

Review of *Acanthodoris* Gray, 1850 with a Phylogenetic Analysis of Onchidorididae Alder and Hancock, 1845 (Mollusca, Nudibranchia)

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The phylogenetic relationships of *Acanthodoris* Gray, 1850 within the Onchidorididae are examined based upon morphological characters. The present phylogenetic analysis supports the monophyly of *Acanthodoris*. Most of the described species of *Acanthodoris* and a newly described species from South Africa are examined. Species included in the present analysis are: *Acanthodoris brunnea*, *A. falklandica*, *A. hudsoni*, *A. lutea*, *A. nanaimoensis*, *A. nanega*, *A. pilosa*, *A. pina*, *A. rhodoceras* and *A. serpentinotus*. The new species has some external similarities to *Acanthodoris pilosa* (Abildgaard in Müller, 1789) from the East Coast of North America and to *Acanthodoris lutea* MacFarland, 1925 from the West Coast of North America. Differences in the reproductive and radular morphology distinguish this new species. Those differences include a shorter deferent duct, vaginal duct and receptaculum seminis duct in the new species than found in *A. lutea* or *A. piosa*. Radula differences include multifid jaw rods and 6 or 7 elongate, pointed outer lateral teeth in the new species. This is in contrast to the triangular hook-like jaw structures and 5 or 6 flattened, triangular outer lateral plates in *A. lutea*. *Acanthodoris pilosa* has no jaw rods and 3 flat outer lateral plates. Phylogenetic analysis place the new species in a basal position to the remaining *Acanthodoris* species and closely related to *Acanthodoris falklandica* Eliot, 1907 from South America and *Acanthodoris nanega* Burn, 1969 from New Zealand. The species from the west coast of North America form a derived clade, separate from the Southern Hemisphere species.

The phylogenetic relationships among the Onchidorididae are presented. Morphological characters of several species from the currently recognized family group are examined. Taxa included in the analysis are: *Adalaria jannae* Millen, 1987, *Adalaria loveni* (Alder and Hancock, 1862), *Adalaria proxima* (Alder and Hancock, 1854), *Calycidoris guentheri* Abraham, 1876, *Diaphorodoris luteocincta* Iredale and O'Donoghue, 1923, *Diaphorodoris lirulatocauda* Millen, 1985, *Diaphorodoris mitsuii* (Baba, 1938), *Diaphorodoris papillata* Portmann and Sandmeier, 1960, *Onchidoris bilamellata* (Linnaeus, 1767) *Onchidoris muricata* (Müller, 1776) and the *Acanthodoris* species listed above. Characters for the phylogenetic analysis are taken from the literature and from dissection of specimens when available. Characters were polarized using *Bathydoris clavigera* Thiele, 1912, *Akiodoris salacia* Miller, 2005 and *Cadlina luteomarginata* MacFarland, 1966.

The phylogeny supports the monophyly of *Adalaria* and *Onchidoris* both situated in a basal clade to *Acanthodoris*. In addition, *Calycidoris* is basally situated to the clade containing the monophyletic *Diaphorodoris*, sister taxa to the clade of *Goniodoris* plus *Okenia*.

The Onchidorididae have traditionally been placed within the Phanerobranchia (Anadoridoidea, Families: Corambidae, Goniodorididae, Polyceridae, Gymnodorididae, Aegiridae and Onchidorididae) (Rudman and Willan 1998). Although it was previously thought that the Phanerobranchia formed a monophyletic clade, recent studies have concluded that it is a paraphyletic group (Wägele and Willan 2000; Valdés 2002; Vallès 2002; Fahey and Gosliner 2004).

Until recently, the following genera had been placed within the Onchidorididae: *Onchidoris*, *Adalaria*, *Arctadalaria*, *Acanthodoris*, *Doridunculus*, *Prodoridunculus*, *Actodoris*, *Calycidoris*, *Akiodoris* (as *Aciodoris*) and *Diaphorodoris* (Millen 1987, Rudman 1998).

However, the most recent phylogeny that includes the Onchidorididae (Millen and Martynov 2005) shows that the traditional Onchidorididae is a paraphyletic group that includes *Goniodoris* and no other members of the traditional Goniodorididae (e.g., *Goniodoris*, *Okenia* and *Trapania*). Millen and Martynov's analysis places the remaining Goniodorididae in a separate clade that they name the Akiodorididae. Their analysis also shows that there are four radular characters supporting a clade of phanerobranch dorids that includes *Acanthodoris*, along with three other Onchidorididae genera.

Previous work that included a detailed examination of *Acanthodoris* (Williams and Gosliner 1979), the group examined for the present study, included a review of all *Acanthodoris* described to date.

The present study reviews the literature of all described *Acanthodoris* species and corroborates the descriptions and illustrations by dissection of additional specimens when available. Species of other Onchidorididae are examined and compared with the literature to provide morphological characters for the phylogenetic analysis.

MATERIAL AND METHODS

Eleven species of *Acanthodoris* were included in the analysis. Type material and additional non-type material was obtained from the following sources: The California Academy of Sciences (CAS), the Natural History Museum of Los Angeles County (LACM), the National Museum of Natural History, Smithsonian Institution (USNM), the South African Museum (A) and the Museo Nacional de Ciencias Naturales, Madrid (MNCM). Specimens were drawn under a dissecting microscope using a camera lucida then dissected by dorsal incision. The internal anatomy was drawn as described and then examined either by dissecting and compound or scanning electron microscopes (SEM). External features were examined directly when specimens were available, by photographs, or by literature review. Special attention was given to the reproductive anatomy, as some of these features were infrequently (or cursorily) described in the literature. Table 1 shows the list of character states derived from dissections and from the literature reviewed for the present study. Specimens from each group of Onchidorididae are included: *Adalaria*, *Calycidoris*, *Diaphorodoris* and *Onchidoris*. Members of the family group Goniodorididae are included for comparison (*Goniodoris*, *Okenia*).

SPECIES DESCRIPTIONS

Family Onchidorididae Gray, 1827

[= Acanthodoridinae P. Fischer, 1881 = Pseudodorididae Eliot, 1910 (n.a.) = Ancyldorididae Thiele, 1926 = Lamellidorididae Pruvot-Fol, 1933 = Villiersiidae Abbott, 1974 (n.a.) = Calycidorididae Roginskaya, 1972]

DIAGNOSIS.— Williams and Gosliner (1979): a moderately depressed body with a simple mantle edging the foot, elongate rhinophores and soft elongate dorsal papillae. The branchial leaves

retract into separate cavities that are interconnected, labial cuticle with rodlets, rachidian absent, two main lateral teeth with a varying number of denticles and a varying number of outer laterals.

Genus *Acanthodoris* Gray, 1850

TYPE SPECIES: *Acanthodoris pilosa* (Abildgaard in Müller, 1789) by monotypy.

[= *Lamellidoris* Alder and Hancock, 1855.]

DIAGNOSIS.— Bergh (1880) and O'Donoghue (1921) provided concise diagnoses of this genus and these are summarized as follows: Body soft depressed; notum thickly covered with short villi; margin of the rhinophore aperture lobed; few branchial plumes, tripinnate, arranged in a circle; head wide, veliform; tentacles short, lobiform. Armature of the labial disc of minute hooks below with projecting thickenings of the cuticle. Narrow radula, naked rachis, first pleural tooth very large, hooked, few external pleural teeth. Armed penis, long vagina.

Diagnosis based on characters examined for the present phylogenetic analysis: Narrow radula with no rachidian tooth; first lateral tooth large and hooked; labial disk with thickened cuticle; jaw rodlets blunt or pointed, single or multiple apices; triaulic reproductive system.

Acanthodoris pilosa (Abildgaard in Müller, 1789)

Figs. 1A–B, 2–3.

Doris pilosa Abildgaard in Müller, 1789:7.

Doris stellata Gmelin, 1791:3107.

Doris nigricans Fleming, 1820:618.

Doris flemingi Forbes, 1838:3.

Doris sublaevis Thompson, 1840:87.

Doris similis Alder and Hancock, 1842:32.

Doris subquadrata Alder and Hancock, 1845:313.

Doris sparsa Alder and Hancock, 1846:293.

Doris fusca Lovén, 1846:4.

Doris rocinella Leach, 1847:268.

Doris quadrangulata Jeffreys, 1869:93.

Doris bifida Verrill, 1870:406.

Doris pilosa stellata Sauvage, 1873:30.

Acanthodoris citrina Verrill, 1879:313.

Acanthodoris ornata Verrill, 1879:313.

Acanthodoris stellata Verrill, 1879:313.

Acanthodoris pilosa var. *albescens* Bergh, 1880:246.

Acanthodoris pilosa var. *purpurea* Bergh, 1880:247.

Acanthodoris pilosa var. *pallida* Bergh, 1905:97.

Acanthodoris pilosa var. *novzealandiae* Bergh, 1905:94.

MATERIAL EXAMINED.— NEOTYPE: CASIZ 118891 Dale County, Wales. Intertidal. 1 specimen, 21 mm dissected. August 1992, D. Geiger. HOLOTYPE of *Acanthodoris ornata* USNM 842118 Eastport Maine, USA. Intertidal. 10 mm. August 1872, Verrill. OTHER MATERIAL: *Acanthodoris pilosa* CASIZ 074711 Washington County, Maine, USA. No depth data. 2 specimens, 12, 15 mm. July 1977. T. Gosliner. MNCN 15.05/21439 (*Onchidoris sparsa*) Artedo, Oviedo, Spain. No depth data. 1 specimen, 10 mm. April 1993, G. Rodríguez. LACM 153980 Cutter Rock, Ketchikan, Alaska. No depth data. 1 specimen, 7 mm dissected, June 1987, S. Millen.

DISTRIBUTION.— North Atlantic (Europe and North America), North Pacific (Aleutian Islands south to Central California).

EXTERNAL MORPHOLOGY.— Numerous descriptions of the external morphology of this species have been provided in the literature (See in particular Abraham 1877; Bergh 1880; O'Donoghue 1921; Pruvot-Fol 1954; Thompson and Brown 1984). See Fig. 1A for a photo of the living animal and Fig. 1B for the original drawing by Abildgaard (1789) See Fig. 2F for a drawing of the ventral anterior surface of a specimen from Wales.

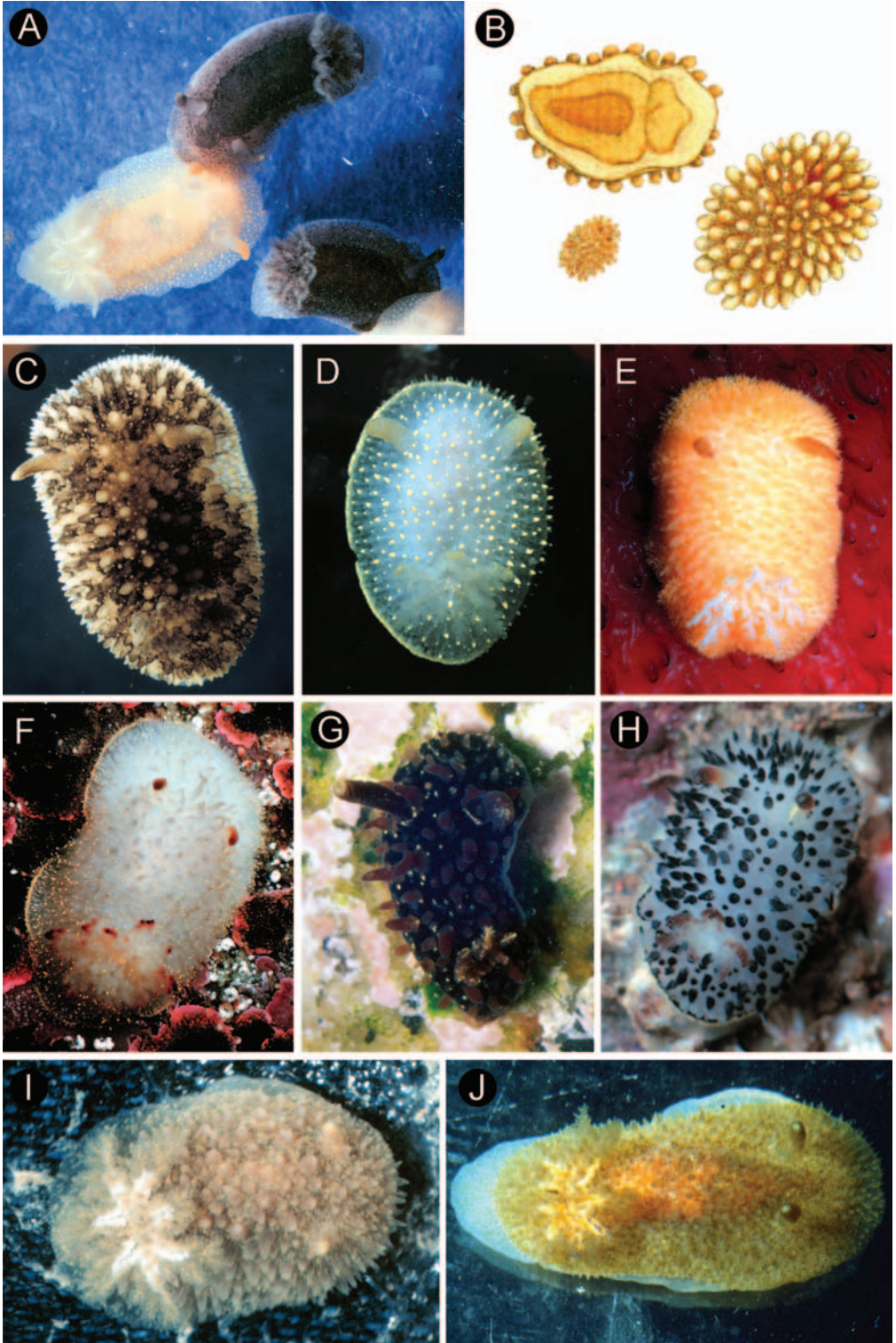
DIGESTIVE SYSTEM.— *Acanthodoris pilosa* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 3E). The radular sac protrudes noticeably from the bulb, under the esophagus. There is a prominent spherical buccal pump with a longitudinal crease. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have multi-tipped, rounded apices (Fig. 2D). The radular formula is 29x3.1.0.1.3 (CASIZ 118891), with all teeth similar to the descriptions of Bergh (1880), O'Donoghue (1921) and Thompson and Brown (1984). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the three outer lateral teeth are flattened plates with a distinct ridge along the inner edge (Figs. 2A–C). The large innermost tooth is flattened with a pointed hook. The inner margin of each tooth has a large, thickened heel that blends into a large shoulder. The shoulder merges with a prominent ridge that has no distinct denticles, but some irregular thickenings or rounded knobs near the end of the ridge.

REPRODUCTIVE SYSTEM.— The ampulla is elongate and tubular (Fig. 3C). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is a thin, elongate tube. It coils and twists, then narrows into the deferent duct, which folds back once on itself before entering the penis. The penis is elongate and wider than the deferent duct and terminates into a common genital atrium. There are penial hooks at the tip of the penis (Fig. 3D). The vaginal duct is short and thinner than the deferent duct. At the distal end, the vagina is as much thinner than the penis. The proximal end widens before terminating into the large round bursa copulatrix. From the bursa the long oviduct connects to the smaller ovoid seminal receptacle. A short uterine duct leads from the base of the bursa into the female gland mass.

CENTRAL NERVOUS SYSTEM.— As with other species of Onchidorididae, the cerebral and pleural ganglia are fused together (Fig. 3B). The two pedal ganglia are located below the cerebro-pleural complex and are joined by an elongate commissure. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. The eyes are sessile at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and two large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

REMARKS.— The specimens we examined of *A. pilosa* closely match the descriptions of Bergh (1880) and subsequent authors (O'Donoghue 1921, Pruvot-Fol 1954, Thompson and Brown 1984). Only the reproductive system of the animal we examined differed slightly from Pruvot-Fol's illustration. In her drawing, the vaginal duct is narrower and the oviduct is shorter than we found.

Picton *in* Rudman (accessed 2004) reviewed the identity of *Acanthodoris pilosa* and the apparent historical misidentification of the animal currently recognized as *A. pilosa*. The original description and illustrations of this species (Abildgaard 1789) (see Fig. 1B) do not match the animal now known as *A. pilosa*, (and recognized as such for over 100 years). That is to say, the ani-



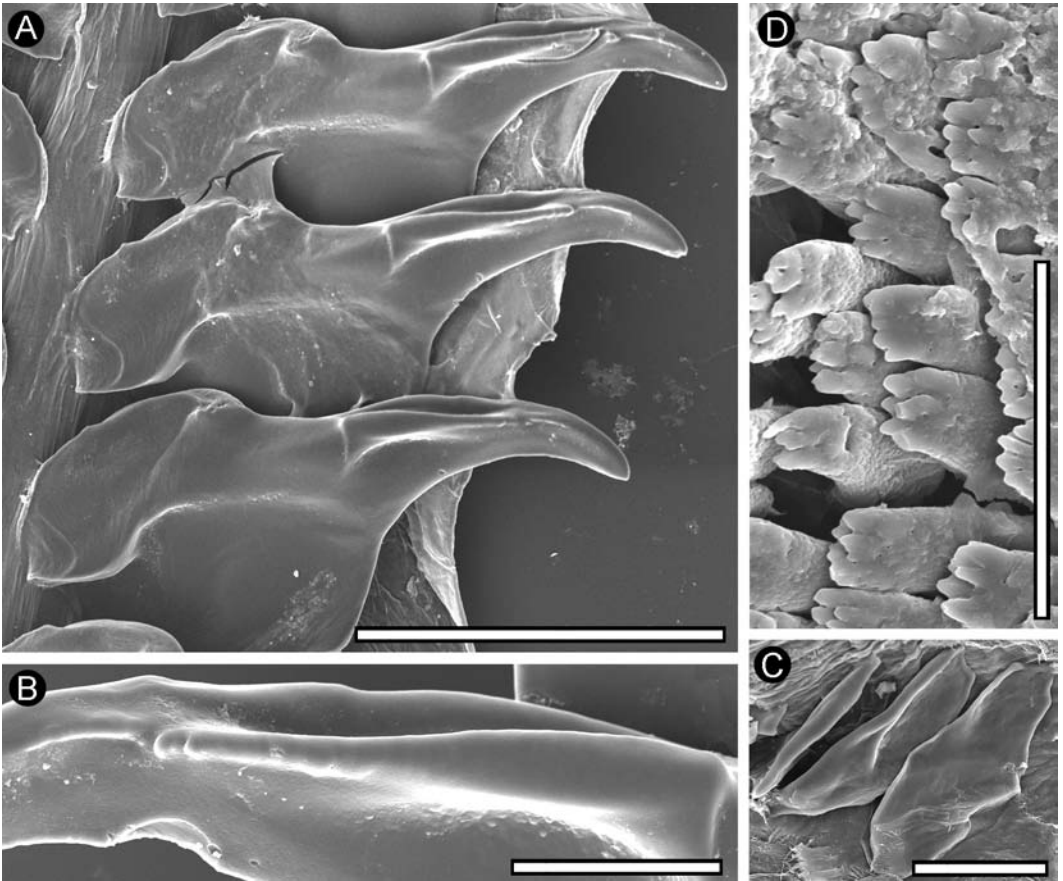


FIGURE 2. *Acanthodoris pilosa* CASIZ 118891. Radular morphology. A First lateral teeth. Scale = 300 µm. B. Close up of denticles. Scale = 50 µm. C. Outer lateral teeth. Scale = 50 µm. D. Jaw rodlets. Scale = 50 µm.

mal illustrated by Abildgaard appears to not have a gill.

Although the original drawing of *A. pilosa* does not resemble the presently recognized species and since the type material is lost (could not be located in any of the major natural history museums), Article 75 of the ICZN allows for the designation of a neotype. Thus, we hereby designate *Acanthodoris pilosa* CASIZ 118891 from Dale County, Wales as the neotype.

***Acanthodoris brunnea* MacFarland, 1905**

Figs. 1C, 4–5.

Acanthodoris brunnea MacFarland, 1905:52.

MATERIAL EXAMINED.— CASIZ 105621 Monterey Bay, Monterey County, California. 50 m depth. 2 specimens, 14 mm, 15 mm dissected. May 1996, C. Mah. CASIZ 000443 San Juan Passage, Puget Sound, Washington. 146 m depth. 1 specimen, 15 mm. July 1925. No collector information.

DISTRIBUTION.— West coast of North America, from California, USA to Vancouver Island, Canada (MacFarland 1905; O'Donoghue 1921 and present study).

