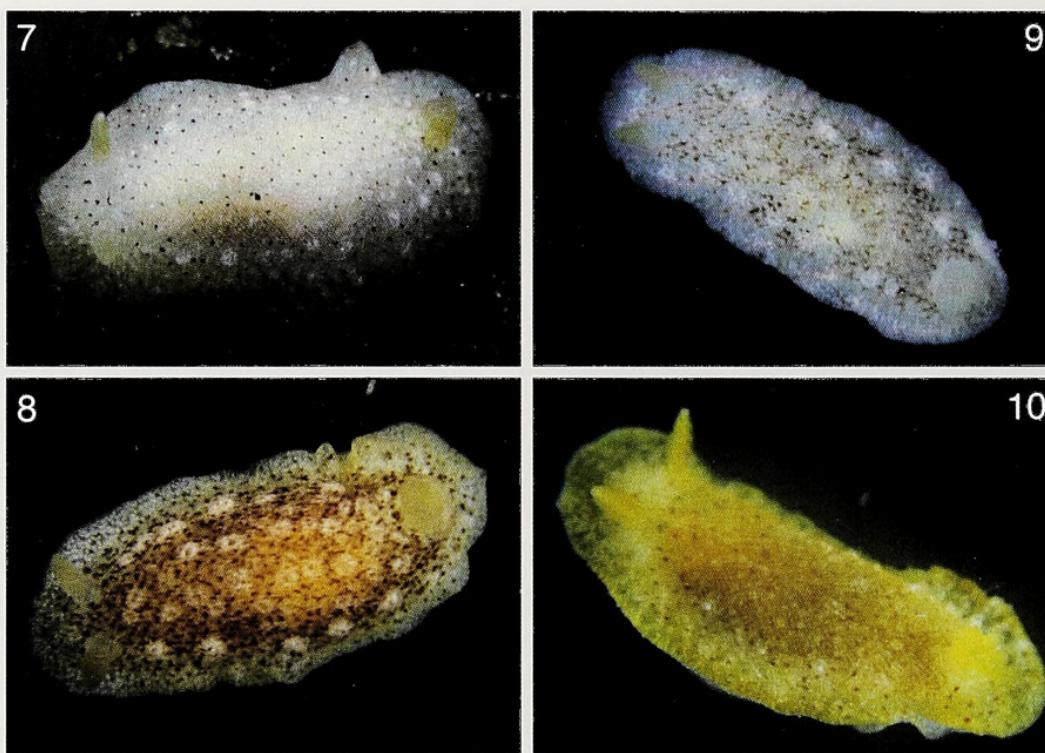
Figures 1–6. Type specimens. **1.** *Dendrodoris nigromaculata* (NHMUK 1904.7.7.1). Photo by Harry Taylor. **2–6.** *Doriopsilla rowena* (USMNH 678413). Photos by Chris Meyer.

heading “*Doriopsilla nigromaculata* (Cockerell and Eliot, 1905) Figs. 1–7.” The figures for this description and legend are on a separate sheet and are a composite of copies of the six pen and ink illustrations from the Species Folder for *Doriopsilla rowena*, plus a map of California with a single red ink dot showing “Distribution in California.” The description is based on the four specimens Lance found in La Jolla on 25 June 1967 but refers to the specimen from La Jolla described by Cockerell and Eliot 70 years earlier. (5) Two sheets with sketches and notes on egg masses laid by specimens collected at Windansea Reef in 1968, San Quintín in 2001, and South Casa Reef in 1998. (6) Two sheets containing 35 mm photographic slides, one with images of adult specimens, the other with images of egg masses and hatching juveniles.

3. Species Folder: White Porostome Spotted contains: (1) A sheet titled “Crenulate dorid” with sketches in pencil of two specimens and a brief description, including dimensions of 24×5 mm and 27×5 mm. This sheet is undated but the dimensions of the larger specimen, combined with information in (2) below indicate that these specimens were collected in either 1961 from the Coronados Islands or in 1963 from Point Loma,

San Diego. (2) A hand-written description of this species with the manuscript name “*Dendrodoris barbarensis*,” based on a single specimen collected from 8 m depth at Naples Reef, Santa Barbara County 30 Oct 1966, two specimens collected at 30 m depth 1.6 km south of South Coronado Island by Nan Limbaugh on 22 Apr 1961, and two specimens collected intertidally at Point Loma by Wesley Farmer on 29 Oct 1963. (3) A typed sheet with information on three specimens collected intertidally at Lunada Bay, Palos Verdes Peninsula, by William Jaeckle, 20 Apr 1983. A note indicates that one of these specimens laid an egg mass on 4 May 1983. (4) Pencil notes and sketches of an egg mass laid by an individual collected from South Casa Reef, La Jolla, 20 July 1974, and sketches of the subsequent direct development to hatching juveniles from that egg mass.

4. Field Account 181 (June 25, 1967, South Casa Reef, La Jolla) contains, in addition to the annotated list of opisthobranchs found on that date by Lance (and Barbara Good), contains notes, from three separate dates, on the development of embryos in an egg mass deposited by *Doriopsilla rowena* (cited as “doriopsillids,” with a later notation as “*Doriopsilla nigromaculata*?”) collected on that date.



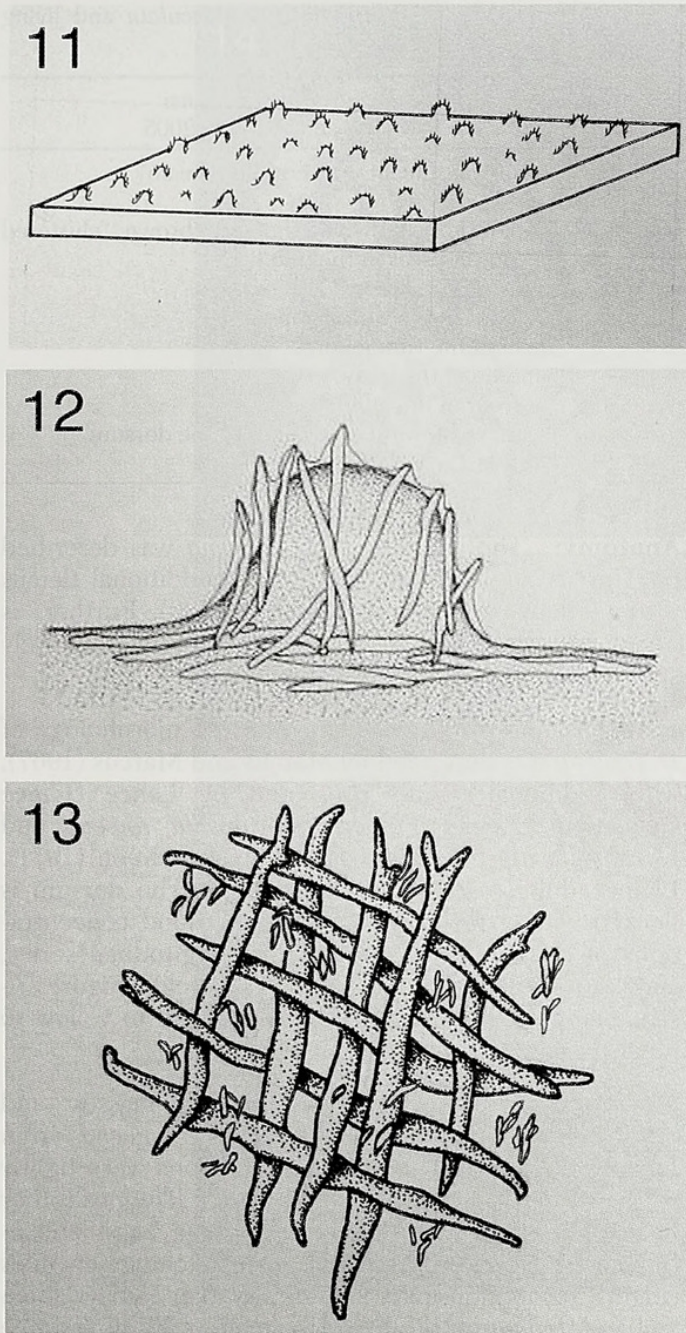
Figures 7–10. Living adult *Doriopsilla rowena*. **7.** Percebu, Gulf of California, Baja California, 7 April 1966 (35 mm slide in Lance Collection, Species Folder: *Doriopsilla rowena*). **8.** Total length 9.2 mm, San Quintin, Baja California, 16 November 2001 (35 mm slide in Lance Collection, Species Folder: *Doriopsilla nigromaculata*). **9.** South Casa Reef, La Jolla, California, 25 June 1967 (35 mm slide in Lance Collection, Folder: *Doriopsilla nigromaculata*). **10.** Total length (in $MgCl_2$) 6.7 mm, Lindo Mar, Bahía de Banderas, Jalisco, Mexico, 26 Feb. 2006 (CASIZ 174055; Goddard and Hermosillo, 2008, as *Doriopsilla nigromaculata*).

GENUS-LEVEL TAXONOMY

***Doriopsilla nigromaculata*.** In the original description of *D. nigromaculata* Cockerell and Eliot (1905) described the mantle of a single preserved specimen as “smooth, not tuberculate,” with a “rather narrow” margin. The latter is consistent with the delicate margin characteristic of living specimens of *Dendrodoris* (Table 1) and is visible in the type specimen (NHMUK 1904.7.7.1) as upturned, crenulate and soft in appearance (Figure 1). Cockerell and Eliot (1905) mentioned “a number of glistening white spicules, . . . imbedded in the skin” of the mantle and described them as “mostly fairly straight long rods, but some of the smaller ones are bent and have an irregular outline.” The spicules are not described as being regularly or densely arrayed and are visible in the type specimen where the mantle tissue had been carefully scraped away, presumably by Eliot in his original examination of the specimen (Figure 1). The position of the anus can be inferred as centered based on their description of the gill plume as “set in a semicircle open behind.” Internally, they described a “folliculate” mouth gland “with a fairly long duct,” which is clearly a ptyaline gland (e.g., illustrations in Valdés et al., 1996; Millen and Bertsch, 2005). No esophageal glands were mentioned, but these are minute (Valdés et al. 1996; Millen and Bertsch, 2005, Figure 2) and likely would not have garnered attention. All of these traits, as well as the extreme anterior and posterior position of the rhinophores and

gills, respectively, in the type specimen, are consistent with contemporary descriptions of species of *Dendrodoris* and clearly indicate the correct generic of *D. nigromaculata* is *Dendrodoris* (Table 1).

***Doriopsilla rowena*.** Marcus and Marcus (1967) described *D. rowena* based on seven preserved syntypes, five of which remain (USMNH 678413), and notes by the collector on the color of the living animals, which were collected in Puerto Peñasco, Sonora, Mexico, in the northern Gulf of California (Figures 2–6). They described the mantle as “smooth,” with evidence of large, but dissolved, diagonally crossed spicules in the “connective tissue of the back.” They noted that “the thick anal papilla and the renal pore in front of it lie to the left of the branchial tuft,” clearly indicating the eccentric position of the anus. The anterior part of the alimentary tract is illustrated in their figure 62B, and does not show either ptyaline or esophageal glands. Elsewhere, Marcus and Marcus (1967: 99) state that the absence of a ptyaline gland is one characteristic of *Doriopsilla*. Marcus and Marcus (1967) did not describe any dorsal tubercles in *D. rowena*. However, James Lance, who found and observed living specimens of this species from Puertecitos, Baja California, and Puerto Peñasco, both in the northern Gulf of California (Figures 11–12), illustrated minute, spiculate dorsal tubercles, which was confirmed with examination of Lance’s original specimens (CASIZ 182606). Lance also illustrated the pattern and



Figures 11–13. *Doriopsilla rowena*, details of notum; all from Lance Collection, Species Folder: *Doriopsilla rowena*. **11.** 1×1 mm detail of notal surface. **12.** Notal tubercle with spicule detail. **13.** Notal spicule pattern.

shapes of the notal spicules (Figure 13), which consist of diagonally crossed rods and forks (Lance Collection, Species Folder: *Doriopsilla rowena*). Taken together, these traits indicate that *D. rowena* is indeed a *Doriopsilla*, as originally described by Marcus and Marcus (1967) (Table 1). This was further confirmed with the examination of the syntypes (Figures 2–6), which are relatively flat and wide animals covered with small spiculate tubercles and an eccentric anus. All these traits are consistent with the diagnosis of *Doriopsilla* by Valdés and Gosliner (1999).