EXTERNAL MORPHOLOGY.— MacFarland (MacFarland 1905; MacFarland 1926) gave thorough descriptions of the external morphology of this species. The specimens examined for the pres-

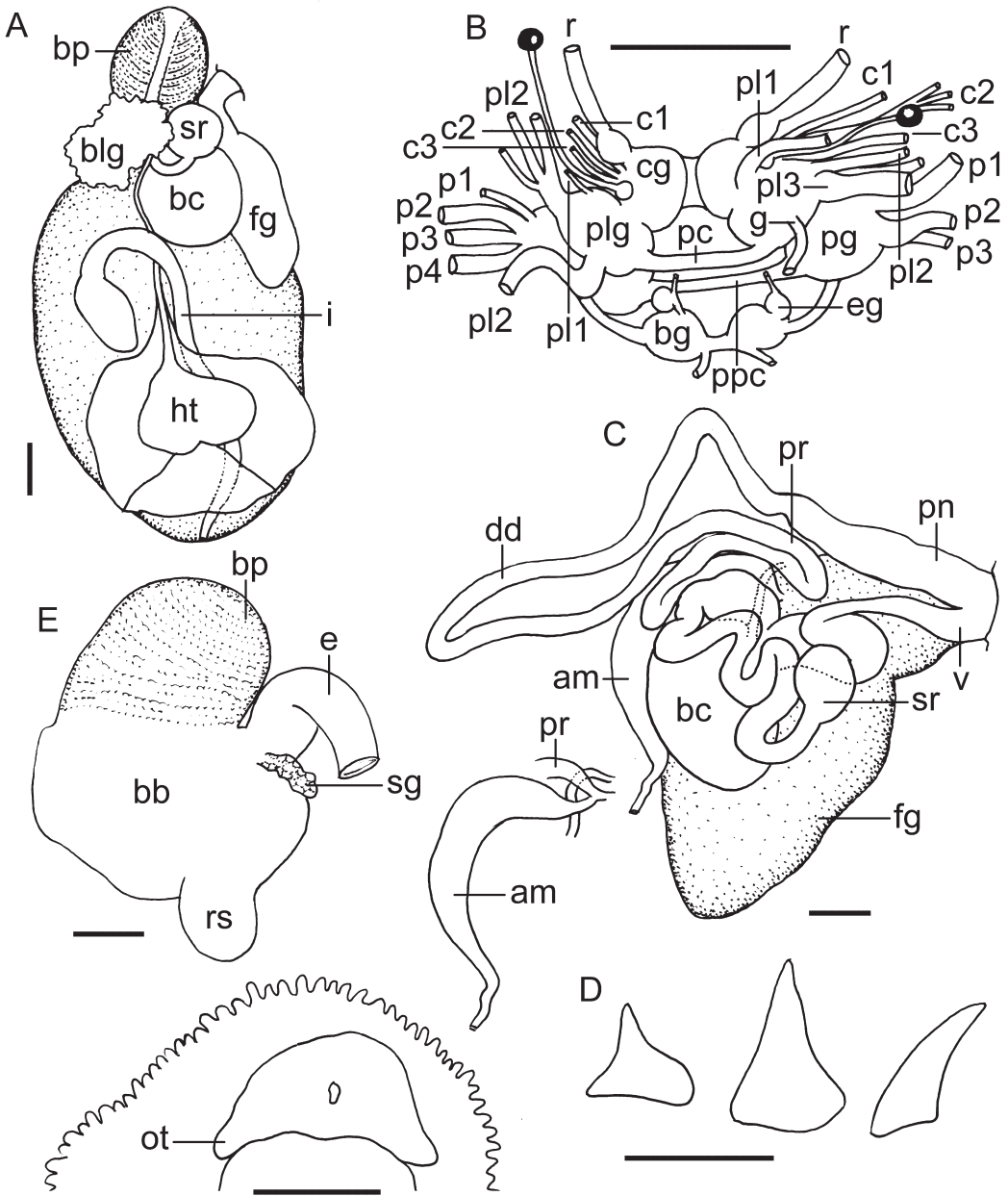


FIGURE 3. *Acanthodoris pilosa* CASIZ 070677 A. Digestive system. B. Cerebro-pleural ganglia. C. Reproductive morphology. D. Detail of penial spines. E. Buccal bulb. F. Anterior ventral surface. Scale bars = 1 mm.

ent study matched his descriptions and thus there is no additional information to present. See Fig. 1 for a photo of the living animal and Fig. 5A for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM.—*Acanthodoris brunnea* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach.

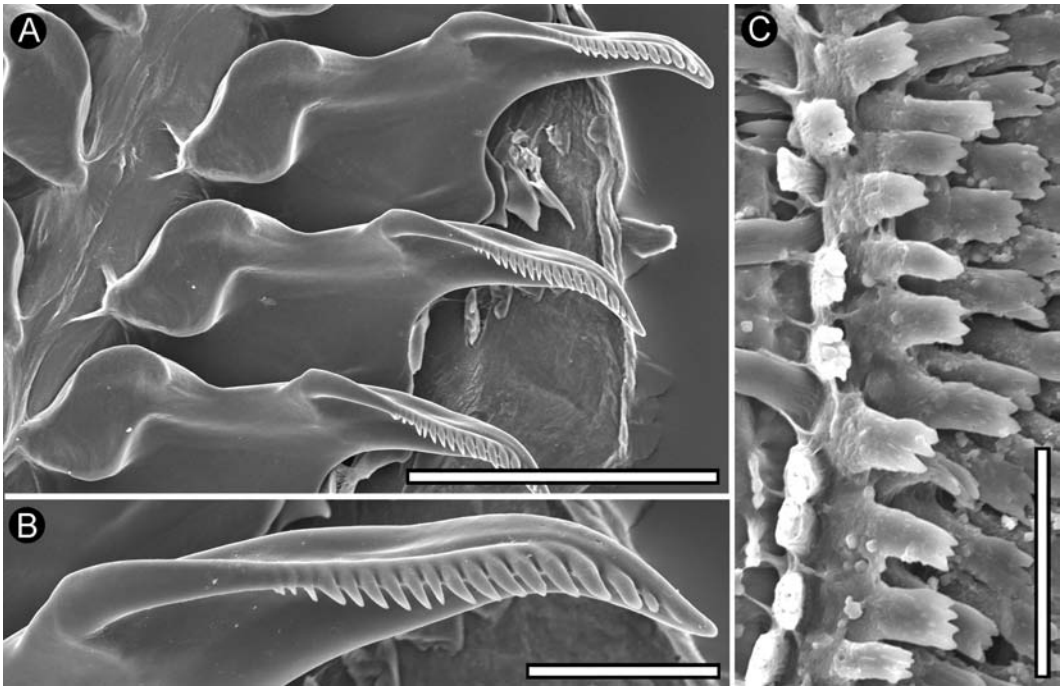


FIGURE 4. *Acanthodoris brunnea* CASIZ 105621. Radular morphology. A First lateral teeth. Scale = 200 μm . B. Close up of denticles. Scale = 50 μm . C. Jaw rodlets. Scale = 30 μm .

The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 5C). The radular sac protrudes substantially from the bulb, under the esophagus. There is a large, spherical buccal pump with a longitudinal crease as described by MacFarland (1905). The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have multi-

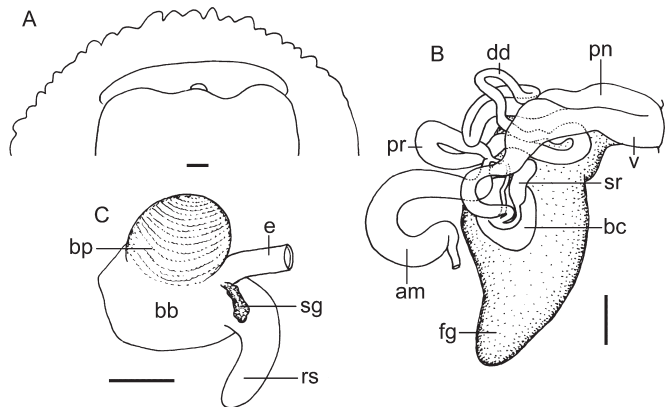


FIGURE 5. *Acanthodoris brunnea* CASIZ 105621. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Scale bars = 1 mm.

tipped, pointed apices (Fig. 4C). The radular formula (CASIZ 105621) is 29x4.1.0.1.4, with all teeth as described by MacFarland (1905). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the four outer lateral teeth are simply pointed plates (Figs. 4A and B). The large first tooth is pointed with 13 to 19 denticles on the inner border of the hook. The inner margin of each tooth has a large, thickened heel that narrows into a nearly straight-edged shoulder. The shoulder merges with a prominent inner edge from which the denticles protrude.

REPRODUCTIVE SYSTEM.— The ampulla is elongate (Fig. 5B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is an elongate, twisted tube. It coils twice before narrowing into the deferent duct, which also coils twice. The penis is elongate and wider than the deferent duct and terminates into a common genital atrium. No penial hooks were observed. The vaginal duct is long and much wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina is slightly wider than the penis. The proximal end narrows and terminates into the round bursa copulatrix. From the bursa the short oviduct connects to the smaller pyriform seminal receptacle. The uterine duct leads from the seminal receptacle into the female gland mass.

REMARKS.— The specimens we examined of *A. brunnea* match MacFarland's descriptions and illustrations (1905, 1925) except for the absence of penial hooks in the specimens we dissected. Williams and Gosliner (1979) noted contradictory information regarding the presence or absence of penial armature in *Acanthodoris*. These authors observed the difficulty in discerning the armature. Although we did perform microscopic examination of our specimens, in no instance did we observe penial spines in this species. Morphological characters for the present phylogenetic analysis are taken from our dissections and the original literature.

Acanthodoris falklandica Eliot, 1907

Figs. 6–7.

Acanthodoris falklandica Eliot, 1907:358.

MATERIAL EXAMINED.— LACM 153981. Puerto Mott, Chili. 7 m depth. 3 specimens, 6–7 mm dissected. January 1995, S. Millen.

DISTRIBUTION.— Falkland Islands (Eliot 1907; Odhner 1926), Chile (Schrödl 1996; Schrödl 1997) and present study).

EXTERNAL MORPHOLOGY.— Eliot 1907:358, Marcus 1959:60 and Odhner 1926:46 all described the external morphology of this species. The specimens examined for the present study matched their descriptions and thus there is no additional information to present. See Fig. 7A for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM.— *Acanthodoris falklandica* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 7C). The radular sac protrudes substantially from an angular extension of the bulb, under the esophagus. There is a large, spherical buccal pump with a longitudinal crease as described by Eliot (1907). There is a thick plate at the top of the opening, with rods at the edge. The rods have multi-tipped, pointed apices (Fig. 6D). The radular formula is 23x2.1.0.1.2 (LACM 153981). There is no rachidian tooth and the large lateral teeth are similar in form while the two outer lateral teeth are simply flat plates with slightly scalloped edges (Figs. 6A and B). The large first tooth has a thickened heel that graduates into a ridge. There are 4–5 denticles on the ridge. The tip of each tooth ends in a pointed hook.

REPRODUCTIVE SYSTEM.— The ampulla is short and tubular (Fig. 7B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is an elongate, thickly coiled tube. It narrows into the deferent duct, which loops once, then widens into the penis. The penis is wide, elongate and terminates into a common genital atrium. The penis does not contain penial hooks. The

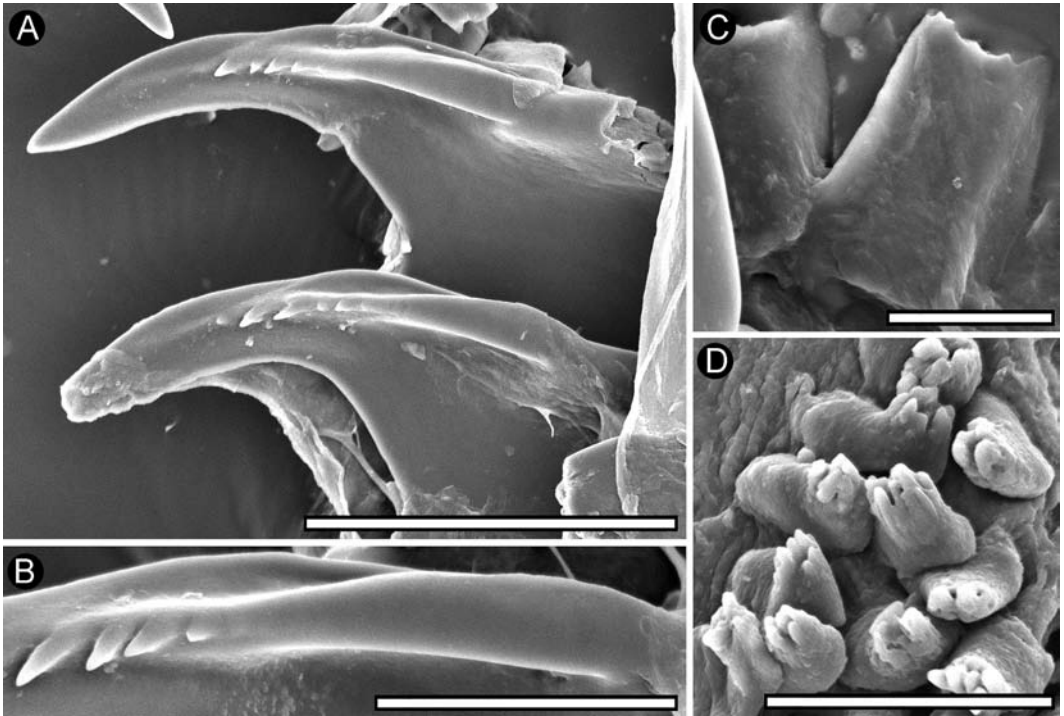


FIGURE 6. *Acanthodoris falklandica* LACM 153981. Radular morphology. A First lateral teeth. Scale = 50 μ m. B. Close up of denticles. Scale = 20 μ m. C. Outer lateral teeth. Scale = 10 μ m. D. Jaw rodlets. Scale = 20 μ m.

vaginal duct is as wide as the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina is large and as wide as the penis. At the proximal end, the vaginal duct narrows before terminating into the large, round bursa copulatrix. From the bursa the long oviduct connects to the smaller round seminal receptacle. The uterine duct leaves the base of the bursa and enters the female gland mass.

REMARKS.— The specimens we examined of *A. falklandica* nearly match Eliot's (1907), Odhner's (Odhner 1926) or Marcus' (1959) description and illustrations of the radula. The specimen we examined has a formula of 23 x 5.1.0.1.5. Eliot's description of the new species included a radular formula of 33x7.1.0.1.7 with up to seven pointed, flattened outer plates. Odhner described

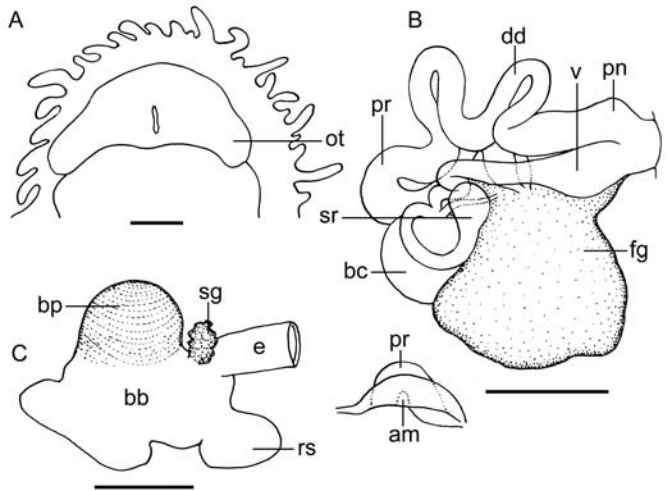


FIGURE 7. *Acanthodoris falklandica* LACM 153981. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Scale bars = 0.5 mm.

a radular formula of 30x4.1.0.1.4 and illustrated four pointed outer lateral teeth. Marcus described and illustrated a radular formula of 4–7.1.0.1.4–7. He illustrated the outer lateral teeth as pointed and elongate. The radula formula of the specimens we examined fall within the range described by Marcus (1959).

Morphological characters for the present phylogenetic analysis are taken from our dissections and the original literature.

Acanthodoris hudsoni MacFarland, 1905

Figs. 1D, 8–9

Acanthodoris hudsoni MacFarland, 1905:51.

MATERIAL EXAMINED.— CASIZ 070785 Monastery Beach, Monterey County, California. 8–10 m depth. 2 specimens, 13 mm, 14 mm dissected. August 1978, G. McDonald. LACM 71-86 Seal Rocks State Park, Lincoln County, Oregon. Intertidal. 4 specimens, 20–40 mm. August 1971, G. Sphon. LACM 71-87 Neptune State Park, Lane County, Oregon. Intertidal. 6 specimens, 6–35 mm. August 1971, G. Sphon.

DISTRIBUTION.— West coast of North America, from California, USA to Vancouver Island, Canada (MacFarland 1905; O'Donoghue 1921, and present study).

EXTERNAL MORPHOLOGY.— MacFarland (1905, 1926) and O'Donoghue (1921) gave thorough descriptions of the external morphology of this species. The specimens examined for the present study matched these descriptions and thus there is no additional information to present. See Fig. 1D for a photo of the living animal and Fig. 9A for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM.— *Acanthodoris hudsoni* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is pear-shaped, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 9C). The radular sac protrudes substantially from an angular extension of the bulb, under the esophagus. There is a large, spherical buccal pump with a longitudinal crease as described by MacFarland (1905). The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have multi-tipped, pointed apices (Fig. 8D). The radular formula is 24x5.1.0.1.5 (CASIZ 070785), with all teeth as described by MacFarland. That is, there is no rachidian tooth and the large lateral teeth are similar in form while the two outer lateral teeth are simply pointed hooks (Figs. 8A–C). The large first tooth is pointed with 10 denticles on the inner border of the hook. The inner margin of each tooth has a large, thickened heel that graduates into a ridge. The ridge merges into a shoulder from which the denticles protrude. The ridge continues to the point of the tooth.

REPRODUCTIVE SYSTEM.— The ampulla is elongate (Fig. 9B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is an elongate, coiled tube. It narrows into the deferent duct, which coils once, then widens into the penis. The penis is wide, elongate and terminates into a common genital atrium. We could not confirm the presence of penial hooks. The vaginal duct is wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina is not as wide as the penis. The middle portion of the vaginal duct expands substantially and then narrows for the last one-third length before terminating into the round bursa copulatrix. From the bursa the oviduct connects to the smaller round seminal receptacle. The uterine duct leaves the base of the bursa and enters the

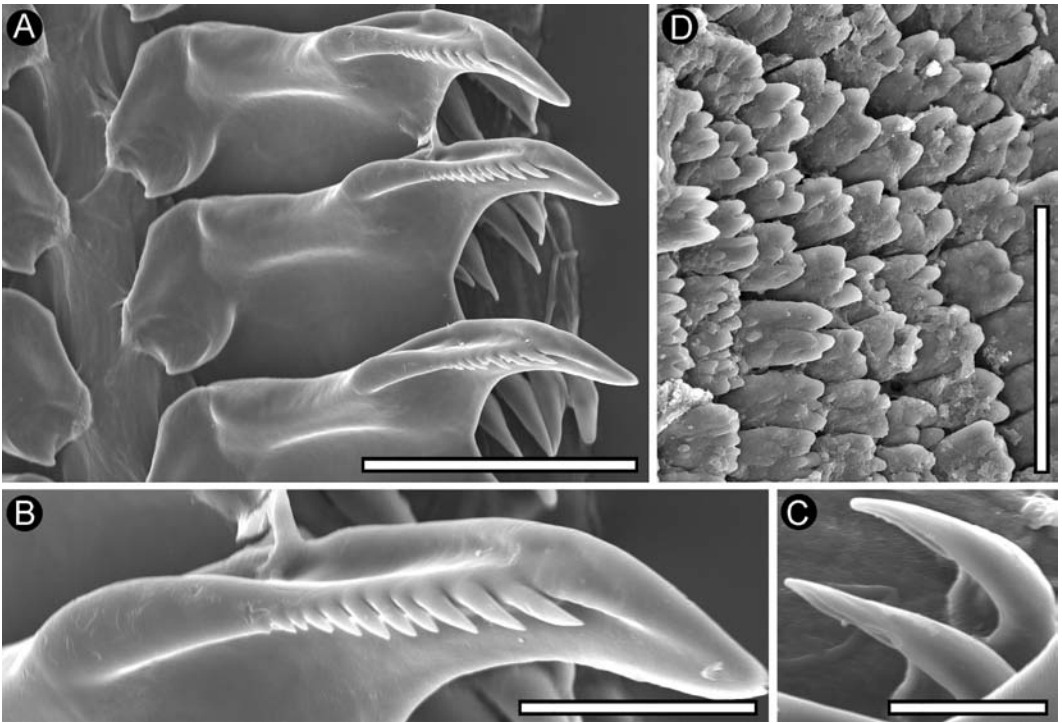


FIGURE 8. *Acanthodoris hudsoni* CASIZ 070785. Radular morphology. A First lateral teeth. Scale = 100 μ m. B. Close up of denticles. Scale = 30 μ m. C. Outer lateral teeth. Scale = 20 μ m. D. Jaw rodlets. Scale = 50 μ m.

female gland mass.

REMARKS.— The specimens we examined of *A. hudsoni* match MacFarland's descriptions and illustrations (1905, 1925). Morphological characters for the present phylogenetic analysis are taken from our dissections and the original literature.

***Acanthodoris lutea* MacFarland, 1925**

Figs. 1E, 10–11.

Acanthodoris lutea MacFarland, 1925:60.