SPECIES-LEVEL TAXONOMY

***Doriopsilla rowena*.** Based on the above morphological and anatomical differences, *Doriopsilla rowena* cannot be a synonym of *Dendrodoris nigromaculata*. *Doriopsilla rowena* differs externally from all other congeners known from the region in its small adult size (up to 12 mm total length) and unique color pattern, consisting of small reddish-brown flecks scattered over the dorsum, as well as larger, round concentrations of opaque white, frequently arranged in longitudinal series, against a ground color of off white to pale yellow, pink or orange (Marcus and Marcus, 1967; Lance in Keen 1971; Behrens and Hermosillo, 2005, cited as *Doriopsilla nigromaculata*; Camacho-García et al., 2005) (Figures 2–10). *Doriopsilla rowena* is therefore a valid species.

***Dendrodoris nigromaculata*.** Cockerell and Eliot (1905) based their original description of *D. nigromaculata* on a single specimen, 10 mm long preserved, that was collected in July 1901 from La Jolla, California (Figure 1). The color of the preserved specimen was described as “yellowish-drab with a slight inclination to lilac in places,” with “a double border of black spots round the dorsal margin, and a few larger black blotches symmetrically disposed, one in front of the rhinophores, two behind them, two in the middle of the back, and five in front of the branchiae.” These larger blotches are still visible in the type specimen (Figure 1). Two nominal species of *Dendrodoris* from the northeast Pacific Ocean have dark spots against a pale background: *D. behrensi* Millen and Bertsch, 2005 (Figure 17) and *D. stohleri* Millen and Bertsch, 2005. In *D. stohleri* the black spots are relatively uniform in size and scattered over the entire dorsum, save its margin (Millen and Bertsch, 2005). However, comparison of the color patterns originally described for *D. nigromaculata* and *D. behrensi* reveals a virtually identical match (Table 2). Indeed, the only discrepancy between the descriptions of these two species is that Millen and Bertsch (2005: 195) state that *D. behrensi* lacks mantle spicules. However, in the companion paper to Millen and Bertsch (2005), Goddard (2005) illustrated and described “slightly curved, spindle-shaped spicules” arranged in a lattice in *D. behrensi* recently hatched (Figure 21) from egg masses laid by adults (Figure 17) included as paratypes of *D. behrensi* by Millen and Bertsch (2005). Lance was also familiar with this species and observed egg masses and hatching juveniles virtually identical to those described by Goddard (2005) (Lance Collection, Species Folder: White Porostome Spotted) (Figures 18–20). Moreover, Lance described the adult body of this species as “very slightly spiculose with notal margins non spiculose” (Lance Collection, Species Folder: White Porostome Spotted). The density of notal spicules therefore decreases as juveniles grow into adults, which could make the spicules easily overlooked in living adult specimens. A similar phenomenon was recently documented by Sánchez-Tocino et al. (2014) for some chromodid nudibranchs.

Table 2. Comparison of original descriptions of external color of a single preserved *Dendrodoris nigromaculata* and living *Dendrodoris behrensi* by Cockerell and Eliot (1905) and Millen and Bertsch (2005), respectively.

	<i>Dendrodoris nigromaculata</i> (Cockerell and Eliot, 1905)	<i>Dendrodoris behrensi</i> Millen and Bertsch, 2005
Background color	"yellowish-drab with a slight inclination to lilac in places"	"semi-translucent white or pale cream"
Larger spots	Black, "symmetrically disposed:"	Dark reddish brown or chocolate brown, "clustered in four areas in the mid line:"
Position		
Group 1	"in front of the rhinophores"	"in front of the rhinophores"
2	"behind [rhinophores]"	"behind the rhinophores"
3	"middle of back"	"middle of the body"
4	"in front of the branchiae"	"in front of the gills"
Smaller spots	"double border. . . round the dorsal margin"	"scattered towards the edges of the dorsum"
Other color elements	None	None

With no significant differences between their original descriptions, *Dendrodoris behrensi* is therefore a junior synonym of *Dendrodoris nigromaculata*.

SYSTEMATICS

Based on the taxonomic results described above, a new systematic arrangement and list of synonyms is proposed for *D. rowena* and *D. nigromaculata*.

Family Dendrodorididae O'Donoghue, 1924

Genus *Doriopsilla* Bergh, 1880

Doriopsilla rowena Marcus and Marcus, 1967

(Figures 2–16)

Doriopsilla rowena Marcus and Marcus, 1967: 205–207; Keen, 1971: 830; Poorman and Poorman, 1978: 373; Bertsch and Kerstitch, 1984: 267; Valdés and Ortea, 1997: 253; Gosliner et al., 1999: 209; Valdés and Gosliner, 1999: 338–340; Camacho-García et al., 2005: 80; Goddard and Hermosillo, 2008: 87; Angulo-Campillo, 2005: Table 2.

Dendrodoris (?) *nigromaculata* [non Cockerell in Cockerell and Eliot, 1905] – Behrens, 1980: 58.

Dendrodoris nigromaculata [non Cockerell in Cockerell and Eliot, 1905].—Steinberg 1961: 59; Sphon 1972: 61; McDonald and Nybakken, 1980: 52; Lance, 1982: 29; McDonald, 1983: 170–171; Behrens, 1991: 71; Angulo-Campillo, 2003: Table 2; Goddard, 2004: 1959, 1963; Goddard, 2005: 206.