MATERIAL EXAMINED.—

CASIZ 070677 Pigeon Point, San Mateo County, California. No depth data. 3 specimens, 20 mm, 25 mm, 28 mm, dissected. November 1975, G. McDonald. CASIZ 101570 Angel Island, San Francisco Bay, California. No depth data. 1 specimen, 20 mm, dissected. January 1976, Lindberg, Weitbrecht and Gray. LACM 70-74 Naples Reef, Santa Barbara County, California. 15 m depth. 1 specimen, 15 mm. October 1970, C. Swift, W. Stewart, D. Divine. LACM

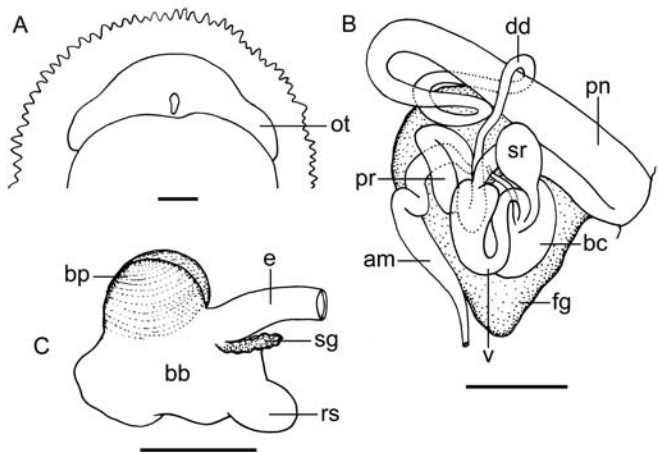


FIGURE 9. *Acanthodoris hudsoni* CASIZ 070785 A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Scale bars = 1 mm.

71-1 Palos Verdes, Los Angeles, California. Intertidal. 2 specimens, 30 mm. January 1971, G. Sphon, E. Marcus, R. Roller, D. Cadien. LACM 73-55 Pirates Cove, California. No depth data. 1 specimen, 21 mm. November, 1973, G. McDonald. LACM 74-30 Palos Verdes, California. Intertidal. 1 specimen, 5 mm. February 1974, G. Sphon, G. Kennedy. LACM 140753 Zuma Beach, California. No depth data. 2 specimens, 22 mm, 25 mm. Spring, 1966.

DISTRIBUTION.— West coast of the USA (MacFarland 1925 and present study).

EXTERNAL MORPHOLOGY.— MacFarland (1925) provided a thorough description of the external morphology of this species. The specimens examined for the present study matched his descriptions and thus there is no additional information to present. See Fig. 1E for a photo of the living animal and Fig. 11A for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM.— *Acanthodoris lutea* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 11C). The radular sac protrudes from an angular extension of the bulb, under the esophagus. There is a large, spherical buccal pump with a longitudinal crease as described by MacFarland (1925). The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have rounded, scalloped apices (Fig. 10D). The radular formula is 34x7.1.0.1.7 (CASIZ 070677), with all teeth as described by MacFarland (1925). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the seven outer lateral teeth are pointed plates (Figs. 10A–C). The large first tooth is pointed with 2 to 3 rounded denticles on the inner border of the hook. The inner margin of each tooth has a large, thickened heel that narrows into a wide, nearly straight-edged shoulder. The shoulder merges with a prominent ridge from which the denticles protrude near the anterior of the ridge. The ridge then continues smoothly to the point of the tooth.

REPRODUCTIVE SYSTEM.— The ampulla is large and bulbous (Fig. 11B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The oviduct enters the large female gland mass. The prostate is an elongate, thick, coiled tube. It narrows into the deferent duct, which twists and coils, then widens into the penis. The penis is tubular, elongate and terminates into a common genital atrium. The penis does not contain penial hooks. The vaginal duct is very long and slightly wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina does not widen from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct widens and then terminates into the round bursa copulatrix. At the base of the bursa the short oviduct connects to the slightly smaller pyriform seminal receptacle. The thin uterine duct leaves the base of the bursa and enters the female gland mass.

REMARKS.— The specimens we examined of *A. lutea* match MacFarland's descriptions and illustrations (1905, 1925). The only difference between our description of the reproductive system and MacFarland's is in regard to the vaginal duct. MacFarland noted a "glandular portion" of the duct at the proximal end. We observed a widening of the duct at this end, however, we cannot confirm that it was glandular.

Morphological characters for the present phylogenetic analysis are taken from our dissections and the original literature.

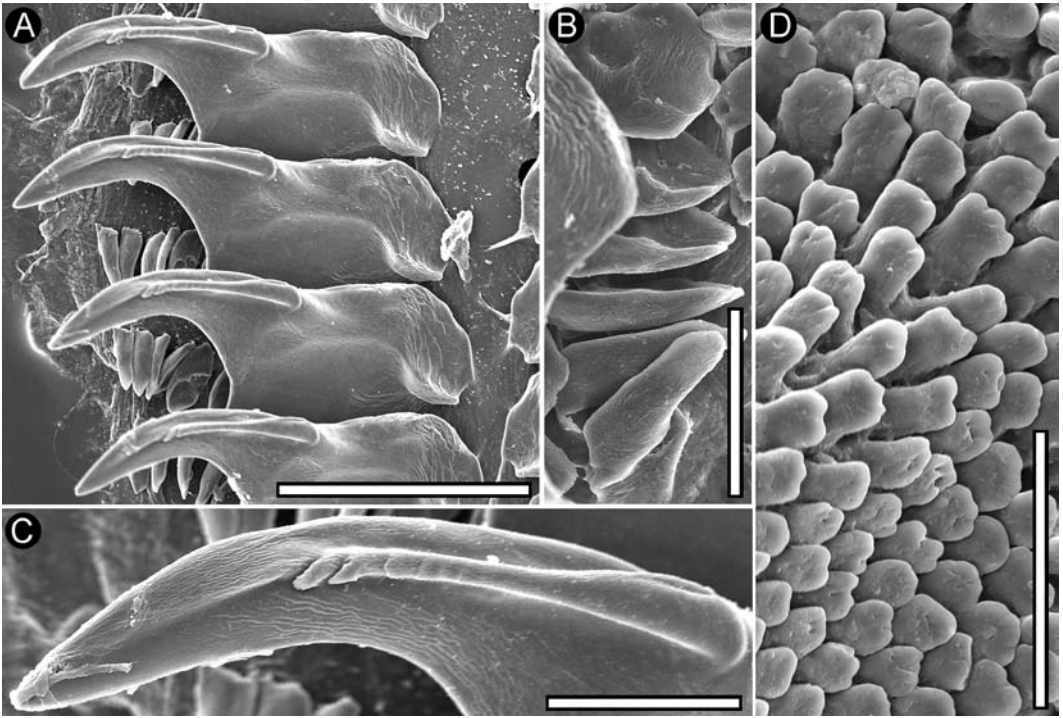


FIGURE 10. *Acanthodoris lutea* CASIZ 070677. Radular morphology. A First lateral teeth. Scale = 200 μm . B. Outer lateral teeth. Scale = 20 μm . C. Close up of denticles. Scale = 50 μm . D. Jaw rodlets. Scale = 50 μm .

Acanthodoris nanaimoensis

O'Donoghue, 1921

Figs. 1F, 12–13.

Acanthodoris nanaimoensis O'Donoghue, 1921:172.

Acanthodoris columbina MacFarland, 1926:94.

MATERIAL EXAMINED.—

CASIZ 076409 Salt Point, Sonoma County, California. 15 m depth. 1 specimen, 20 mm, dissected. October 1962, D. Sullivan. CASIZ 074558 Clayoquot Sound, Vancouver Island, Canada. No depth data. 4 specimens, 10–20 mm dissected. February 1991, G. MacGinitie. CASIZ 068331 Vancouver Island, Canada. No depth or collector data. 1 specimen, 25 mm dissected. LACM

72-103 Neptune National Park, Lincoln County, Oregon. Intertidal. 3 specimens, 10 mm, 20 mm, dissected, 20 mm. August 1972, G. Kennedy & G. Sphon. LACM 72-108 Cape Arano State Park, Oregon. Intertidal. 1 specimen, 20 mm. August 1972, G. Sphon & G. Kennedy. LACM 71-113 Whale Rock, Del Norte County,

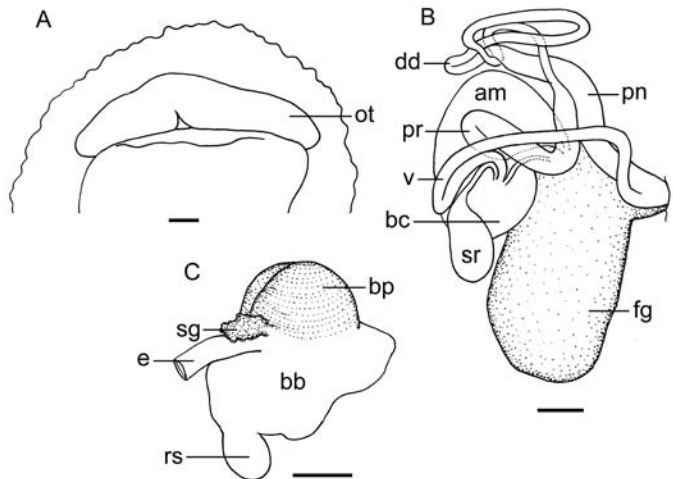


FIGURE 11. *Acanthodoris lutea* CASIZ 070677 A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Scale bars = 1 mm.

California. 10–15 m depth. 5 specimens, 13–30 mm. August 1971, C. Swift. LACM 71-109 Prisoner's Rock, Trinidad, Humboldt County, California. 8–17 m depth. 1 specimen, 20 mm. July 1971, C. Swift.

DISTRIBUTION.— West coast of North America, from Alaska to southern California (MacFarland 1926 and present study).

EXTERNAL MORPHOLOGY.— O'Donoghue (1921) and MacFarland (1926) gave thorough descriptions of the external morphology of this species. The specimens examined for the present study matched these descriptions and thus there is no additional information to present. See Fig. 1X for a drawing of the ventral anterior surface of a specimen from Oregon.

DIGESTIVE SYSTEM.— *Acanthodoris nanaimoensis* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 13D). The knob-shaped radular sac protrudes from the bulb, under the esophagus. There is a large, spherical buccal pump with a longitudinal crease as found in other *Acanthodoris* species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have blunt, deeply scalloped apices (Fig. 12D). The radular formula (LACM 72-103) is 33x3.1.0.1.3, with all teeth as described by O'Donoghue (1921). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the five outer lateral teeth are small plates (Figs. 12A–C). The large first tooth is plate-shaped with a pointed hook that has 3–6 tiny pointed denticles on the inner border of the hook. The inner margin of each tooth has a large, thickened heel that narrows into a wide, nearly straight-edged shoulder. The shoulder merges with a prominent inner edge from which the denticles protrude.

REPRODUCTIVE SYSTEM.— The ampulla is long and thin (Fig. 12B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the female gland mass. The prostate is an elongate, thick tube. It narrows into the long, thinner deferent duct, which twists and coils, then widens into the penis. The penis is tubular, elongate and terminates into the common genital atrium. The penis does not contain penial hooks. The vaginal duct is very long and wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina widens slightly from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large round bursa copulatrix. From the bursa the long oviduct connects to the smaller round seminal receptacle. The thin uterine duct leaves the base of the bursa and enters the female gland mass.

REMARKS.— The specimens we examined of *A. nanaimoensis* match O'Donoghue (1921) description of the external morphology. However, our observations of the radular morphology differ from O'Donoghue's illustrations or descriptions. He reported 6–7 lateral teeth with six smaller outer teeth and we observed a formula of 31x3.1.0.1.3. O'Donoghue also found no signs of denticulation on the ridge of the large main tooth. We found the teeth to be denticulate, with two rounded outermost denticles and 3–5 smaller, pointed denticles next to these. In addition, O'Donoghue reported the labial armature as closely packed tiny triangular denticles. However we observed denticles having multifid tips as reported by MacFarland (1926) for *Acanthodoris columbina*. Thus, our specimens match the description and illustrations of the radular teeth as presented by MacFarland (1926).

MacFarland (1926) reported that the specimens he examined were devoid of penial hooks and that the penis was very short and blunt. But O'Donoghue (1921) reported that his specimens had long, sub-conical and armed with minute hooks. Our specimens match MacFarland's (1926)

description of the reproductive organs. O'Donoghue (1921) did not illustrate the reproductive sys-

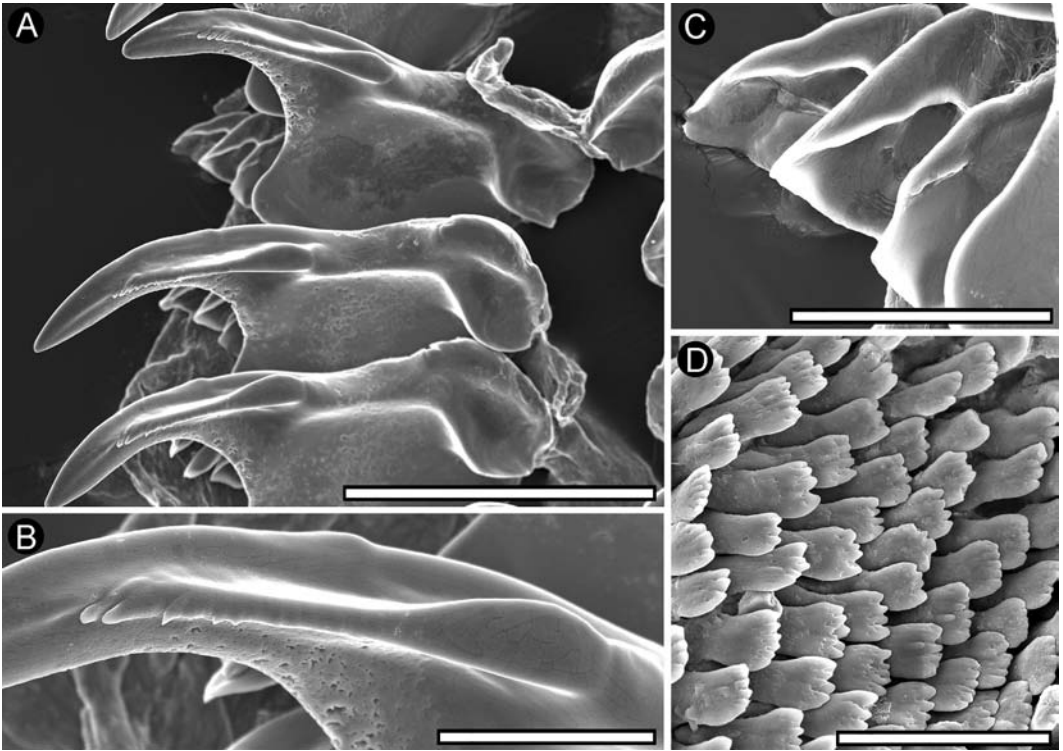


FIGURE 12. *Acanthodoris nanaimoensis* LACM 72-103. Radular morphology. A First lateral teeth. Scale = 200 μ m. B. Close up of denticles. Scale = 50 μ m. C. Outer lateral teeth. Scale = 50 μ m. D. Jaw rodlets. Scale = 50 μ m.

tem of his specimens, but only described the penial morphology.

Steinberg (Steinberg 1963) synonymized *Acanthodoris nanaimoensis* and *A. columbina* stating that the variation noted between the specimens examined by O'Donoghue and MacFarland were not enough to justify two separate species.

Morphological characters for the present phylogenetic analysis are taken from our dissections and the original literature.

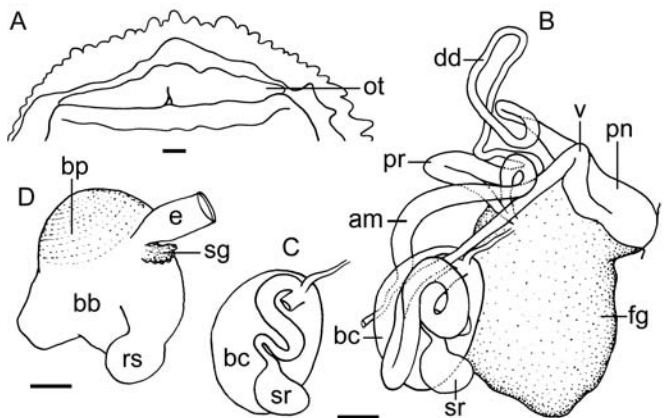


FIGURE 13. *Acanthodoris nanaimoensis* CASIZ 070677 A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Scale bars = 1 mm.

***Acanthodoris nanega* Burn, 1969**

Figs. 14–15.

Acanthodoris nanega Burn, 1969.

MATERIAL EXAMINED.— CASIZ 100574 Victor Harbour, South Australia. 3.6 m depth. 2 specimens, 7–10 mm, 7 mm dissected. August 1994, T. Gosliner.

DISTRIBUTION.— South coast of Australia (Burn and present study).

EXTERNAL MORPHOLOGY.— Burn (1969) described the external morphology of this species. The specimens examined for the present study matched his descriptions and thus there is no additional information to present. Burn stated that the foot was bilabiate in front but the preserved specimens we examined did not display this morphology. See Fig. 15A for a drawing of the ventral anterior surface of a specimen from South Australia.

DIGESTIVE SYSTEM.— *Acanthodoris nanega* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 15A). The long radular sac protrudes substantially from the bulb, under the esophagus. There is a large buccal pump with a longitudinal crease and a pointed apex. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have blunt, deeply scalloped apices (Fig. 14B). The radular formula is 27x5.1.0.1.5 (LACM 72-103), with all teeth as described by Burn (1969). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the five outer lateral teeth are small, seed-shaped plates (Figs. 14A, C, D). The large first tooth is plate-shaped with a pointed hook that has 3–6 pointed denticles on the inner border of the hook. The inner margin of each tooth has a large, thickened heel that blends into a wide, nearly straight-edged shoulder. The shoulder merges into a prominent inner edge from which the denticles protrude.

REPRODUCTIVE SYSTEM.— The ampulla is elongate (Fig. 15B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is an elongate, serpentine tube. It does not narrow into the long deferent duct, which curves once before widening into the penis. The penis is short and bulbous and terminates into the common genital atrium. The penis does not contain penial hooks. The vaginal duct is very long and wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina does not widen from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large round bursa copulatrix. From the bursa the oviduct connects to the slightly smaller ovoid seminal receptacle. The uterine duct could not be seen.

REMARKS.— The specimens we examined of *A. nanega* match the external description provided by Burn (1969) except for the bilabiate anterior foot that Burn observed.

The radular morphology of the specimens we examined matches the illustrations and description by Burn. However, Burn did not examine the reproductive organs of his specimens, so the descriptions provided herein are used for the characters in the present phylogenetic analysis.

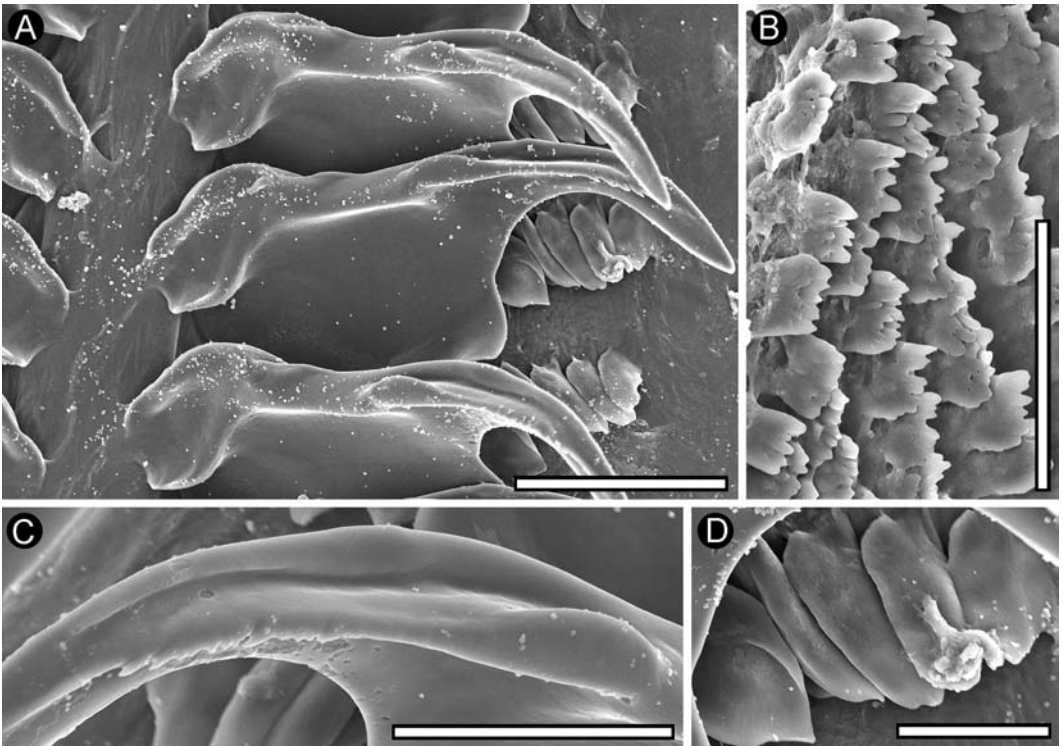


FIGURE 14. *Acanthodoris nanega* CASIZ 100574. Radular morphology. A First lateral teeth. Scale = 100 μ m. B. Jaw rodlets. Scale = 50 μ m. C. Close up of denticles. Scale = 50 μ m. D. Outer lateral teeth. Scale = 30 μ m.