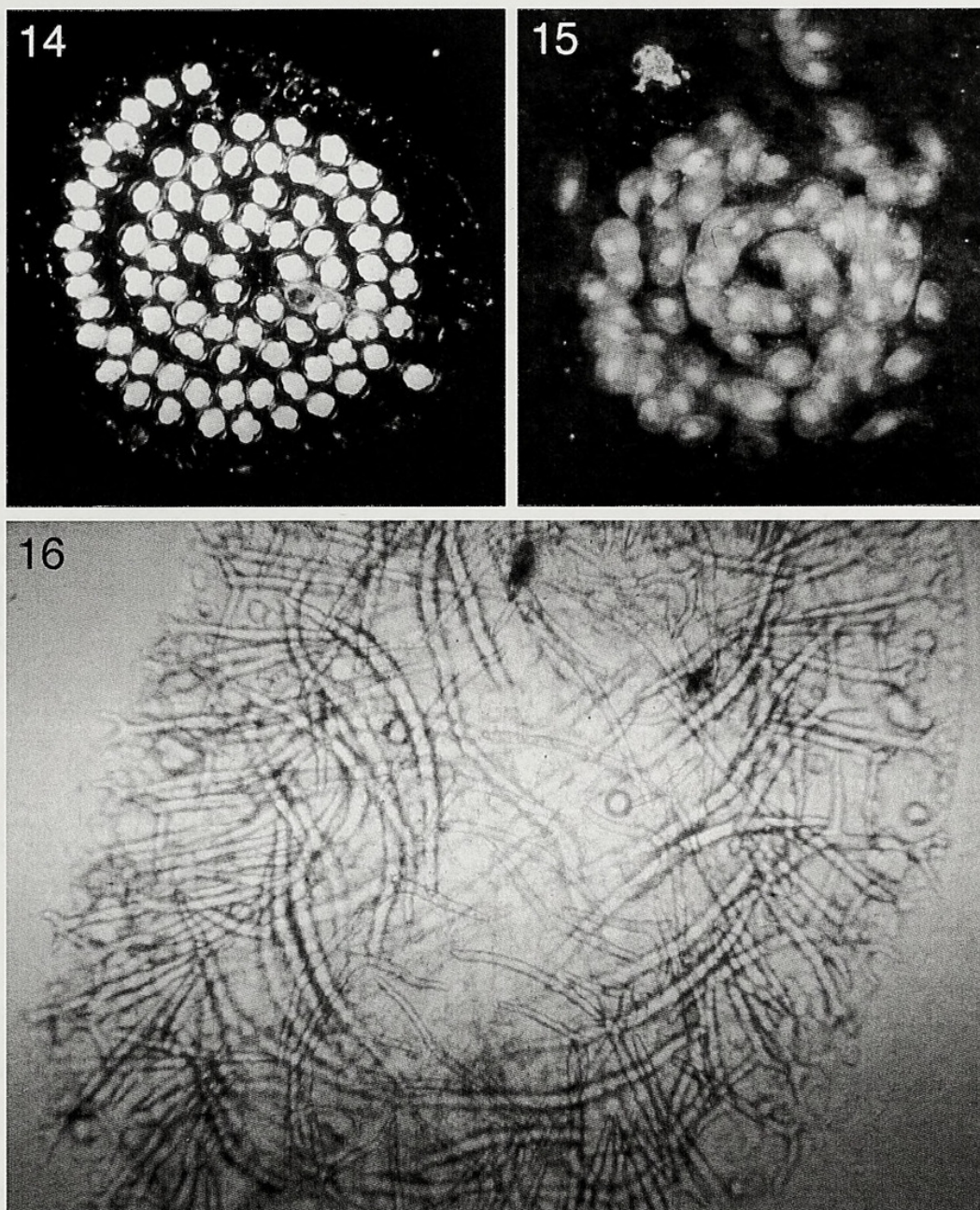
Doriopsilla nigromaculata [non Cockerell in Cockerell and Eliot, 1905].—Behrens and Hermosillo, 2005: 88; Lance Collection, Species Folder: *Doriopsilla nigromaculata*. California Academy of Sciences and Goddard, 2013: worksheets for Ladera St., False Point, Windansea, and So. Casa Reef (data from unpublished field accounts, no page numbers).

Type Material: *Doriopsilla rowena* – Syntypes: 5 specimens, Puerto Peñasco, Sonora, Mexico (USMNH 678413).

Anatomy: The anatomy of *D. rowena* was described by Marcus and Marcus (1967), with additional details presented by Valdés and Gosliner (1999). Further, as noted and illustrated by Lance, the notum is densely spiculate with rods and forks (Figures 12–13, 16).

External Morphology: The external morphology of *D. rowena* was described by Marcus and Marcus (1967), with additional details presented by Lance (Lance Collection, Species Folders: *Doriopsilla rowena* and *Doriopsilla nigromaculata*) and Lance in Keen (1971). Living adults reach 12 mm in length. The dorsum is flecked with dark brown, has larger, round concentrations of opaque white, typically in longitudinal series, and is covered by minute, spiculate tubercles (Figures 7–12). The ground color varies from whitish to yellow to pinkish orange.

Development: Lance obtained egg masses and observed development of *Doriopsilla rowena* from La Jolla (Figures 14–16). The egg ribbons were tightly coiled and laid flat, rather than on edge like most other dorid nudibranchs, and contained large eggs, encapsulated singly, that developed into hatching juveniles (Figure 15) in more than 26, but less than 38 days, at an ambient temperature of approximately 20° C (Lance Collection, Species Folder: *Doriopsilla nigromaculata*; Field Account 181, South Casa Reef, 25 June 1967). Recently hatched juveniles possess the same notal spicule complement of rods and forks as adults (Figures 13 and 16). Lance sketched another egg mass, laid by a specimen 9.5 mm long collected from Windansea Reef in June 1968. This egg mass was also laid flat and had 4 whorls in a closed spiral and a total diameter of 5 mm, as indicated by a scale bar. Based on that scale bar, the eggs illustrated by Lance measured approximately 215 µm in diameter. A note on Lance Field Account 181 indicates that the embryos did not develop a shell. Taken together, this information indicates that *D. rowena* from La Jolla have ametamorphic direct development (Bonar 1978; Goddard 2004). Lance's sketch and notes on an egg mass laid by a *D. rowena* from San Quintin, Baja California are also consistent with this mode of development.



Figures 14–16. *Doriopsilla rowena*, egg mass and hatching juveniles; all from 35 mm slides in Lance Collection, Species Folder: *Doriopsilla nigromaculata*. **14.** Egg mass from South Casa Reef, 26 Apr. 1998. **15.** Hatching juveniles, no date or locality (35 mm slide processed Sep. 1974). **16.** Spicule detail, hatched juvenile, South Casa Reef, no date (35 mm slide processed Sep. 1974).

(Lance Collection, Species Folder: *Doriopsilla nigromaculata*).

A specimen of *D. rowena* (Figure 10; CASIZ 174055), 6.7 mm long, collected from Nayarit, Mexico laid a flat egg ribbon of 6 turns in a closed spiral 6 mm across, virtually identical to the egg masses described above from La Jolla (JG, unpublished data). However, the eggs from Nayarit averaged 97.4 μm in diameter, indicating planktotrophic development (Goddard and Hermosillo, 2008). Lance described similar egg masses laid by specimens of *D. rowena* from the northern Gulf of California but mode of development cannot be inferred based on any of the information included (Lance Collection, Species Folder: *Doriopsilla rowena*).

Geographic Distribution: *Doriopsilla rowena* is known from the northern Gulf of California to Panama, (Marcus and Marcus 1967; Keen 1971; Poorman and Poorman 1978; Bertsch and Kerstitch 1984; Camacho-García et al. 2005; Goddard and Hermosillo 2008; Angulo-Campillo 2005; CASIZ 171209, 171229), the Galapagos Islands (CASIZ 78390, 78408), and La Jolla, California to El Campo, near Punta Eugenia, Baja California Sur (Lance Collection, Species Folder: *Doriopsilla nigromaculata*; CASIZ 71519; Behrens and Hermosillo 2005) (Figure 22).

Remarks: As evidenced in the Lance Collection (Species Folder: *Doriopsilla rowena*), Jim Lance started to

describe *D. rowena* under the manuscript name “*D. puertecitensis*,” based on three specimens he collected at Puertecitos, on the Baja California side of the northern Gulf of California. Sometime following the publication of Marcus and Marcus (1967), Lance added in red ink the name *D. rowena* on his original pencil sketches of these specimens. Later he executed a set of undated pen and ink illustrations, some of which are reproduced here in Figures 11–13 and labeled them all as *Doriopsilla rowena* (these illustrations were likely made for the monograph on Panamic opisthobranchs that Lance intended but never completed). In the drawing of the dorsal view of an adult (not reproduced here) Lance depicted six thin, widely spread, bipinnate gills and a centered anus. However, examination of his original specimens from Puertecitos (CASIZ 182606) reveal more tightly clustered gills and an eccentric anus, indicating that Lance’s drawing in these respects was purely schematic.

On 25 June 1967 at South Casa Reef in La Jolla, Lance found four specimens of a small (up to 9 mm long) “doriopsillid” that he first referred to in his notes and illustrations as the “Brown-spotted *Doriopsilla*” but later changed in red ink to “? *D. nigromaculata*” (Lance Collection, Field Account 181 and Species Folder: *Doriopsilla nigromaculata*). He eventually found this species at three more sites on the outer coast of San Diego County, as well as in Bahía San Quintín, Baja California, and in his field accounts for these sites consistently used the name *Doriopsilla nigromaculata* for this species (Lance Collection; California Academy of Sciences and Goddard 2013).

Lance’s Species Folder for *Doriopsilla nigromaculata* includes a typed description, titled *Doriopsilla nigromaculata* (Cockerell and Eliot, 1905), which was based on the four specimens from La Jolla, California in June 1967. This description is accompanied by and references a composite figure, also labeled as *Doriopsilla nigromaculata*, but which was comprised solely of his earlier illustrations (eventually labelled as *D. rowena*) of “*D. puertecitensis*” from the Gulf of California (some of which are reproduced here in Figures 11–13). In the text of this description Lance states “it is likely that the present species and an unnamed one, frequently encountered in the Gulf of California, will eventually prove to be conspecific.” This indicates that Lance wrote this description after June 1967, but prior to receiving a copy of Marcus and Marcus (1967), and also suggests that after receiving the latter, he considered *D. rowena* a junior synonym of *D. nigromaculata*. Further, as mentioned above, hatching juveniles from La Jolla possess the same notal spicule complement of rods and forks as adults from the Gulf of California (Figures 13 and 16). Although morphologically the specimens from La Jolla are very similar to *D. rowena* from the Gulf of California, Lance never applied the name *D. nigromaculata* to the latter, and in conversation with at least one colleague, maintained that the two were probably distinct (T.M. Gosliner, personal communication to JG, 12 Dec 2014).

Lance (1982) illustrated a hatching juvenile, labeled as “*Dendrodoris nigromaculata* (Cockerell in Cockerell and

Eliot, 1905)”, the name used by California workers during this time period for what we have shown here to be *Doriopsilla rowena*. Lance noted publication of this illustration on a separate sheet in his Species Folder “*Doriopsilla nigromaculata*”. However, comparison of this illustration with his sketches of direct development in his species folder “White Porostome Spotted” reveals it to be copied from a sketch for that species, which we demonstrate here to be *Dendrodoris nigromaculata*. Although their egg masses and spicule complement as hatching juveniles are different, both species have ametamorphic direct development (see below), and Lance (1982) was probably mainly making a statement about developmental mode in the one. The unexpected twist is that the binomial used in the figure caption turns out to be accurate for the species actually illustrated.