Acanthodoris pina Ev. Marcus
& Er. Marcus, 1967

Figs. 1G, 16–17.

Acanthodoris pina Marcus &
Marcus, 1967:201.

Acanthodoris stohleri Lance 1968:8.

MATERIAL EXAMINED.—

LACM 153100 Bahia de los Angeles, Baja California. 8.8 m. 1 specimen, 15 mm dissected. March 2000, M. Miller. LACM 140754 Punta Lobos, Sonora, Mexico. No depth data. 6 specimens, 6–30 mm. March 1975, F. and R. Poorman. LACM 67-17 Libertad, Sonora, Mexico. Intertidal. 1 specimen, 20 mm. March 1967, J. McLean. CASIZ 118701 Baja California Norte, Mexico. No depth data. 8 specimens, 5–20 mm. December 1964, W. Farmer.

DISTRIBUTION.— Baja California (Marcus and Marcus 1967, Lance 1968 and present study).

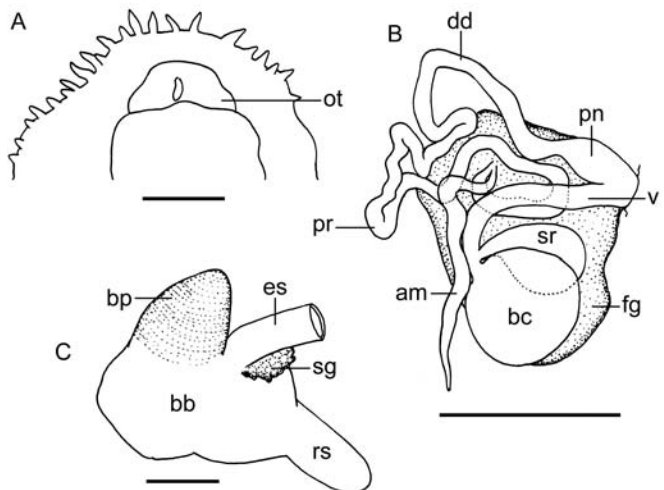


FIGURE 15. *Acanthodoris nanega* CASIZ 100574. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Scale bars = 1 mm.

EXTERNAL MORPHOLOGY.— Marcus and Marcus (1967) described the external morphology of this species. The specimens examined for the present study matched their descriptions and thus there is no additional information to present. See Fig. 1G for a photo of the living animal and Fig. 17A for a drawing of the ventral anterior surface of a specimen from Baja California.

DIGESTIVE SYSTEM.— *Acanthodoris pina* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 17D). The radular sac protrudes from the bulb, under the esophagus. There is a large buccal pump with a longitudinal crease as found in other *Acanthodoris* species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have blunt, deeply scalloped apices (Fig. 16D). The radular formula is 31x5.1.0.1.5 (LACM 153100), with all teeth as described by Marcus and Marcus (1967). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the five outer lateral teeth are small plates with a ridge on the top (Figs. 16A–C). The large first tooth is plate-shaped with a pointed hook that has 3–4 blunt denticles on the inner border of the hook. The inner margin of each tooth has a large, thickened heel that blends into a wide, nearly straight-edged shoulder. The shoulder merges into a prominent inner edge from which the denticles protrude.

REPRODUCTIVE SYSTEM.— The ampulla is thick and elongate (Fig. 17B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is an elongate tube. It narrows into the long deferent duct, which loops and curves back on itself before widening into the penis. The penis is elongate and wide and terminates into the common genital atrium. There is a glandular portion of the penis located at the distal end. There are no penial hooks. The vaginal duct is very long, curved and wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina narrows slightly as compared to the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the round bursa copulatrix. From the bursa the oviduct connects to the much smaller round seminal receptacle. The thin uterine duct connects at the base of the bursa and enters the female gland mass.

REMARKS.— The specimens we examined of *A. pina* match Marcus & Marcus (1967) description of the external and radular morphology. The only difference between the specimens we examined and those examined by Marcus and Marcus is the presence of a glandular portion of the penis. Marcus and Marcus did not mention this glandular portion, but we observed it in the specimens we dissected. Morphological characters of the radular and reproductive systems used in the present phylogenetic analysis are taken from dissection of the specimens noted above.

Lance (1968) described several specimens collected in Bahía San Luis Gonzaga, Baja California. His publication, which described a new species *Acanthodoris stohleri*, was preceded by Marcus and Marcus (1967) publication of *A. pina* sp. nov. by only two months. We examined the type specimens of *A. stohleri* and concur with Keen's (1971:828) synonymy of the two species.

Acanthodoris rhodoceras Cockerell in Cockerell and Eliot, 1905

Figs. 1H, 18–19.

Acanthodoris rhodoceras Cockerell in Cockerell & Eliot, 1905:38.

Acanthodoris sp. MacGinitie and MacGinitie, 1949:363.

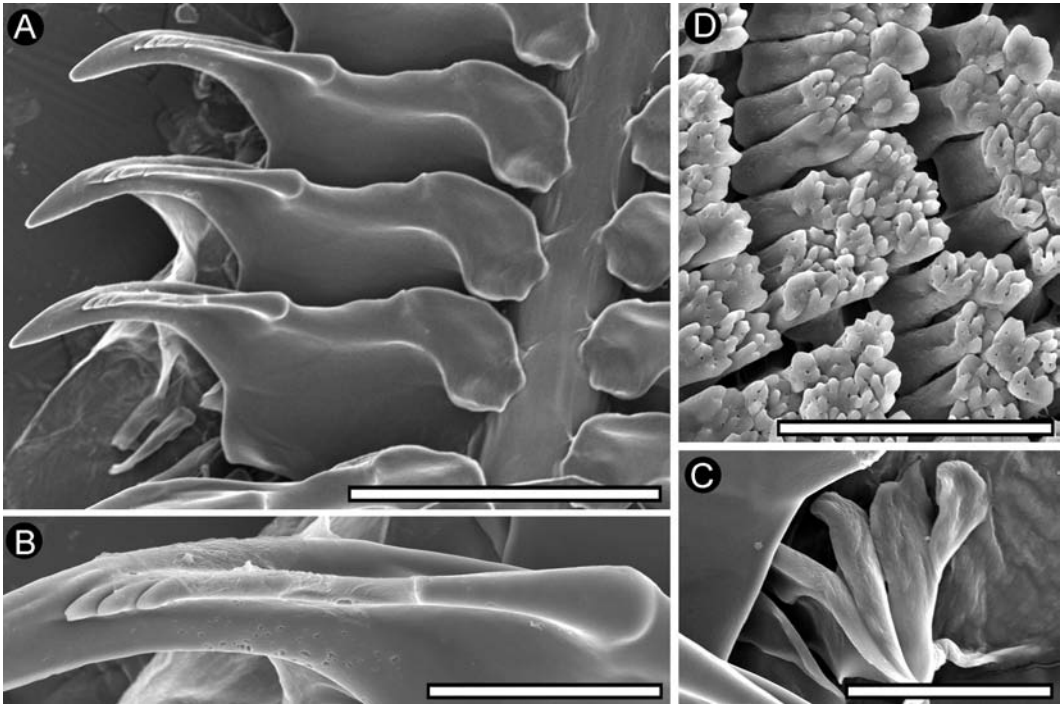


FIGURE 16. *Acanthodoris pina* CASIZ 153100. Radular morphology. A First lateral teeth. Scale = 200 μm . B. Close up of denticles. Scale = 50 μm . C. Outer lateral teeth. Scale = 50 μm . D. Jaw rodlets. Scale = 50 μm .

MATERIAL EXAMINED.—

CASIZ 068334 Orange County, California. 7 fathoms depth. 1 specimen, 18 mm dissected. May 1934, G. MacGinitie. CASIZ 072355 San Luis Obispo County, California. 6 m depth. 1 specimen, 20 mm. October 1985, D. Behrens. CASIZ 069078 Monterey County, California. No depth data. 1 specimen, 30 mm. April 1972, G. McDonald. CASIZ 169829 San Francisco Marina, California. 1 m depth. 1 specimen, 4 mm. April 2003, R. Ayres, C. Brown, M. Walton, S. Lattanzio. CASIZ 068322 Duxbury Reef, Marin County, California. No depth data. 2 specimens, 7–10 mm. November 1989, D. Contress. LACM 126371 Duxbury Reef, California. No depth data. 1 specimen, 15 mm. July 1986, R. Willan. LACM 140755 Corona del Mar, California. No depth data. 1 specimen, 15 mm. February 1963, no

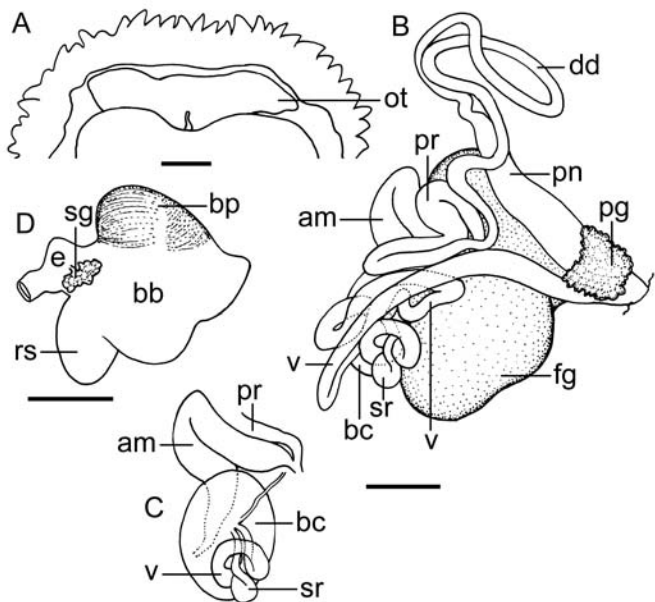


FIGURE 17. *Acanthodoris pina* CASIZ 153100 A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Scale bars = 1 mm.

collector data. LACM 70-78 Government Point, Santa Barbara County, California. 24 m depth. 1 specimen, 13 mm. December 1970, C. Swift. LACM 73-32 Kodiak Island, Alaska. Intertidal. 1 specimen, 12 mm. August 1973, J. McLean. LACM 73-23 Kenai Peninsula, Alaska, 5 fathoms. 1 specimen, 20 mm. August 1973, J. McLean. LACM 1971-362.6 Beaufort Sea, Arctic Ocean. 360 m. 4 specimens, 10–15 mm. September 1971, R/V Glacier. LACM 66-35 Vancouver, Canada. Intertidal. 1 specimen, 10 mm. June 1966, J. McLean. USNM 576629 San Francisco Bay, California. 46 fms. 1 specimen, 12 mm. October 1912, no collector data. USNM 791507 Point Loma, California. No depth data. 1 specimen, 8 mm. July 1956, J. Morrison.

DISTRIBUTION.— West coast of North America, from Oregon to Baja California (Cockerell and Eliot 1905 and present study).

EXTERNAL MORPHOLOGY.— Cockerell and Eliot (1905) and MacFarland (1925) described the external morphology of this species. The specimens examined for the present study matched their descriptions and thus there is no additional information to present. See Fig. 1H for a photo of the living animal and Fig. 19A for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM. — *Acanthodoris rhodoceras* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 19C). The radular sac protrudes from the bulb, under the

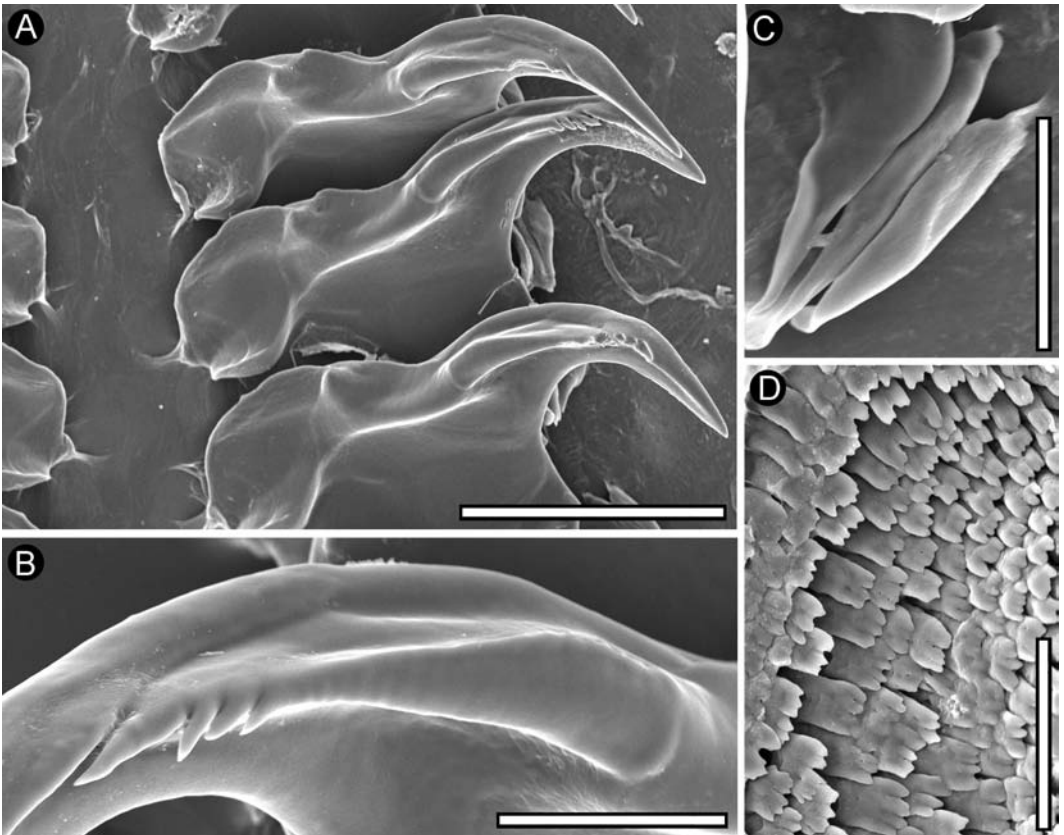


FIGURE 18. *Acanthodoris rhodoceras* CASIZ 068334. Radular morphology. A First lateral teeth. Scale = 200 μm . B. Close up of denticles. Scale = 50 μm . C. Outer lateral teeth. Scale = 30 μm . D. Jaw rodlets. Scale = 50 μm .

esophagus. There is a large ovoid buccal pump with a longitudinal crease as found in other *Acanthodoris* species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have pointed, deeply scalloped apices (Fig. 18D). The radular formula is 32x3.1.0.1.3 (CASIZ 068334), with all teeth as described by Cockerell and Eliot (1905). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the three or four outer lateral teeth are small plates (Figs. 18A–C). The large first tooth is rather flat with a long pointed hook that has up to 4 pointed denticles on the inner border of the hook. The inner margin of each tooth has a large, thickened heel that blends into a wide shoulder. The shoulder ends and there is a prominent ridge from which the denticles protrude. The ridge then continues to the tip of the hook, but has no further denticulation.

REPRODUCTIVE SYSTEM.—

The ampulla is sausage shaped and elongate (Fig. 19B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The oviduct enters the large female gland mass. The prostate is an elongate tube. It narrows into the long deferent duct, which curves back on itself before widening into the penis. The penis is wide and terminates into the common genital atrium. The penis contains minute pointed hooks. The vaginal duct is very long and wider than the deferent duct. At the distal end, the vagina widens slightly from the vaginal duct as it joins with the penis at the common genital atrium. The proximal end of the vaginal duct widens into a bulb before it terminates into the large round bursa copulatrix. From the bursa the oviduct connects to the smaller ovid seminal receptacle. The long uterine duct connects at the base of the bursa.

REMARKS.— The specimens we examined of *A. rhodoceras* match Cockerell and Eliot's (1905) and MacFarland's (1925) descriptions of the external, radular and reproductive morphology. Morphological characters of the radular and reproductive systems used in the present phylogenetic analysis are taken from the literature and corroborated with the dissection of the specimens noted above.

Acanthodoris serpentinitus Williams and Gosliner, 1979

Fig 11.

Acanthodoris serpentinitus Williams and Gosliner 1979:216.

DISTRIBUTION.— Known only from San Felipe, Baja California, Mexico (Williams and Gosliner 1979).

REMARKS.— This species was examined and described in detail by Williams and Gosliner

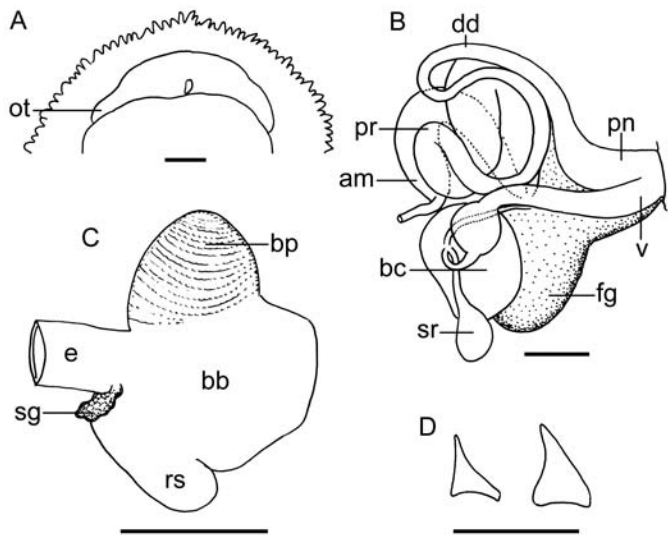


FIGURE 19. *Acanthodoris rhodoceras* CASIZ 068334. A. Anterior ventral surface. Scale bar = 1 mm. B. Reproductive morphology. Scale bar = 1 mm. C. Buccal bulb. Scale bar = 1 mm. D. Sketch of penial spines. Scale = 30 μ m.

(1979). Morphological characters for the present phylogenetic analysis were taken from the original literature and from re-examination of the type specimens held at the California Academy of Sciences.

Other *Acanthodoris* species not included in the phylogenetic analyses

Acanthodoris armata O'Donoghue, 1927:4.

LOCALITY.— Vancouver Island, Canada

REMARKS.— O'Donoghue (1927) described the external and radular morphology of this species. The type material could not be located at any of the major natural history museums. No further revision is possible.

Acanthodoris atrogriseata O'Donoghue, 1927:2.

LOCALITY.— Vancouver Island, Canada

REMARKS.— O'Donoghue (1927) described the external and radular morphology of this species. The type material could not be located at any of the major natural history museums. No further revision is possible.

Acanthodoris caeruleascens Bergh, 1880a:252

LOCALITY.— Bering Sea, Alaska

REMARKS.— Bergh (1880) described the external and radular anatomy of this species. The reproductive anatomy was not illustrated and only partially described. The type material could not be located at any of the major natural history museums, thus no further revision is possible.

Acanthodoris globosa Abraham, 1877:262

LOCALITY.— New Zealand

REMARKS.— Abraham (1877) briefly described the external and radular morphology of this species. Eliot (1907) examined and described the external and radular morphology of Abraham's specimen. The type material could not be located at any of the major natural history museums.

Acanthodoris metulifera Bergh, 1905:98

LOCALITY.— Tasmania

REMARKS.— Bergh (1905) briefly described the external and radular morphology of this species. The type material could not be located at any of the major natural history museums. Marcus and Marcus (1967:203) speculated that this species may be a synonym of *A. globosa* Abraham, 1877. Certainly the descriptions of the external morphology are very similar, as are the descriptions and illustrations of the radular morphology. Without examination of the type material, we cannot formally synonymize two species.

A. mollicella Abraham, 1877:262

LOCALITY.— New Zealand

REMARKS.— Abraham (1877) described the external morphology and briefly the radular morphology of this species. Eliot (1907) examined and described the external and radular morphology of Abraham's specimen. Williams and Gosliner (1979) provided further anatomical details.

Comparisons of the original descriptions and illustrations of *A. mollicella*, *A. metulifera* and *A. globosa* causes one to suspect that the three species are synonymous. However, since the type

material could not be located at any of the major natural history museums, no further revision of this species is possible.

Acanthodoris uchidai Baba 1935c:119

LOCALITY.— Akkeshi Bay, Hokkaido, Japan (Baba 1935).

REMARKS.— Baba (1935) described the external and radular morphology of this species. However, no description of the reproductive anatomy exists for this species and we were unable to obtain the type material. Limited morphological characters were taken from the original literature for the present phylogenetic analysis.

Acanthodoris vatheleti Rochebrune and Mabile, 1891:11

LOCALITY.— Cape Horn

REMARKS.— This species was only perfunctorily described by Rochebrune and Mabile (Rochebrune and Mabile 1891). Schrödl (2003) reported that *A. vatheleti* may be conspecific with *A. falklandica* Eliot, 1907. However, the type specimen of *A. vatheleti* cannot be located and thus no further revision is possible.

NEW SPECIES

Acanthodoris planca Fahey and Valdés sp. nov.

Figs. 1J, 20–21.

Acanthodoris sp. Gosliner, 1987:91

MATERIAL EXAMINED.— Holotype: CASIZ 171754 Cove Rock, False Bay, South Africa. No depth data. 20 mm. January 1991, M. Bursey. Paratype: ELM W1647 Igada-Gulu, False Bay, South Africa. No depth data. 18 mm dissected. February 1990, M. Bursey.

DISTRIBUTION.— This species has only been recorded from South Africa (present study).

ETYMOLOGY.— The specific name *planca* is taken from the Greek word meaning flat-footed. This *Acanthodoris* species has a prominent flat-footed appearance as it crawls.

EXTERNAL MORPHOLOGY.— The body shape of the living animal is oblong and the foot extends beyond the mantle margin (Fig. 1J). The dorsum is covered with elongate papillae that appear short and conical when preserved. The papillae in the preserved specimens are longer at the mantle margin. The oral tentacles are short and blunt. The rhinophores are stout clubs. They angle towards the posterior and have 15–17 lamellae. The gill is broad and spreads to cover the posterior third of the animal. There are ten gill leaves that are bi- and tripinnate. The background color of the dorsum is pale brown or orange and there is a darker orange patch of coloration mid-dorsum. The foot is white with tiny brownish-orange dots. The rhinophores and gill leaves are the same color as the background color, but the rhinophore tips are white. See Fig. 21A for a drawing of the ventral anterior surface of the paratype.

DIGESTIVE SYSTEM.— *Acanthodoris planca* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is a somewhat ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 21B). The radular sac protrudes from the bulb, under the esophagus. There is an ovoid buccal pump with a longitudinal crease as found in other *Acanthodoris* species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods

are elongate, blunt and have multi-apices (Fig. 20D). The radular formula is 32x6.1.0.1.6 (CASIZ 171754), with all teeth similar in shape to other *Acanthodoris*. That is, there is no rachidian tooth and the large lateral teeth are similar in form while the six to seven outer lateral teeth are elongate and have pointed tips (Figs. 20A–C). The large first tooth is plate-shaped with a pointed hook that has approximately 8 blunt denticles on a thickened shoulder along the edge of the hook. The inner margin of each tooth does not have the large, thickened heel that is found on some other *Acanthodoris* species. The thickened shoulder ends abruptly at the inner margin of the each tooth.

REPRODUCTIVE SYSTEM.— The ampulla is an elongate tube (Fig. 21C). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The oviduct enters the large female gland mass. The prostate is an elongate, narrow tube with two folds. It has a short constriction where it enters the short, straight deferent duct, which then widens slightly into the penis. The penis is short and terminates into the common genital atrium. No penial hooks were observed. The vaginal duct is very long and wider than the deferent duct. At the distal end, the vagina widens very slightly from the vaginal duct as it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large ovoid bursa copulatrix. From the bursa the oviduct connects to the smaller ovoid seminal receptacle. The uterine duct is short and enters at the point where the bursa and seminal receptacle connect.

REMARKS.— *Acanthodoris planca* is externally most similar to the description of *A. citrina* Verrill, 1879, later synonymized with *A. pilosa* by Thompson and Brown 1984 and to *A. lutea*

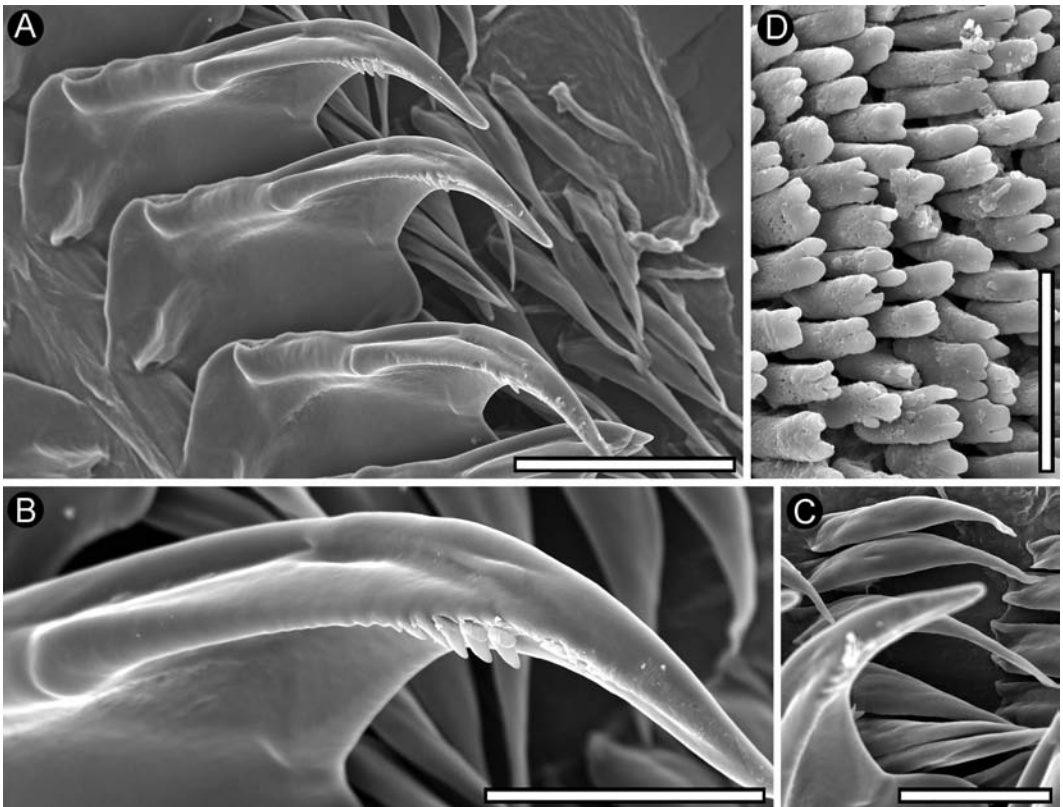


FIGURE 20. *Acanthodoris planca* CASIZ 171754. Radular morphology. A First lateral teeth. Scale = 100 µm. B. Close up of denticles. Scale = 50 µm. C. Outer lateral teeth. Scale = 50 µm. D. Jaw rodlets. Scale = 30 µm.

MacFarland, 1925. All three species are orange yellow or orange and have a large gill that extends the width of the body. All three species have rhinophores that are similar in color as the body. The dorsum of each of these species is densely covered with conical tubercles. *Acanthodoris planca* has ten branchial leaves and both Verrill (1879) and MacFarland (1925) reported nine for both *A. pilosa* and *A. lutea*. The foot color differs between the species. *Acanthodoris planca* has a white foot with tiny brownish-orange spots, while that of *A. lutea* is orange yellow. Verrill did not report the foot color for *A. citrina* but the foot color of *A. pilosa* (*Doris sparsa*) was reported by Alder and Hancock (1846) as colorless and by Bergh (1879) as whitish or yellowish.

The radular morphology differs between these species. *Acanthodoris planca* has densely arranged, multifid jaw rods, whereas *A. lutea* has triangular, hook-like structures. Verrill did not report the radular morphology of *A. citrina* but Thompson and Brown (1984) provided scanning electron micrographs of *A. pilosa*. *Acanthodoris planca* has 6–7 elongate, pointed outer lateral teeth, while *A. lutea* has 5–6 flattened, triangular plates “with a slight basal thickening” (MacFarland 1925). *Acanthodoris pilosa* has three outer lateral teeth that are flattened plates and a frail jaw cuticle with honeycombing (Thompson and Brown 1984).

There are reproductive differences as well. Both the penis and vaginal duct of *Acanthodoris planca* is shorter and thinner than found in either of the other two species. *Acanthodoris planca* has a much shorter deferent duct than found in either *A. lutea* or *A. pilosa*. The receptaculum seminis duct is much shorter in *A. planca* than that of *A. pilosa* but similar in length to that of *A. lutea*.

The combination of morphological characters identifies *Acanthodoris planca* as a previously undescribed species. The phylogenetic analysis performed for the present study shows *A. planca* to be closely related to *A. falklandica* and *A. nanega*.

OTHER SPECIES EXAMINED FOR THE PRESENT PHYLOGENETIC ANALYSIS

Genus *Adalaria* Bergh, 1878

TYPE SPECIES: *Adalaria loveni* (Alder and Hancock, 1854)

Doris loveni Alder and Hancock, 1862:262

REMARKS.— Millen (2005) revised this genus. The characters used in the phylogenetic analysis of the present study are taken from this publication and corroborated with our own examinations of specimens.

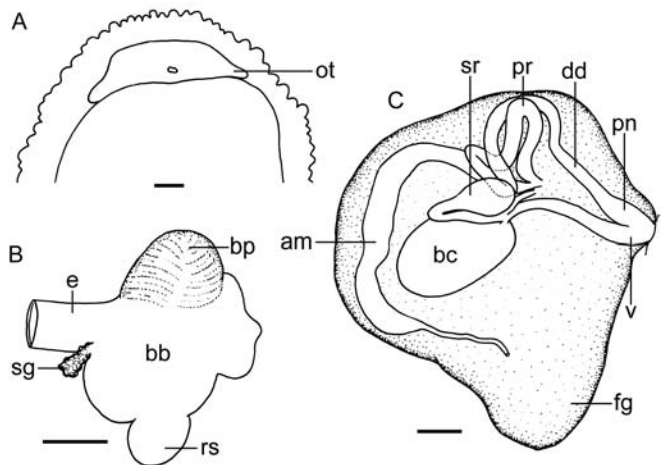


FIGURE 21. *Acanthodoris planca* CASIZ 171754. A. Anterior ventral surface. Scale bar = 1 mm. B. Buccal bulb. C. Reproductive morphology. Scale bars = 1 mm.

***Adalaria jannae* Millen, 1987**

Figs. 22–23.

Adalaria jannae Millen 1987:2696*Adalaria* sp. Behrens 1980:100; Behrens 1991:50*Onchidoris muricata* Roller and Long, 1969:427; McDonald, 1975:531; McDonald and Nybakken, 1978:111; Nybakken, 1978:135; McDonald and Nybakken, 1981:16*Onchidoris* sp. Roller and Long 1969:427; McDonald and Nybakken 1980:44; McDonald and Nybakken 1980:16; McDonald 1983:124, 128

Onchidorididae sp. B Lemche in Just and Edmunds 1985:76

MATERIAL EXAMINED.— CASIZ 142450 Whittier, Prince William Sound, Alaska. No depth data. 8 specimens, 4–6 mm, 1 mm and 5 mm, dissected. August 1999, J. Goddard. LACM 153983 Copper Cove, Vancouver Island, Canada. 1.5 m depth. 1 specimen, 6 mm. September 1985, S. Millen.

DISTRIBUTION.— North Atlantic (Britain to France, and north across Norway, west to Iceland, Greenland and south to Massachusetts) and North Pacific (Bering Sea Alaska, south to California). (Millen 1987, Rudman 2004 and present study).

EXTERNAL MORPHOLOGY.— Millen (1987) described the external morphology of this species. The specimens examined for the present study matched her description and thus there is no additional information to present. See Fig. 23A for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM. — *Adalaria jannae* shares the same general digestive anatomy as other Onchidorididae species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 23B). The radular sac protrudes from the bulb, under the esophagus. There is a large ovoid buccal bulb with a longitudinal crease as found in other Onchidorididae species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have blunt, deeply scalloped apices (Fig. 22A–C). The radular formula is 37x4.1.0.1.4 (CASIZ 142450) with all teeth as described by Millen. That is, there is no rachidian tooth and the large lateral teeth are similar in form while the 4 outer lateral teeth are elongate and multi-tipped. The large first tooth is beak-shaped with a flattened base and a pointed hook that has 17 pointed denticles on the inner border of the hook. The inner margin of each tooth has a large heel that blends into a wide shoulder. The shoulder is on top of the prominent inner edge from which the denticles protrude.

REPRODUCTIVE SYSTEM.— The ampulla is an elongate tube (Fig. 23C). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The oviduct enters the large female gland mass. The prostate is a curved, thickened tube. It does not narrow into the deferent duct, which is straight and widens into the penis. The penis is short and terminates into the common genital atrium. The penis does not contain penial hooks. The vaginal duct is very short. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina widens enormously from the vaginal duct as it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large round bursa copulatrix. From the bursa the oviduct connects to the slightly smaller ovoid seminal receptacle. The uterine duct is very short and connects at the point where the receptaculum joins the vaginal duct.

CENTRAL NERVOUS SYSTEM.— Millen described the central nervous system of this species as similar to other Onchidorididae.

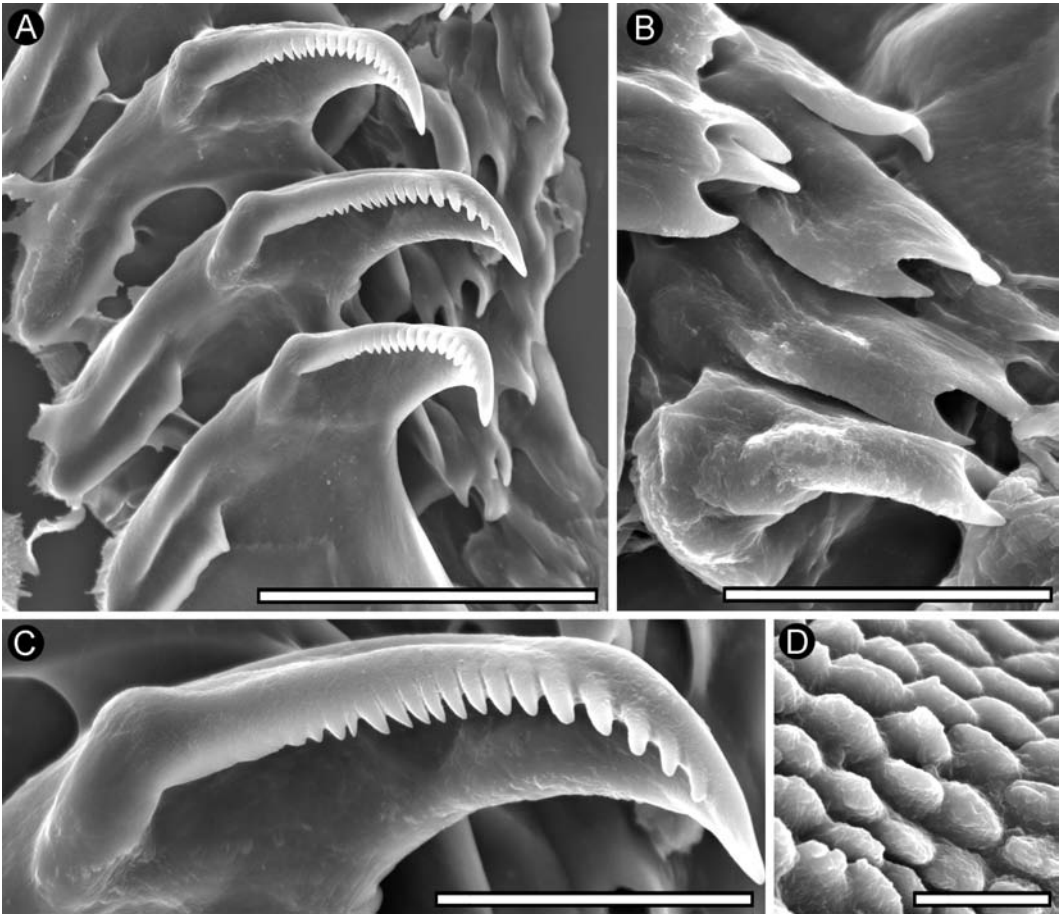


FIGURE 22. *Adalaria jannae* CASIZ 142450. Radular morphology. A First lateral teeth. Scale = 50 µm. B. Close up of outer lateral teeth. Scale = 20 µm. C. Close up of denticles. Scale = 20 µm. D. Jaw rodlets. Scale = 10 µm.

REMARKS.— Millen (1987) thoroughly described and illustrated the reproductive and radular morphology of this species. Our examination of specimens from Alaska concurs with these findings. The only difference we noted in our specimens is that the ampulla is longer than the illustration by Millen of specimens from British Columbia, Canada.

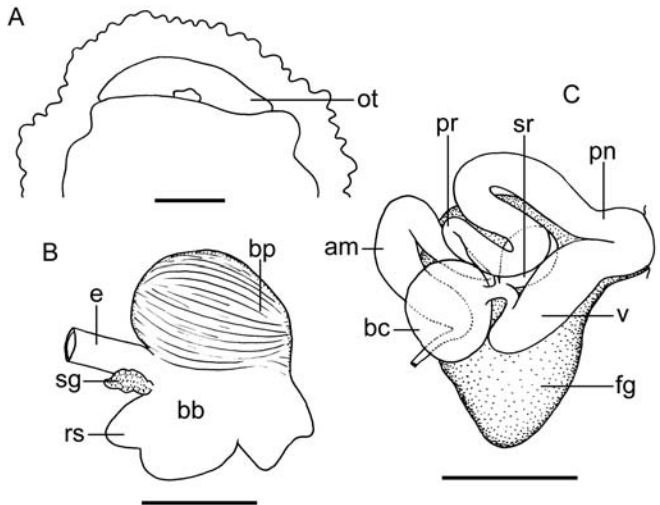


FIGURE 23 (right). *Adalaria jannae* CASIZ 142450. A. Anterior ventral surface. Scale bar = 1 mm. B. Buccal bulb. Scale bar = 0.5 mm. C. Reproductive morphology. Scale bar = 1 mm.

Morphological characters for the present analyses are taken from the literature and corroborated by our own examinations.

***Adalaria proxima* (Alder and Hancock, 1854)**

Figs. 24–25.

Doris proxima Alder and Hancock, 1854:103.

Adalaria albopapillosa Dall, 1871:137.

Adalaria pacifica Bergh, 1880:227.

Adalaria virescens Bergh, 1880:83.

MATERIAL EXAMINED.— CASIZ 087252 Isles of Shoals, York County, Maine. No depth data. 27 specimens, 4–6 mm, 5 mm, dissected. January 1979, T. Gosliner. CASIZ 087250 Rye Harbor, Rockingham County, New Hampshire. No depth data. 1 specimen, dissected. May 1978, T. Gosliner, E. Marcus and A. Kuzirian. CASIZ 070645 Otter Bay, Johnstone Strait, British Columbia. 13–20 m depth. 4 specimens, 12–15 mm, 15 mm, dissected. August 1976, P. Lambert. USNM 804963 Bay of Fundy, Canada. No depth data. 1 specimen, 10 mm. 1872. LACM 153982 Bamfield, Vancouver Island, Canada. 6 m depth. 1 specimen, 11 mm. September 1970, S. Millen.

DISTRIBUTION.— North Atlantic (Britain to France, and north across Norway, west to Iceland, Greenland and south to Connecticut) and North Pacific (Bering Sea Alaska, south to California). (Millen 1987, Rudman 2004 and present study).

EXTERNAL MORPHOLOGY.— Bergh (1880), Alder and Hancock (1854), Thompson (1984) and Millen (1987) described the external morphology of this species. The specimens examined for the present study matched these descriptions and thus there is no additional information to present. See Fig. 25A for a drawing of the ventral anterior surface of a specimen from Maine.

DIGESTIVE SYSTEM. — *Adalaria proxima* shares the same general digestive anatomy as other Onchidorididae species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 25D). The radular sac protrudes from the bulb, under the esophagus. There is a large ovoid buccal bulb with a longitudinal crease as found in other Onchidorididae species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods are very small, blunt and have rounded tops (Fig. 24C). The radular formula is 43x.9.1.1.1.9 (CASIZ 087252) with all teeth as described by Bergh and Thompson. That is, there is a distinct rachidian tooth and the large lateral teeth are similar in form while the 9 outer lateral teeth have hooked tips (Figs. 24A and B). The large first tooth has a wide base and a long, pointed hook. The inner margin of each tooth is flattened. A thickened ridge extends from the flat inner margin into the pointed tip of the tooth. There are no denticles on the inner border of the hook. The outer edge of the tooth is thick and rounded.