The specimens described and identified as *D. rowena* by Bertsch and Aguilar-Rosas (1984) from El Tomatal, on the Pacific coast of Baja California, are, based on their larger size (up to 30 mm long) and color pattern, actually *Diaulula aurila* Marcus and Marcus (1967), which is common in that region (Bertsch et al. 1999, cited as “*Sal y pimienta*” (Salt and pepper [doris]); Goddard and Schickel 2000, cited as *Discodoris* sp. 1 of Behrens 1991; personal observations).

Genus *Dendrodoris* Ehrenberg, 1831

Dendrodoris nigromaculata (Cockerell in Cockerell and Eliot, 1905)

(Figures 1, 17–21)

Doridopsis vidua (?) [non Bergh, 1878].—Cockerell and Eliot, 1905: 40–41.

Doris nigromaculata Cockerell in Cockerell and Eliot, 1905: 40–41.

Doridopsis nigromaculata (Cockerell in Cockerell and Eliot, 1905).—Cockerell, 1908: 106.

Dendrodoris vidua [non Bergh, 1878].—O’Donoghue, 1926: 212.

Dendrodoris nigromaculata (Cockerell in Cockerell and Eliot, 1905).—O’Donoghue, 1926: 213; Steinberg, 1961: 59. Lance, 1982: 29.

Dendrodoris sp. Lee and Brophy, 1969: 20.

Dendrodoris sp. Behrens, 1980: 100; Behrens and Gatewood, 1986: 139, 142.

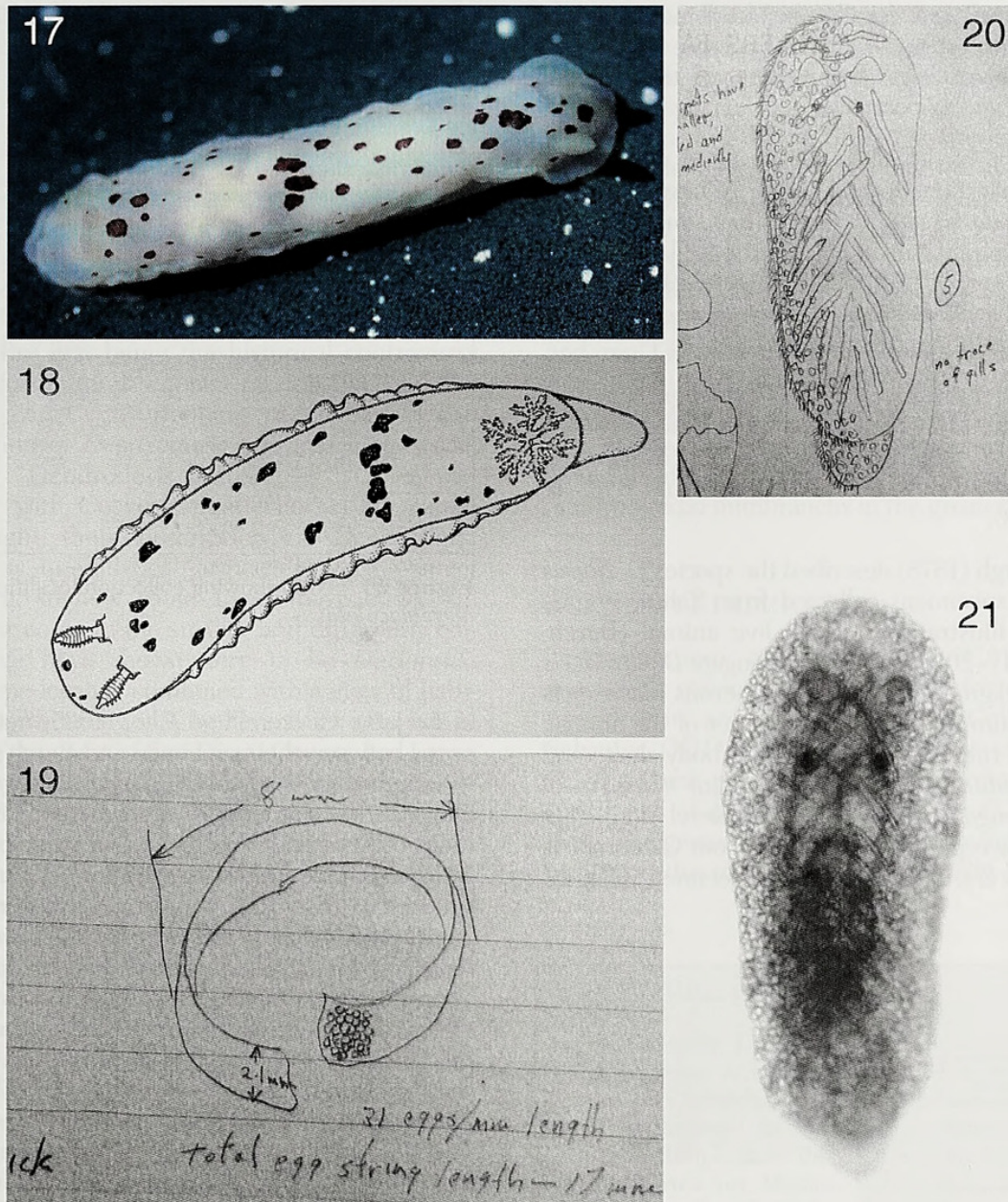
Dendrodoris sp. b McDonald and Nybakken, 1980: 54; McDonald, 1983: 171.

Dendrodoris sp. 3 Behrens, 1991: 72; Goddard, 2004: 1957, 1959, 1963.

Dendrodoris behrensi Millen and Bertsch, 2005: 189–199; Goddard, 2005: 201–211; Behrens and Hermosillo, 2005: 86; California Academy of Sciences and Goddard, 2013: worksheets for Hill St. and So. Casa Reef.

Type Material:

Doris nigromaculata – Holotype: La Jolla, California, July 1901 (NHMUK 1904.7.7.1), dissected by Sir C. Eliot in 1905.