REPRODUCTIVE SYSTEM.— The ampulla is sausage shaped (Fig. 25B and C). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The oviduct enters the large female gland mass. The prostate is a thick, coiled tube. It does not narrow into the deferent duct, which coils once before curving into the penis. The penis is long and as wide as the deferent duct and it terminates into the common genital atrium. The penis contains minute, closely set penial hooks throughout the length of the penis? The vaginal duct is short. At the distal end, the vagina widens enormously from the vaginal duct as it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the small ovoid bursa copula-

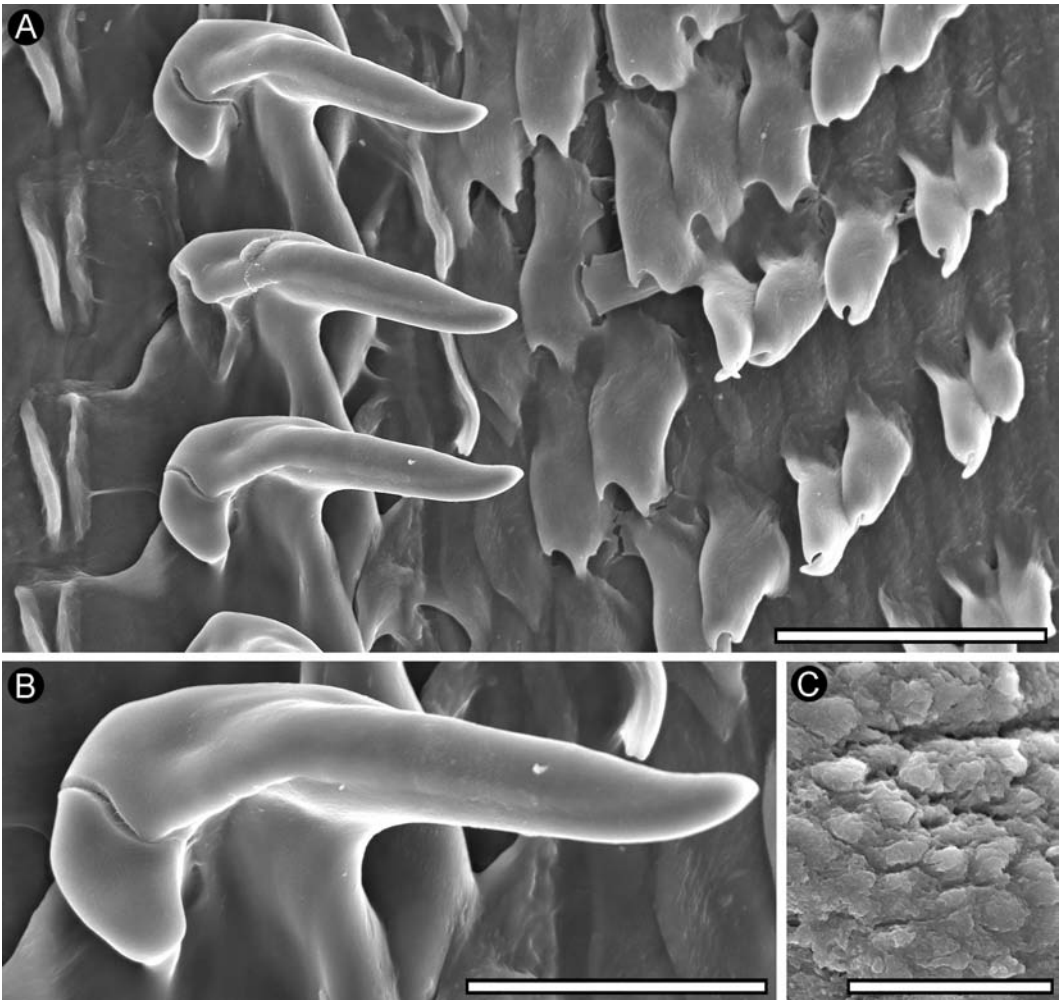


FIGURE 24. *Adalaria proxima* CASIZ 087252. Radular morphology. A. First and outer lateral teeth. Scale = 50 μ m. B. Close up of first lateral tooth. Scale = 30 μ m. C. Jaw rodlets. Scale = 20 μ m.

trix. The tiny seminal receptacle is sessile on the vaginal duct. The uterine duct is very short and connects at the vaginal duct.

REMARKS.— Bergh (1880), Thompson (1958) and Millen (1987) described and/or illustrated the reproductive and radular morphology of this species. Our examination of specimens from the east and west coasts of North America concur with these findings. The only difference we noted in our specimens is that the vaginal duct is longer than those illustrated by Millen from Great Britain and Canada. Morphological characters for the present analyses are taken from the literature and corroborated by our own examinations.

Genus *Calycidoris* Abraham, 1876

TYPE SPECIES: *Calycidoris guentheri* Abraham, 1876

DIAGNOSIS.— Abraham (1876) provided the following diagnosis for the genus: Body

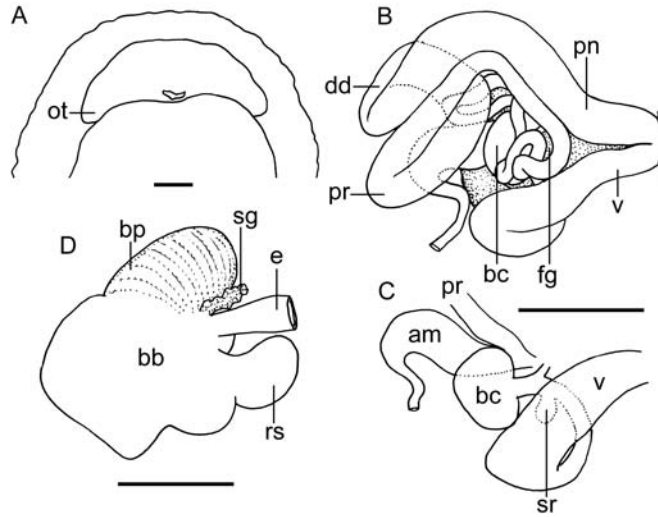


FIGURE 25. *Adalaria proxima* CASIZ 087252. A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Scale bars = 1 mm.

depressed, mantle ample extending over the head and the foot, and bearing soft conical papillae. Dorsal tentacles short and laminated, and retractile within sheathless cavities. Branchia simply laminate, forming a cup around the anus, together contained in a common mantle cavity, wall being not completely contractile over them. Oral tentacles represented by a fleshy, laterally extended veil. Odontophore narrow, bearing two bicuspid spines in each row, no central spine, spinous collar or under jaw.

The present study confirms this diagnosis.

Calycidoris guentheri Abraham, 1876a:133

Figs. 26–27.

Doris sibirica Aurivillius, 1887:372.

MATERIAL EXAMINED.— CASIZ 086915 Wainwright, Alaska. 10 m depth. 1 specimen, 25 mm dissected. September 1973, unknown collector. CASIZ 086920 Arctic Ocean. 48 m depth. 1 specimen, 14 mm. August 1977, K. Frost.

DISTRIBUTION.— Alaska, Arctic Ocean (Roginskaya 1972 and present study).

EXTERNAL MORPHOLOGY.— Abraham (1876) and Roginskaya (1972) described the external morphology of this species. The specimens examined for the present study match their descriptions and thus there is no additional information to present. See Fig. 27E for a drawing of the ventral anterior surface of a specimen from Alaska.

DIGESTIVE SYSTEM.— *Calycidoris guentheri* shares the same general digestive anatomy as other Onchidorididae species (Fig. 27A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two long salivary glands at the side of the oral tube, near the radular sac (Fig. 27D). The radular sac protrudes as an oval from the bulb, under the esophagus. There is a large ovoid buccal pump with a longitudinal crease as found in other Onchidorididae species. The labial disk frames the triangular opening to the buccal

bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods are elongate and have mostly blunt tips (Fig. 26D). The radular formula (CASIZ 086915) is 29x.3.1.0.1.3 with all teeth as described by Roginskaya (1972). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the 3 outer lateral teeth are flattened plates (Figs. 26A–C). The large first tooth has a wide base and a long, pointed hook that has no denticles on the inner border of the hook. The inner margin of each tooth does not have a flattened heel as found in *Acanthodoris*. There is a ridge that extends along the hooked portion of the tooth. The outer edge of the tooth is long and extends much longer than the inner edge.

REPRODUCTIVE SYSTEM.— The ampulla is an elongate tube (Fig. 27C). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The oviduct enters the large female gland mass. The prostate is a curved, thickened tube. It does not narrow into the deferent duct, which is straight and widens into the penis. The penis is very wide and terminates into the common genital atrium. The penis does not contain penial hooks. The vaginal duct is very short. At the distal end, the vagina widens only slightly from the vaginal duct as it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large round bursa copulatrix. From the bursa the thick and very elongate oviduct connects to the small round seminal receptacle. The uterine duct is long and connects at the base of the bursa.

CENTRAL NERVOUS SYSTEM.— As with other species of Onchidorididae, the cerebral and pleural ganglia are fused together (Fig. 27B). The two pedal ganglia are located below the cerebro-pleu-

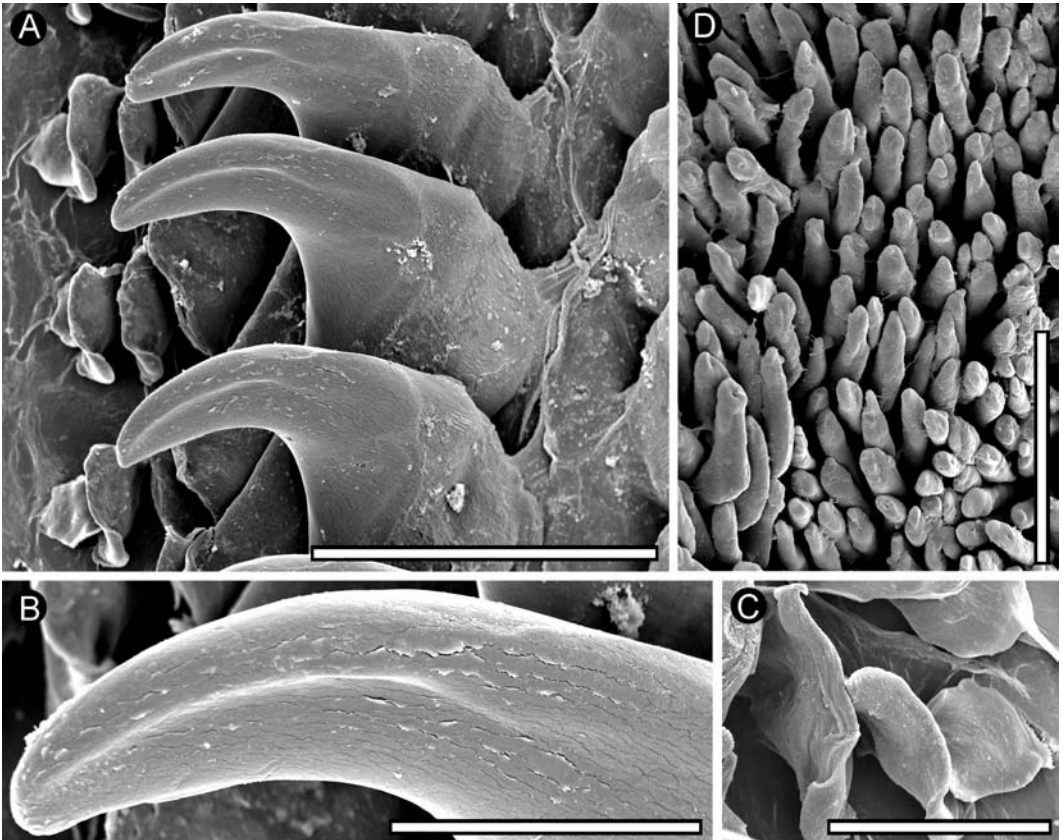


FIGURE 26. *Calycidoris guentheri* CASIZ 086915. Radular morphology. A First lateral teeth. Scale = 300 μ m. B. Close up of first lateral tooth. Scale = 100 μ m. C. Close up of outer lateral teeth. Scale = 100 μ m. D. Jaw rodlets. Scale = 50 μ m.

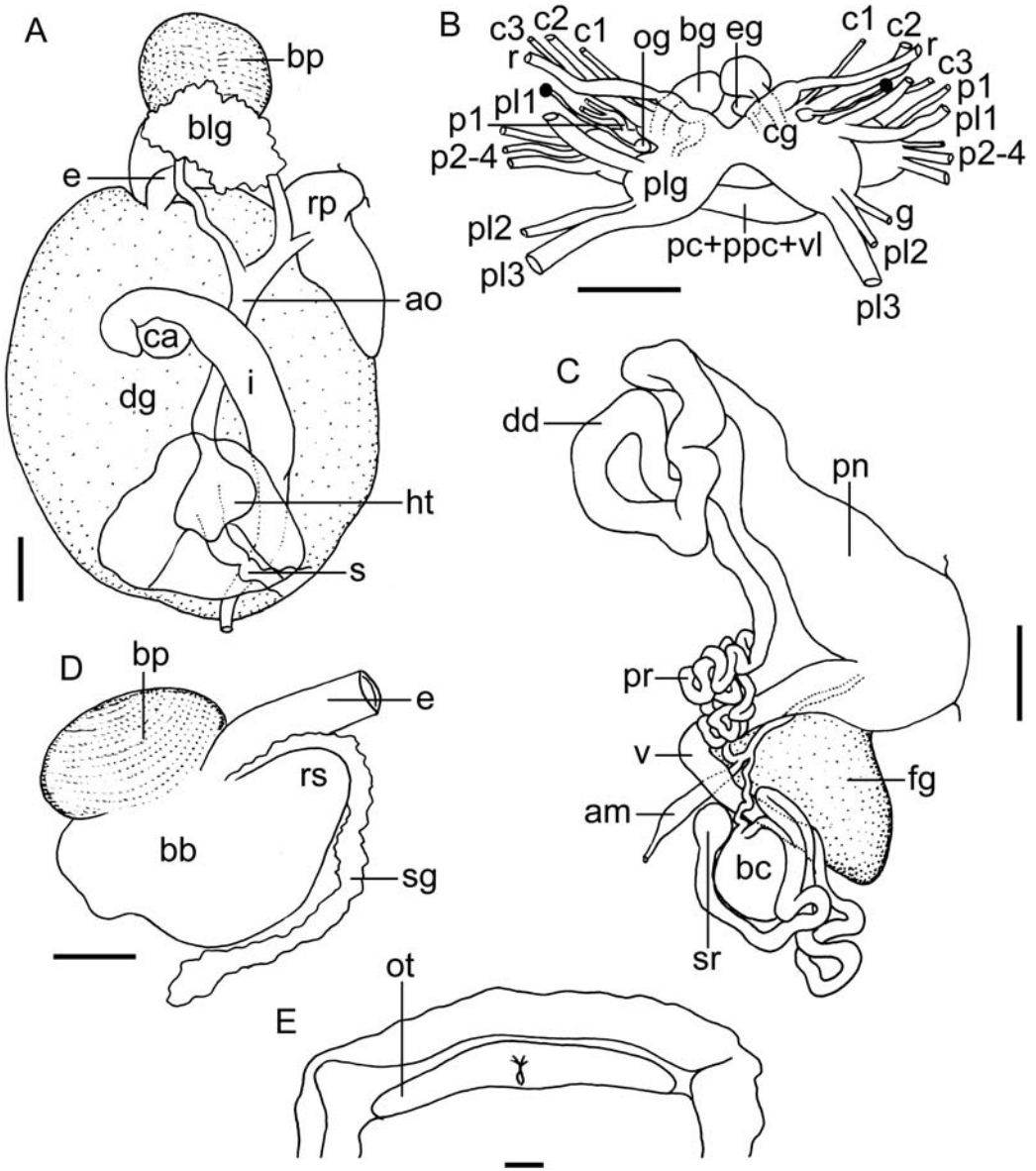


FIGURE 27. *Calycidoris guentheri* CASIZ 086915. A. Digestive system. B. Central nervous system. C. Reproductive morphology. D. Buccal bulb. E. Anterior ventral surface. Scale bars = 1 mm.

ral complex and are joined by an elongate commissure. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. The eyes are sessile at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and two large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

REMARKS.— Phylogenetic characters for the present analyses are taken from the material examined herein, from Millen and Martynov (Millen and Martynov 2005) and from Fahey and Gosliner (2004).

Genus *Diaphorodoris* Iredale and O'Donoghue, 1923

TYPE SPECIES: *Diaphorodoris luteocincta* (Sars, 1870)

DIAGNOSIS.— Iredale and O'Donoghue (1923) did not provide a diagnosis for the genus when they established this name in the List of British Nudibranchiate Molluscs. However, Pruvot-Fol (1954) gave a brief comparison of *Diaphorodoris* with *Lamellidoris*. She stated that *Diaphorodoris* differs from *Lamellidoris* in the body form, which is higher and narrower than the former. The oral tentacles are not flattened but are two rounded bumps above the mouth. The tubercles of *Diaphorodoris* are fewer, long, conical and pointed.

Diagnosis based on characters examined for the present phylogenetic analysis: Narrow radula with no rachidian tooth; first lateral tooth large and hooked with multiple pointed denticles; labial disk with thickened cuticle; one outer lateral tooth hooked; jaw rodlets pointed, single apex; triaulic reproductive system.

***Diaphorodoris luteocincta* (Sars, 1870)**

Figs. 28–29.

Doris luteocincta Sars 1870:191.

Doris beaumonti Farran 1903:126.

Diaphorodoris luteocincta var. *alba* Portmann and Sandmeier 1960a:182.

Diaphorodoris luteocincta var. *reticulata* Portmann and Sandmeier 1960a:181.

MATERIAL EXAMINED.— CASIZ 087443 Horta Harbor, Azores, Atlantic Ocean. 5–7 m depth. 7 specimens, 5–8 mm, 1, 7 mm dissected. November 1992, P. Wirtz. CASIZ 072580 Ilha San Miguel, Azores, Atlantic Ocean. 20 m depth. 6 specimens, 5–10 mm. 1988, T. Gosliner.

DISTRIBUTION.— Mediterranean, north and eastern Atlantic (Sars 1870, Eliot 1910; Portmann 1960; Schmekel and Portmann 1982; and present study).

EXTERNAL MORPHOLOGY.— Portmann and Sandmeier (1960), Schmekel and Portmann (1982) and Pruvot-Fol (1954) all described the external morphology of this species. The specimens examined for the present study matched these descriptions and thus there is no additional information to present. See Fig. 29E for a drawing of the ventral anterior surface of a specimen from the Atlantic Ocean.

DIGESTIVE SYSTEM. — *Diaphorodoris luteocincta* shares the same general digestive anatomy as other *Diaphorodoris* species (Fig. 29A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two very small glands at the side of the oral tube, near the radular sac (Fig. 29C). The trapezoidal radular sac protrudes from the bulb, under the esophagus. There is a very large buccal pump with a longitudinal crease as found in other *Diaphorodoris* species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have multi-tipped apices that are blunt (Fig. 28B). The radular formula (CASIZ 087443) is 28x1.1.0.1.1, with all teeth as described by the authors noted above. That is, there is no rachidian tooth and the large first lateral teeth are similar in form while the outer lateral tooth is a small plate with a blunt hook (Figs. 28A and C). The large first tooth is beak-shaped with a long pointed hook that has 13–16 pointed denticles on the inner border of the hook. There

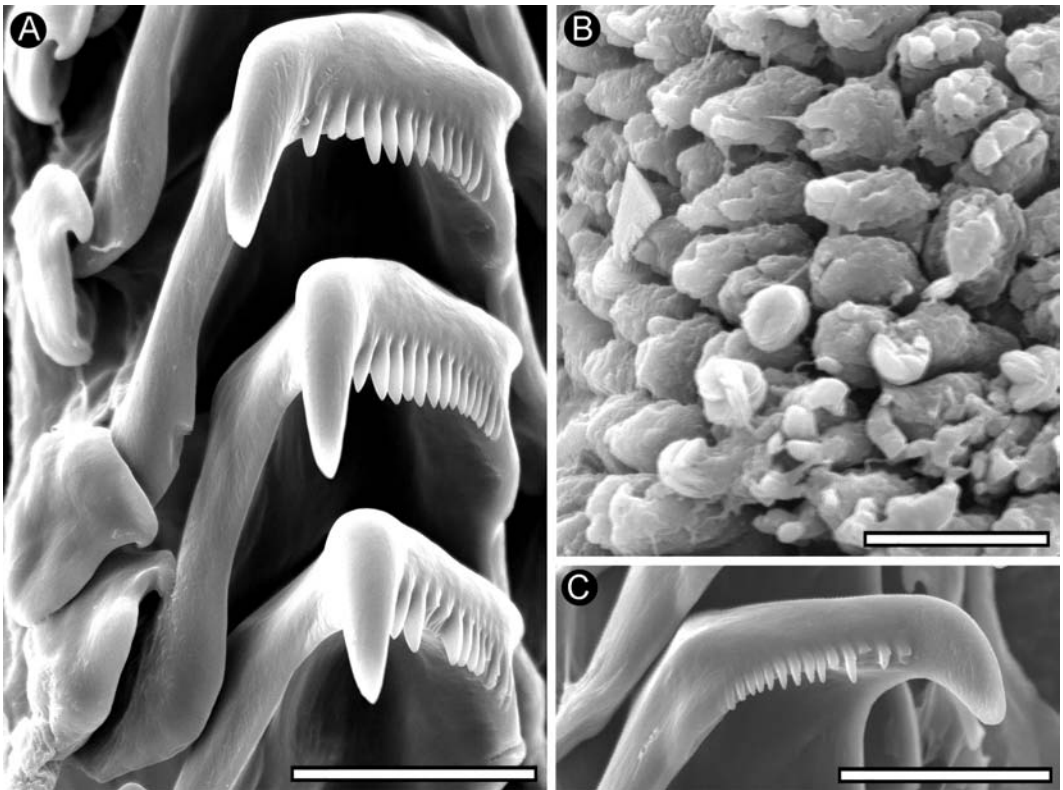


FIGURE 28. *Diaphorodoris luteocinta* CASIZ 087443. Radular morphology. A First lateral teeth. Scale = 20 μm . B. Jaw rodlets. Scale = 10 μm . C. Close up of denticles. Scale = 25 μm .

is no large, thickened heel or shoulder as found in species of *Diaphorodoris*. The denticles protrude from the edge of the tooth.

REPRODUCTIVE SYSTEM.— The ampulla is elongate and tubular (Fig. 29D). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is a thick elongate tube. It doesn't narrow appreciably into the long deferent duct, which curves and twists before widening into the penis. The penis is short and bulbous and terminates into the common genital atrium. We did not observe penial hooks in the penis. The vaginal duct is elongate and as wide as the deferent duct. At the distal end, the vagina does not widen from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large rounded bursa copulatrix. From the bursa the oviduct connects to the slightly smaller ovoid seminal receptacle. The long uterine duct connects at the point where the seminal receptacle joins the bursa.

CENTRAL NERVOUS SYSTEM.— As with other species of Onchidorididae, the cerebral and pleural ganglia are fused together (Fig. 29B). The two pedal ganglia are located below the cerebro-pleural complex and are joined by an elongate commissure. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. The eyes are sessile at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and two large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion

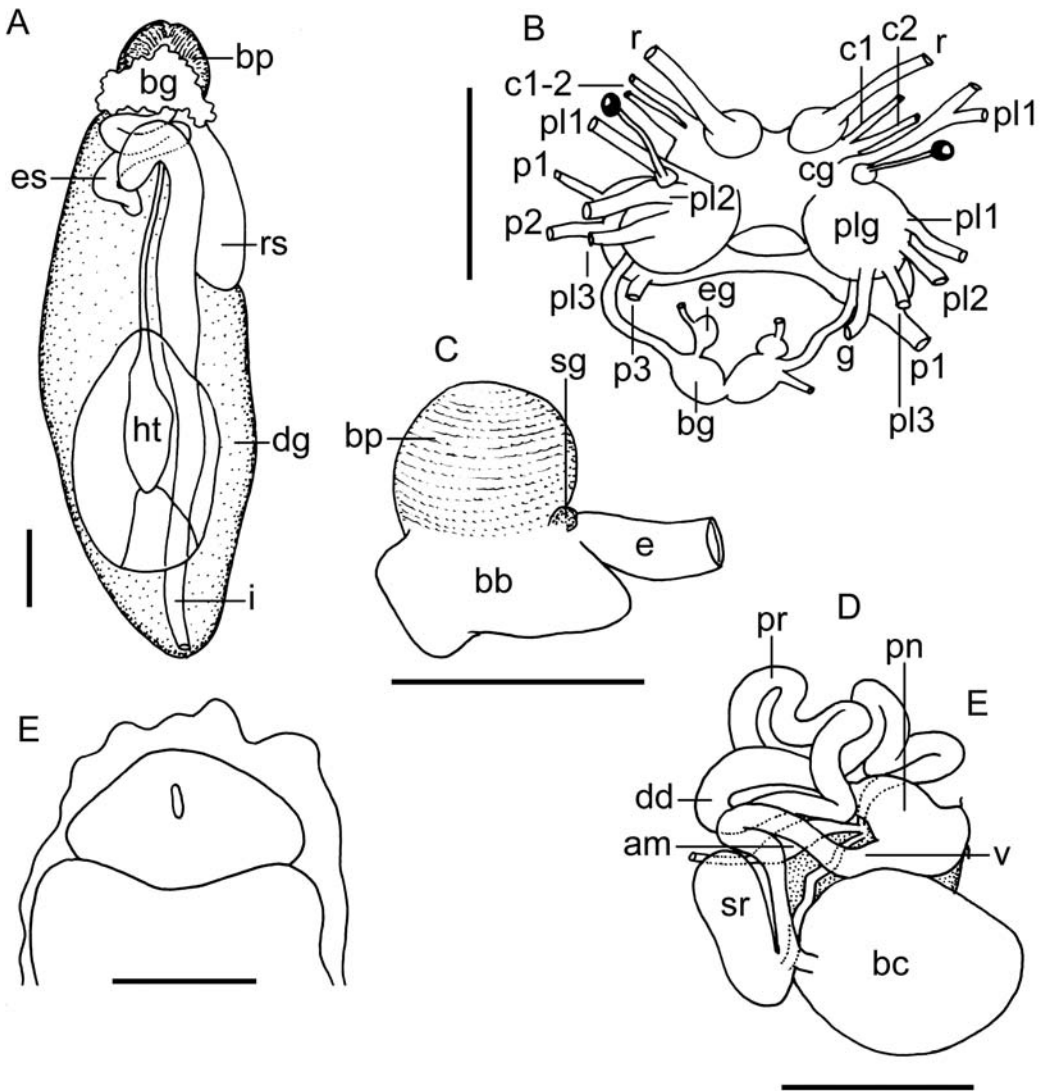


FIGURE 29. *Diaphorodoris luteocinta* CASIZ 087443. A. Digestive system. B. Cerebro-pleural ganglia. C. Buccal bulb. D. Reproductive morphology. E. Anterior ventral surface. Scale bars = 1 mm.

on the right side of the visceral loop. Gastro-esophageal, rhynchophoral and optical ganglia are present.

REMARKS.— Millen (1985) and Millen and Martynov (2005) described and presented morphological characters for phylogenetic analyses of this species. Characters for the present analyses are taken from these publications, from Fahey and Gosliner (2004) and from our dissections of specimens from the Azores.

***Diaphorodoris lirulatocauda* Millen, 1985**

Figs. 30–31.

Diaphorodoris lirulatocauda Millen, 1985:84.

MATERIAL EXAMINED.— CASIZ 076203 Monterey Bay, Monterey California. No depth data. 2 specimens, 3 mm, 6 mm dissected. August 1978, T. Gosliner. LACM 153984 Cutter Rock, Ketchikan, Alaska, 1 specimen, 3 mm, dissected. No depth data. June 1987, S. Millen.

DISTRIBUTION.— West coast of North America from British Columbia to California (Millen 1985) and present study).

EXTERNAL MORPHOLOGY.— Millen (1985) thoroughly described the external and internal morphology of this species. The specimens examined for the present study matched her description and thus there is no additional external information to present. See Fig. 31A for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM.— *Diaphorodoris lirulatocauda* shares the same general digestive anatomy as other *Diaphorodoris* species (see description in Millen 1985). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small salivary glands at the side of the oral tube, near the radular sac (Fig. 31C). The radular sac protrudes from the bulb, under the esophagus. There is a large buccal pump with a longitudinal crease as found in other *Diaphorodoris* species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have blunt, scalloped apices, some which look like open flowers (Fig. 30B). The radular formula (CASIZ 076203) is 20x1.1.0.1.1, with all teeth as described by Millen (1985). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the outer lateral teeth are small plates with a curved pointed hook at the tip (Figs. 30A and C). The large first tooth is beak-shaped with a pointed hook that has 13–16 pointed denticles on the inner border of the hook. There is no large, thickened heel or shoulder as found in species of *Acanthodoris*. The denticles protrude from the edge of the tooth.

REPRODUCTIVE SYSTEM.— The ampulla is a thick sausage shape (Fig. 31B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is a thin elongate tube. It does not narrow into the long deferent duct, which curves back on itself before widening into the penis. The penis is elongate and wide and terminates into the common genital atrium. Penial hooks were not observed. The vaginal duct is relatively short and wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina does not widen from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the round bursa copulatrix. From the bursa the short oviduct connects to the slightly smaller ovoid seminal receptacle. The uterine duct could not be seen.

REMARKS.— Our examination of specimens from California and Alaska match the description presented by Millen, except that we did not observe penial hooks. Characters for the present phylogenetic analyses are taken from specimens examined herein and from Millen (1985).

Diaphorodoris mitsuui (Baba, 1938)

Figs. 32–33.

Lamellidoridella mitsuui Baba, 1938:130.

Diaphorodoris sp. Gosliner, 1987b:92.

MATERIAL EXAMINED.— CASIZ 069759 Barracuda Point, East side Pig Island [Tab Island], Madang, Papua New Guinea. 6 m depth. 1 specimen 5 mm, dissected. August 1989, T. Gosliner.

DISTRIBUTION.— Japan (Baba 1938; Baba 1949) and Papua New Guinea (present study).

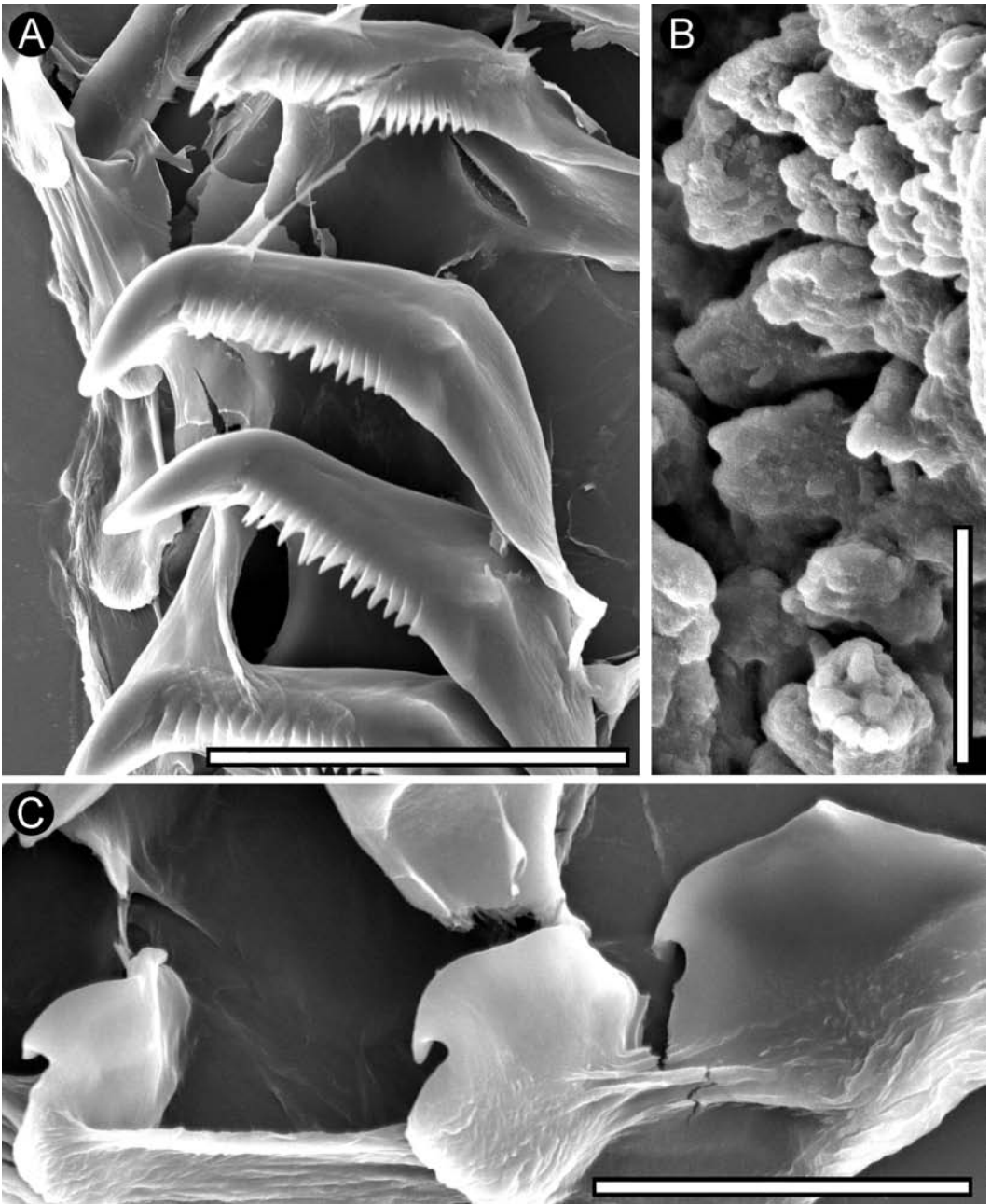


FIGURE 30. *Diaphorodoris lirulatocauda* CASIZ 076203. Radular morphology. A First lateral teeth. Scale = 50 μm . B. Jaw rodlets. Scale = 10 μm . C. Close up of outer lateral teeth. Scale = 20 μm .

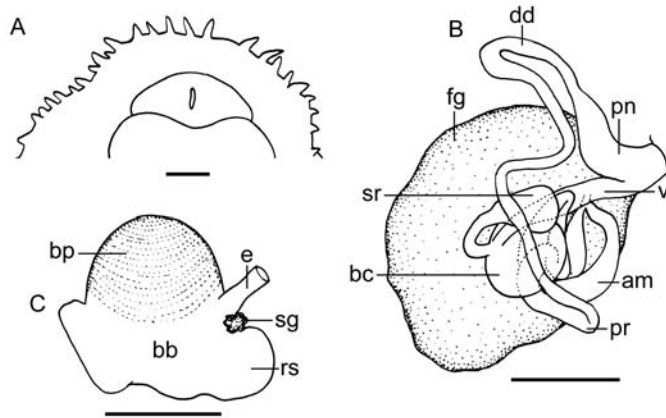


FIGURE 31. *Diaphorodoris lirulatocauda* CASIZ 076203. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Scale bars = 0.5 mm.

EXTERNAL MORPHOLOGY.— Baba (1938) and Millen (1985) described the external morphology of this species. The specimens examined for the present study matched these descriptions and thus there is no additional information to present. See Fig. 33A for a drawing of the ventral anterior surface of a specimen from Papua New Guinea.

DIGESTIVE SYSTEM.— *Diaphorodoris mitsuui* shares the same general digestive anatomy as other *Diaphorodoris* species (Fig. 29A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 33C). The radular sac protrudes slightly from the bulb, under the esophagus. There is a large buccal pump with a longitudinal crease as found in other *Diaphorodoris* species. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods are pointed with a single apex (Fig. 32C). The radular formula (CASIZ 069759) is 20x1.1.0.1.1 with all teeth as described by Baba (1938). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the outer lateral tooth is a small plate with a pointed hook at the tip (Figs. 32A and B). The large first tooth is beak-shaped with a pointed hook that has 13–16 pointed denticles on the inner border of the hook. There is no large, thickened heel or shoulder as found in other species of Onchidorididae. The denticles protrude from the edge of the tooth.

REPRODUCTIVE SYSTEM.— The ampulla is sausage-shaped (Fig. 33B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is a short tube. It doesn't narrow appreciably into the short deferent duct, which widens into the penis. The penis is short and wide and terminates into the common genital atrium. The penis contains minute, closely set penial hooks throughout the length of the penis? The vaginal duct is short and the same width as the deferent duct. At the distal end, the vagina does not widen from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large round bursa copulatrix. From the bursa the oviduct connects to the ovoid seminal receptacle that is the same size as the bursa. The uterine duct connects at the base of the bursa.

REMARKS.— Baba (1938) and Millen (1985) described the external morphology of this species. Baba provided a discussion of the radular morphology. Characters for the present analyses are taken from this literature and from our dissections of specimens from New Guinea.

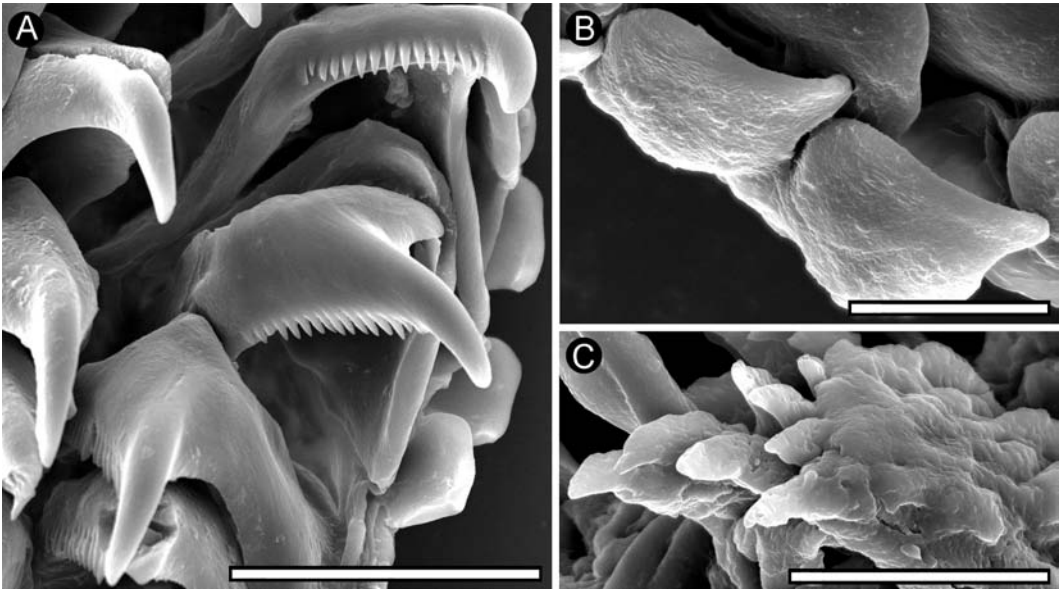


FIGURE 32. *Diaphorodoris mitsuui* CASIZ 069759. Radular morphology. A First lateral teeth. Scale = 30 µm. B. Jaw rodlets. Scale = 10 µm. C. Close up of denticles. Scale = 20 µm.

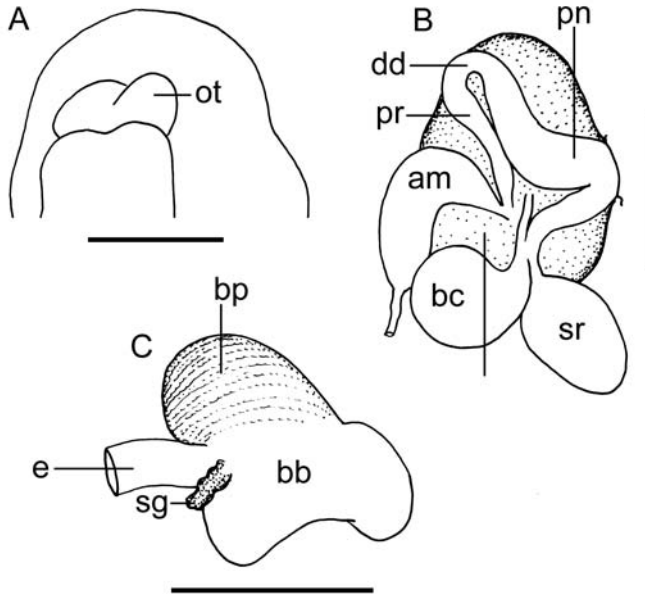


FIGURE 33. *Diaphorodoris mitsuui* CASIZ 069759. A. Anterior ventral surface. Scale bar = 1 mm. B. Reproductive morphology. Scale bar = 0.5 mm. C. Buccal bulb. Scale bar = 0.5 mm.

***Diaphorodoris papillata* Portmann and Sandmeier, 1960**

Figs. 34–35.

Diaphorodoris papillata Portmann and Sandmeier, 1960:182

MATERIAL EXAMINED.— CASIZ 099115 Isla Tarifa, Strait of Gibraltar, Cadiz, Spain. 30 m depth. 2 specimens, 5 mm, 8 mm dissected. September 1994, T. Gosliner.

DISTRIBUTION.— Western Mediterranean (Schmekel and Portmann, 1982 and present study).

EXTERNAL MORPHOLOGY.— Several authors described the external morphology of this species (Portmann and Sandmeier 1960; Schmekel and Portmann 1982). The specimens examined for the present study matched these descriptions and thus there is no additional information to present. See Fig. 35A for a drawing of the ventral anterior surface of a specimen from Spain.