Figures 17–21. *Dendrodoris nigromaculata*. **17.** Living adult, 22 mm long, from Bahía Falsa, Baja California, May 2001. Included as a paratype of *Dendrodoris behrensi* by Millen and Bertsch (2005). **18.** Adult, no date or locality (Lance Collection, Species Folder: White Porostome Spotted). **19.** Egg mass, sketch labelled as South Casa Reef, La Jolla, 20 July 1974, but Lance Field Accounts indicate adults were from Hill Street, San Diego, 19 July 1974 (Lance Collection, Species Folder: White Porostome Spotted). **20.** Recently hatched juvenile, Aug. 1974 (pencil sketch in Lance Collection, Species Folder: White Porostome Spotted). **21.** Juvenile, 570 μ m long, four days after hatching, June 2001. From egg mass laid by adult from Bahía Falsa, Baja California, May 2001 (Goddard 2005, as *Dendrodoris behrensi*).

Dendrodoris behrensi – Holotype: California, 14 Feb 1988 (CASIZ 69303). Paratypes: California, 14 Feb 1988 (CASIZ 171658); San Quintín, Mexico, 27 May 2001 (CASIZ 171659), San Quintín, Mexico, 27 May 2001 (CASIZ 171660).

Anatomy: The anatomy of *Dendrodoris nigromaculata* was described by Cockerell and Eliot (1905) and Millen and Bertsch (2005). As noted by Cockerell and Eliot (1905), Lance (Lance Collection, Species Folder: White Porostome Spotted), and Goddard (2005), notal spicules

are sparse and consist of straight to slightly curved rods only, some of which are irregular in outline (Figures 1, 20–21).

External Morphology: The external morphology of *D. nigromaculata* was described by Cockerell and Eliot (1905) and Millen and Bertsch (2005), with additional details presented by Lance (Lance Collection, Species Folder: White Porostome Spotted). Adults grow to 27 mm long and are distinguished externally by their translucent white ground color and chocolate brown blotches,

the larger of which are usually clustered into three or four groups centered mid-dorsally, and the smaller of which are scattered toward the edges of the dorsum (Figures 17–18).

Development: As described by Goddard (2005) and Lance (Lance Collection, Species Folder: White Porostome Spotted) *Dendrodoris nigromaculata* has ametamorphic direct development in short, stout egg ribbons laid on edge in a loose coil of only a turn or two (Figure 19). Juveniles (Figures 20–21) hatch after an embryonic period of 38 days at 16–19° C and are about 510 microns long.

Geographic Distribution: *Dendrodoris nigromaculata* is known from the Monterey Peninsula, California south to the San Benitos Islands, Baja California (McDonald, 1983; Behrens and Gatewood, 1986; Millen and Bertsch, 2005) (Figure 23).

Remarks: Bergh (1878) described the species *Doriopsis vidua* based on specimens collected from Tahiti, French Polynesia. The illustrations of the live animal (Bergh, 1878: pl. 1, figs. 17–20) represent an elongate *Dendrodoris* with a white background color and numerous black spots all over the dorsum, larger near the center of the animal, and small dorsal tubercles. Based on the body shape and coloration, *D. vidua* is most likely a senior synonym of *Dendrodoris elongata* Baba, 1936. Cockerel and Eliot (1905) tentatively reported this species from California as *Doridopsis vidua* (?), based on a single specimen collected

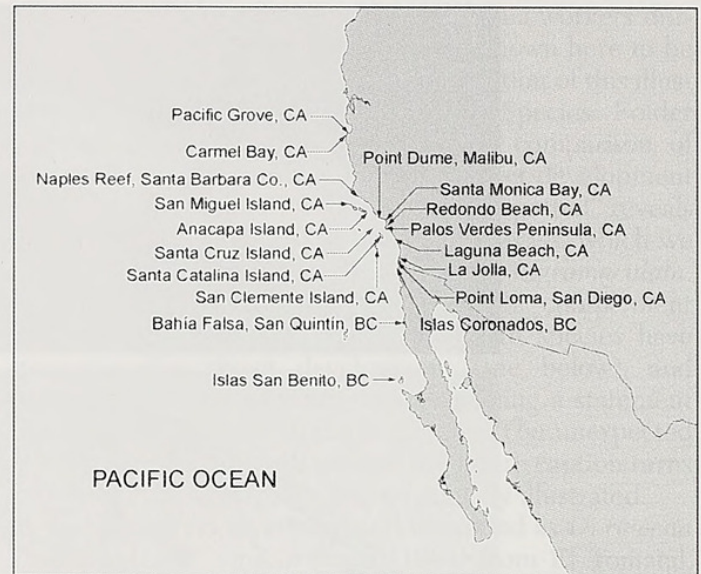


Figure 23. Map showing collection localities of *Dendrodoris nigromaculata*.

in La Jolla. Cockerel and Eliot (1905) noted some differences between their specimen and Bergh's (1878) original description in several details, including the coloration and mantle margin width. Cockerel and Eliot (1905) also indicated that their record was "suspicious" considering the geographic distance between the type locality and California, thus they introduced Cockerell's new name *Doridopsis nigromaculata* in case the specimen was ultimately proven to belong to a distinct species. As mentioned above, examination of the specimen studied by Cockerel and Eliot (1905) and therefore the holotype of *D. nigromaculata* (NHMUK 1904.7.7.1) revealed that it is a species of *Dendrodoris*. The holotype of *D. nigromaculata* has three pairs of large dark spots and several smaller spots irregularly distributed (Figure 1), very different from the original description of *Doriopsis vidua* by Bergh (1878) and references to *D. nigromaculata* by other authors, but nearly identical to the original description of *D. behrensi* by Millen and Bertsch (2005).

Lance was aware of this species as early as 1961 (or possibly even 1953) and referred to it in his notes and illustrations first as the "crenulate dorid," then as the "white dendrodorid" or "brown-spotted *Dendrodoris*" (Lance Collection, Species Folder: White Porostome Spotted), and in his field accounts as "*Dendrodoris* sp. true *dendrodoris*" (19 July 1974, Hill St) and "*Dendrodoris* sp. 3 [following Behrens 1991] white porostome" (26 Apr. 1998, So Casa Reef). As evidenced by an undated, handwritten description and pen and ink illustration of an adult (Figure 18), Lance started to formally describe it under the manuscript name "*Dendrodoris barbarensis*," based on five specimens collected in the 1950's and 60's from Naples Reef, Santa Barbara County; Point Loma, San Diego; and the Coronado Islands. Lance's folder for this species contains no evidence that he ever associated Cockerell and Eliot's (1905) description of *D. nigromaculata* with it.

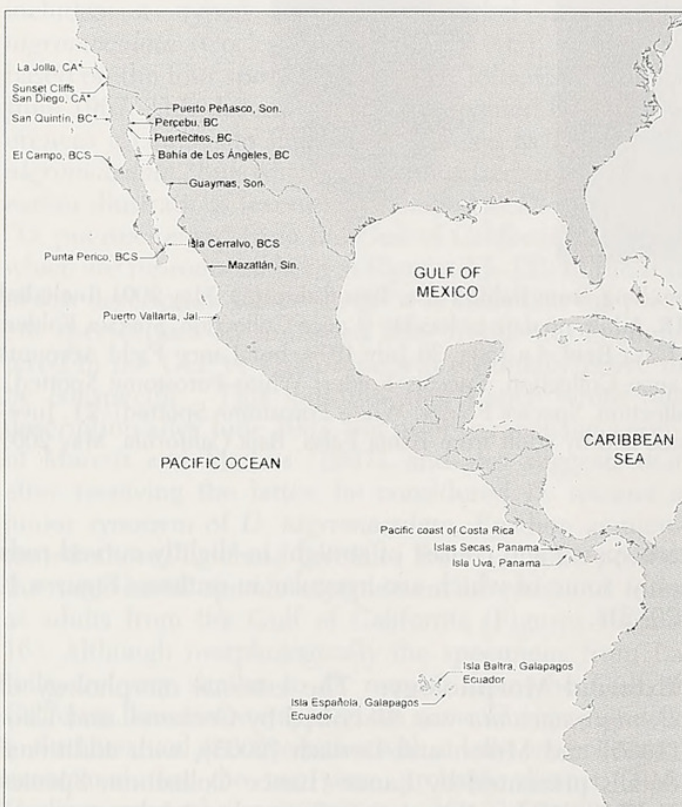


Figure 22. Map showing collection localities of *Doriopsilla rowena*.

F.M. MacFarland collected *D. nigromaculata* on the Monterey Peninsula in the 1920s (see Millen and Bertsch 2005, Material Examined). However, MacFarland (1966) does not mention those specimens nor refer to Cockerell and Eliot's 1905 description of *D. nigromaculata*.

DISCUSSION

The taxonomic confusion surrounding *Dendrodoris nigromaculata* and *Doriopsilla rowena* likely has two main sources, the first being the historical controversy over the validity of Bergh's genus *Doriopsilla*, and the second being Lance's overlooking of Cockerell and Eliot's description of *Dendrodoris nigromaculata* as he was describing "*Dendrodoris barbarensis*." Lance was clearly familiar with Cockerell and Eliot's 1905 paper, and in hindsight their description of *Dendrodoris nigromaculata* is unequivocal, especially with respect to color pattern, so how could Lance have ended up misapplying that name to the smaller and differently colored species we have shown here to be *Doriopsilla rowena*? The type locality, combined with a view of habitat fidelity for nudibranchs, may be keys. After a decade of collecting along the coast of San Diego County Jim Lance considered himself intimately acquainted with the intertidal nudibranchs there (see Steinberg 1961: 59), and must have wondered why he had never found Cockerell's *D. nigromaculata* from 60 years earlier. Thus, in 1967 when Lance did find in La Jolla a dendrodoridid with brown spots that was new to him, he was primed to recognize it as Cockerell's missing *Dendrodoris nigromaculata*, overlooking that that name better applied to his "*Dendrodoris barbarensis*" which he had already seen from other locations in southern California. In any case, once Lance misapplied the name, new workers in the field followed his lead and considerable authority, especially with regards to the fauna of southern California (see Steinberg, 1961; Lance, 1961, 1966). The inertia gained by this use of *nigromaculata* subsumed *rowena* for decades among California workers, helped muddle the generic distinctions between *Dendrodoris* and *Doriopsilla*, and steered Millen and Bertsch (2005) away from considering Cockerell's *nigromaculata* when they described it as *Dendrodoris behrensi*. Cockerell's type specimen of *Dendrodoris nigromaculata* had effectively become a cold case, sitting on a shelf half a world away in the Natural History Museum in London, its type status unknown to the museum curatorial staff.

Doriopsilla rowena from the Pacific coast of California and Baja California lay large eggs and have ameta-morphic direct development. However, based on the limited information presented by Goddard and Hermosillo (2008), members of the Panamic population appears to have planktotrophic development, which is consistent with a geographic range stretching from the northern Gulf of California to Panama and the Galapagos Islands. However, if planktotrophy is confirmed, including at the type locality of *D. rowena* in Puerto Peñasco, then

the directly developing population from California and the Pacific coast of Baja California likely represents an undescribed cryptic species. An alternative explanation is that this species displays poecilogony. Aside from its rarity, there are no confirmed examples of poecilogony that include such disparate modes of development, thus we consider the first hypothesis as the most likely. *Doriopsilla gemela* Gosliner, Schaefer, and Millen, 1999 exhibits a similar but geographically reversed variability, with planktotrophic development in California and direct development in the Gulf of California (Goddard, 2005; and see Lance Collection, Species Folder: Gulf Yellow Porostome), and has recently been found to comprise two species (Hoover et al., in preparation). Genetic confirmation of the two forms of *D. rowena* as separate species would bring the total number of nominal species of dendrodoridid nudibranchs in the greater region to eleven.

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