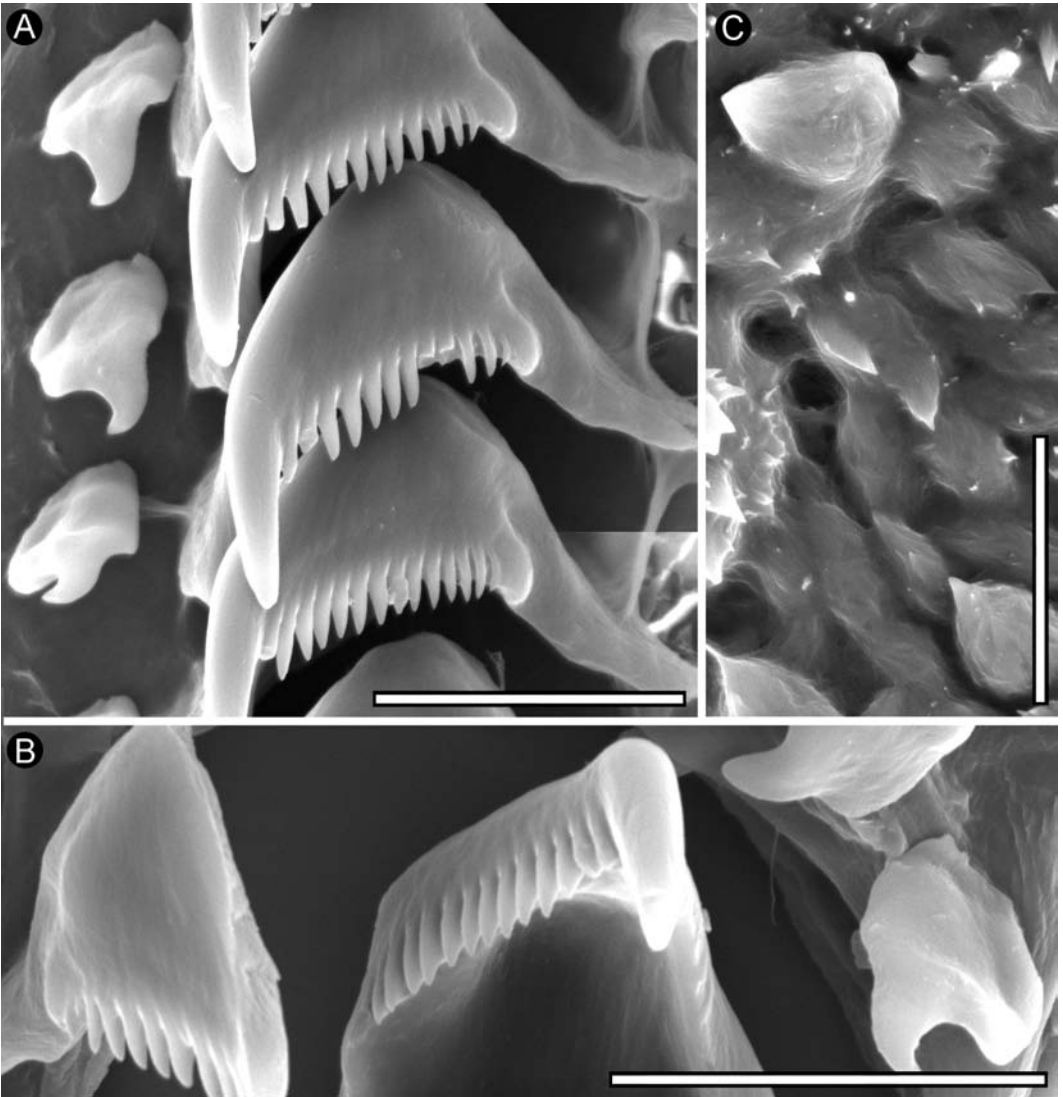


FIGURE 34. *Diaphorodoris papillata* CASIZ 099115. Radular morphology. A First lateral teeth. Scale = 20 μ m. B. Close up of denticles. Scale = 20 μ m. C. Jaw rodlets. Scale = 10 μ m.

DIGESTIVE SYSTEM.— *Diaphorodoris papillata* shares the same general digestive anatomy as other *Diaphorodoris* species (Fig. 29A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is almost elongate, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 35B). The radular sac barely protrudes from the bulb, under the esophagus. There is a large protruding buccal pump with a longitudinal crease as found in other *Diaphorodoris* species. The crop is the largest component of the buccal bulb. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods have pointed apices, some which look like spiked stars (Fig. 34C). The radular formula is 26.1.0.1 (CASIZ 099115), with all teeth as described by Schmekel and Portmann (1982). That is, there is no rachidian tooth and the large lateral teeth are similar in form while the outer lateral tooth is a small plate with a tiny pointed hook at the tip (Figs. 34A and B). The large first tooth is a concave hook with a pointed hook that has a row 14–16 elongate denticles on the inner border of the hook. There is no large, thickened heel or shoulder as found in species of *Acanthodoris*. The denticles protrude from the edge of the tooth.

REPRODUCTIVE SYSTEM.— The ampulla is sausage shaped (Fig. 35C). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is a thin elongate tube. It does not narrow appreciably into the short deferent duct, which curves back on itself before widening into the penis. The penis is a wide, elongate tube and terminates into the common genital atrium. There were no penial hooks observed. The vaginal duct is relatively short and wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina does not widen from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the large ovoid bursa copulatrix. From the bursa the long oviduct connects to the much smaller ovoid seminal receptacle. The long uterine duct connects at the base of the bursa.

REMARKS.— Portmann and Sandmeier (1960) and Schmekel and Portmann (1982) illustrated the radular and reproductive morphology of this species. Our dissections corroborated their findings. Characters for the present analyses are taken from the literature and from our own examination of this species.

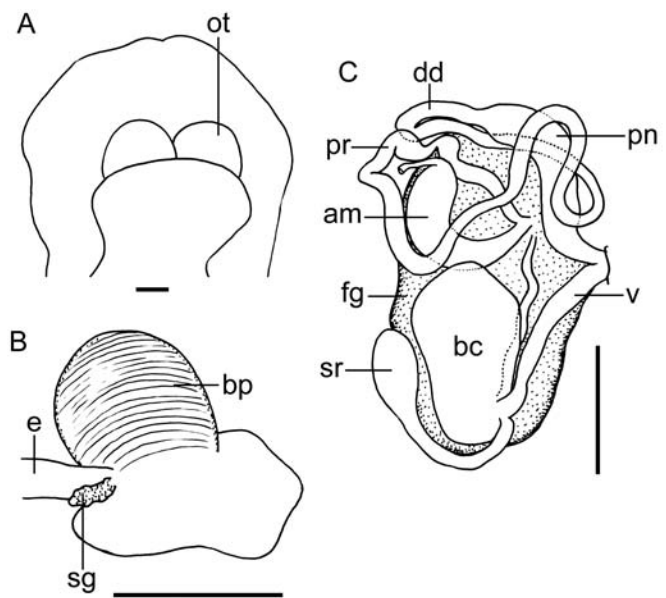


FIGURE 35. *Diaphorodoris papillata* CASIZ 099115. A. Anterior ventral surface. Scale bar = 1 mm. B. Reproductive morphology. Scale bar = 0.5 mm. C. Buccal bulb. Scale bar = 0.5 mm.

Genus *Onchidoris* Blainville, 1816TYPE SPECIES: *Onchidoris bilamellata* (Linnaeus, 1767)

Non *Onchidoris* (sic *Onchidorus*) de Blainville, 1816:96.

Onchidorus, *Onchidora* Cuvier, 1830:52.

Villiersia d'Orbigny, 1837:XI.

Oncidiodoris, *Oncodoris* Agassiz, 1846:417.

Oicodespina (*Okiodespina*) Gistel, 1848:399.

Proctaporis Mörch, 1857:6.

Proctaporis fusca (Fabricius, 1780) Mörch = *Doris pallida*.

Onchidora Desmarest, 1858:142.

Onchidorus Ferussac, 1882:XXVIII.

Ancylodoris Dybowski, 1900:143.

Atalodoris Iredale and O'Donoghue, 1923:221.

DIAGNOSIS.— Schmekel and Portmann (1982) provided a diagnosis for this genus. In summary, the body is oval and more broad than high. The notum is spiculose with dorsal papillae and without labial tentacles. The rhinophores are retractable into low sheaths. The gill is not retractable and is arranged in a circle around the anus. The radula is with or without a central tooth, with 2–3 lateral teeth. The jaw consists of a cuticle with weak jaw elements.

***Onchidoris bilamellata* (Linnaeus, 1767)**

Figs. 36–37.

Doris bilamellata Linnaeus, 1767:1083.

Doris fusca Müller, 1776:229.

Doris elfortiana de Blainville, 1816:95.

Onchidoris leachii de Blainville, 1816:450.

Doris liturata Möller, 1842:5.

Doris liturata Beck, 1842:78.

Lamellidoris bilamellata praecedentis Mörch, 1868:204.

Lamellidoris n. sp. vel. var. *praecedentis* Mörch, 1868:204.

Lamellidoris bilamellata var. *liturata* Bergh, 1878b:609

Lamellidoris bilamellata Eliot, 1910:156.

Lamellidoris bilamellata var. *pacifica* Bergh, 1905:101.

MATERIAL EXAMINED.— CASIZ 068343 Prince William Sound, Alaska. No depth data. 3 specimens, 18–20 mm, 1, 18 mm dissected. August 1965, S. Haven. CASIZ 081942 Woods Hole, Massachusetts. No depth data. 2 specimens, 10–12 mm. September 1906, F. MacFarland. CASIZ 068344 Charleston Yacht Harbor, Coos County, Oregon. No depth data. 3 specimens, 27–30 mm. February 1963, L. Andrews. CASIZ 060106 Sonoma County Coast, California. 50–115 fathoms. 1 specimen, 20 mm. February 1950, L. Miles. LACM 86-180 St. Andrews Bay, Fife, Scotland. Intertidal. 7 specimens, 7–12 mm. September 1986, J. McLean. USNM 574284 (*Onchidoris liturata*) Station 1182, Greenland. No depth data. 1 specimen, 14 mm. No collection date. J. Blake.

DISTRIBUTION.— North Atlantic (Britain to France, and north across Norway, west to Iceland, Greenland and south to Connecticut) and North Pacific (Bering Sea Alaska, south to California).

EXTERNAL MORPHOLOGY.— The external morphology of this species has been described by several authors (Bergh 1878; Eliot 1910). The specimens examined for the present study matched these descriptions and thus there is no additional information to present. See Fig. 37E for a drawing of the ventral anterior surface of a specimen from Alaska.

DIGESTIVE SYSTEM.— *Onchidoris bilamellata* shares the same general digestive anatomy as

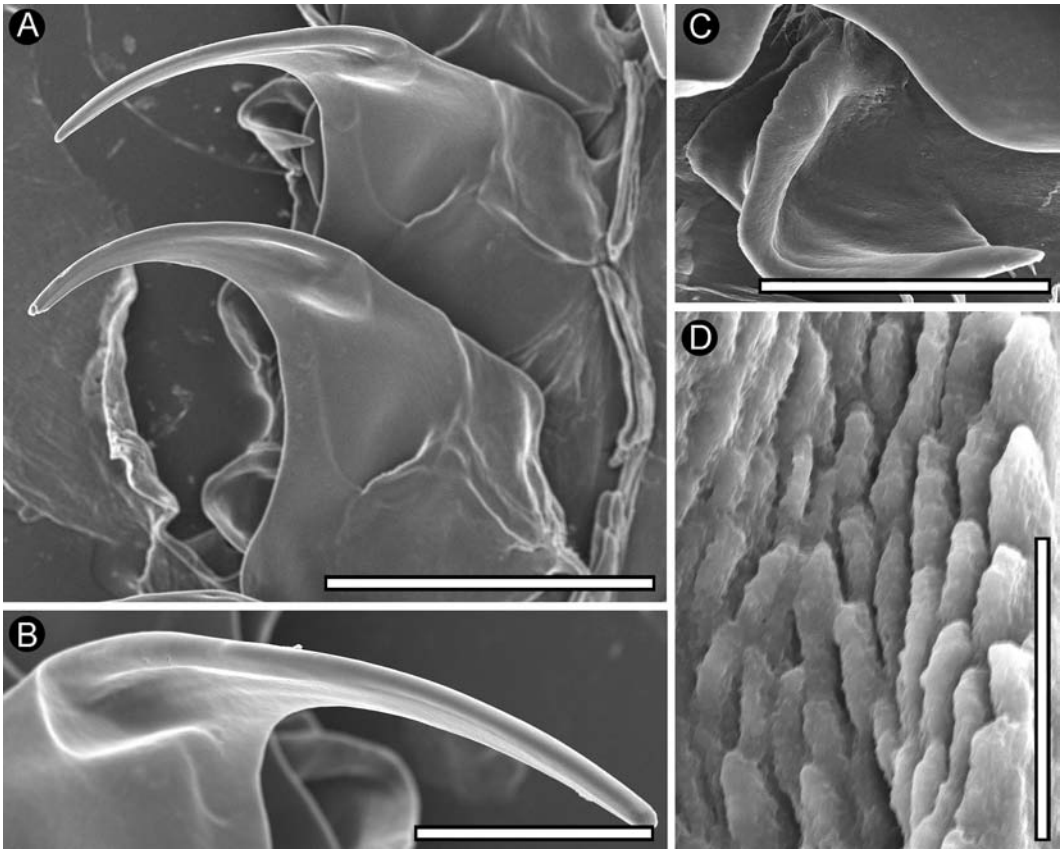


FIGURE 36. *Onchidoris bilamellata* CASIZ 068343. Radular morphology. A First lateral teeth. Scale = 300 μm . B. Close up of first lateral tooth. Scale = 100 μm . C. Close up of outer lateral tooth. Scale = 100 μm . D. Jaw rodlets. Scale = 20 μm .

other Onchidorididae (Fig. 37A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is a flattened oval with four large muscles attached; two per side. There are two small salivary glands at the side of the oral tube, near the radular sac (Fig. 37D). The radular sac protrudes from the bulb, under the esophagus. There is a large protruding buccal pump that has a fold (as found in other *Onchidoris* species) The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods are elongate with single apices (Fig. 36D). The radular formula is 23x1.1.1.1 (CASIZ 068343), with all teeth as described by Thompson and Brown (1984). That is, there is a small vestigial rachidian tooth and the large lateral teeth are similar in form while the outer lateral tooth is a thin, curved hook (Figs. 36A–C). The large first tooth is plate-shaped with a long pointed hook that has no denticles on the inner border of the hook. There is a large, heel or shoulder as found in species of *Acanthodoris* and *Diaphorodoris*.

REPRODUCTIVE SYSTEM.— The ampulla is elongate (Fig. 37C). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is a thin, curved elongate tube. It narrows slightly into the long deferent duct, which has one curve before it widens into the penis. The penis is

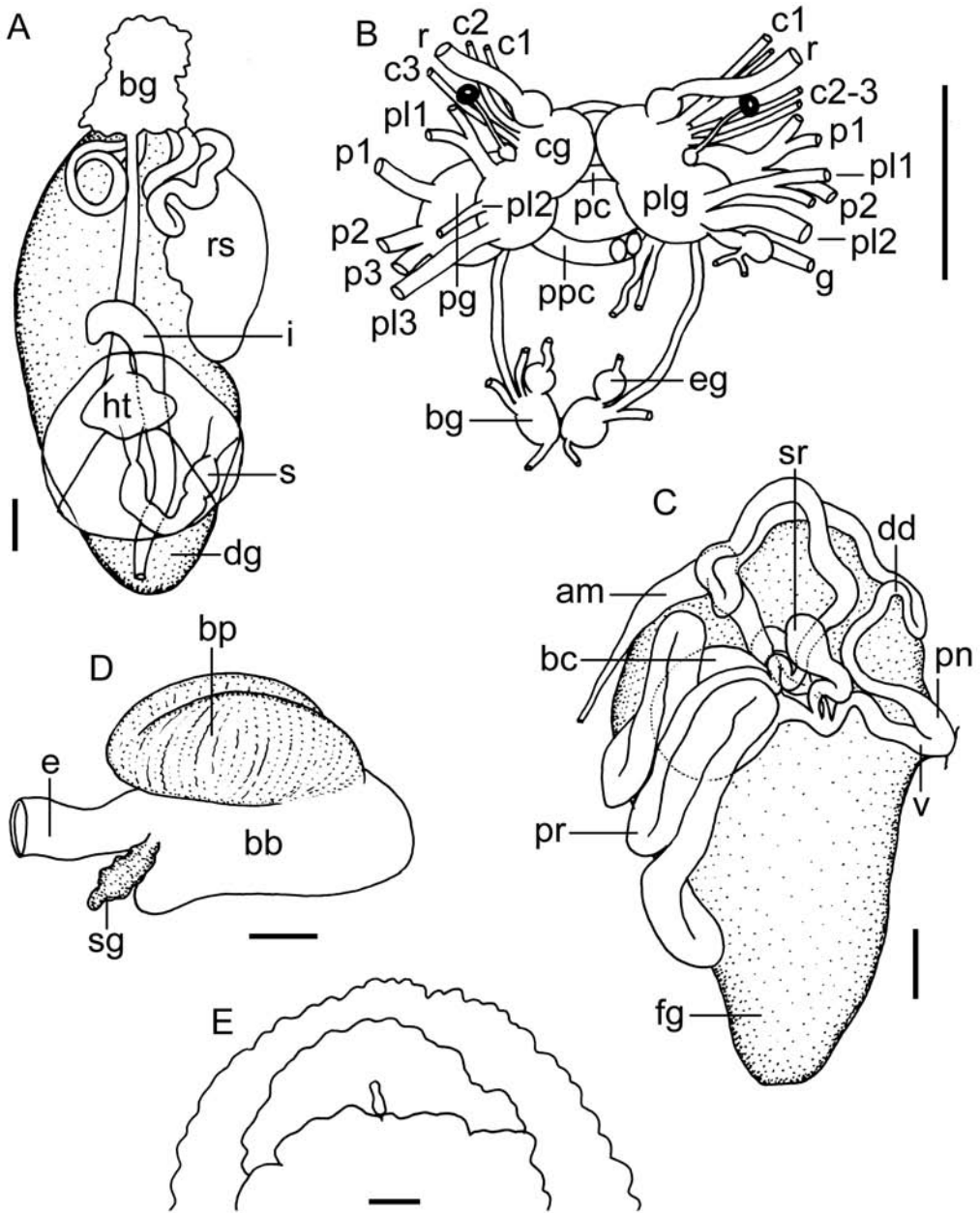


FIGURE 37. *Onchidoris bilamellata* CASIZ 068343. A. Digestive system. B. Cerebro-pleural ganglia. C. Reproductive morphology. D. Buccal bulb. E. Anterior ventral surface. Scale bars = 1 mm.

short and wider than the deferent duct. It terminates into the common genital atrium. The penis does not contain penial hooks. The vaginal duct is relatively short compared to other *Onchidoris* and wider than the deferent duct. The vagina was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the distal end, the vagina slightly widens from the vaginal duct before it joins the penis at the common genital atrium. The proximal end of the vaginal

duct terminates into the large round bursa copulatrix. From the bursa the oviduct connects to the much smaller ovoid seminal receptacle. The short uterine duct connects below the point at which the receptaculum joins the oviduct.

CENTRAL NERVOUS SYSTEM.— As with other Onchidorididae, the cerebral and pleural ganglia are fused together (Fig. 37B). The two pedal ganglia are located below the cerebro-pleural complex and are joined by an elongate commissure. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. The eyes are sessile at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and two large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

REMARKS.— Characters for the present phylogenetic analyses are taken from our examination of material from Massachusetts, Alaska, Scotland and Greenland.

***Onchidoris muricata* (Müller, 1776)**

Figs. 38–39.

Doris muricata Müller, 1776:229.

Doris aspera Alder and Hancock, 1842:32.

Doris diaphana Alder and Hancock, 1845:313.

Doris pallida Agassiz, 1850:229.

Lamellidoris hystricina Bergh, 1878b:605.

Lamellidoris varians Bergh, 1878:613.

Onchidoris muricata Nybakken and McDonald, 1980:44.

Onchidoris sp. Goddard, 1984:152.

(See Millen 1985 for a complete synonymy and discussion).

MATERIAL EXAMINED.— CASIZ 087251 Isles of Shoals, York County, Maine. 8–15 m depth, 15 specimens, 8 mm dissected. January 1979, T. Gosliner. CASIZ 067705 Friday Harbor, Puget Sound, Washington. 0 m depth. 3 specimens, 3–5 mm. July 1950, P. Illg. USNM 574287 Provincetown, Massachusetts. No depth or collector data. 3 specimens, 15–20 mm. No collection date, J. Blake. USNM 804964 Bay of Fundy, Canada. No depth or collector data. 3 specimens, 6–12 mm. 1872. USNM 810779 Massachusetts Bay, Massachusetts. No depth or collector data. 1 specimen, 5 mm. 1878. USNM 810783 Bay of Fundy, Canada. No depth or collector data. 3 specimens, 5–10 mm. 1872. USNM 827473 (*Lamellidoris aspera* sic) Georges Bank, Massachusetts. 82 m depth. 1 specimen, 4 mm. November 1982, Battelle. USNM 827901 (*Lamellidoris aspera* sic) Georges Bank, Massachusetts. 82 m depth. 1 specimen, 4 mm. November 1982, Battelle. LACM 153985 Cutter Rock, Ketchikan County Alaska. No depth data. 1 specimen, 7 mm. June 1987, S. Millen.

DISTRIBUTION.— North Atlantic (Britain to France, and north across Norway, west to Iceland, Greenland and south to Connecticut) and North Pacific (Bering Sea Alaska, south to California). (Rudman 2004 and present study).

EXTERNAL MORPHOLOGY.— Several authors have described the external morphology of this species, by most recently by Millen (1985). The specimens examined for the present study matched her description and thus there is no additional information to present. See Fig. 1X for a drawing of the ventral anterior surface of a specimen from California.

DIGESTIVE SYSTEM.— *Onchidoris muricata* shares the same general digestive anatomy as other Onchidorididae (Fig. 37A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached; two per side. There are two small glands at the side of the oral tube, near the radular sac (Fig. 37D). The radular sac protrudes noticeably from the bulb, under

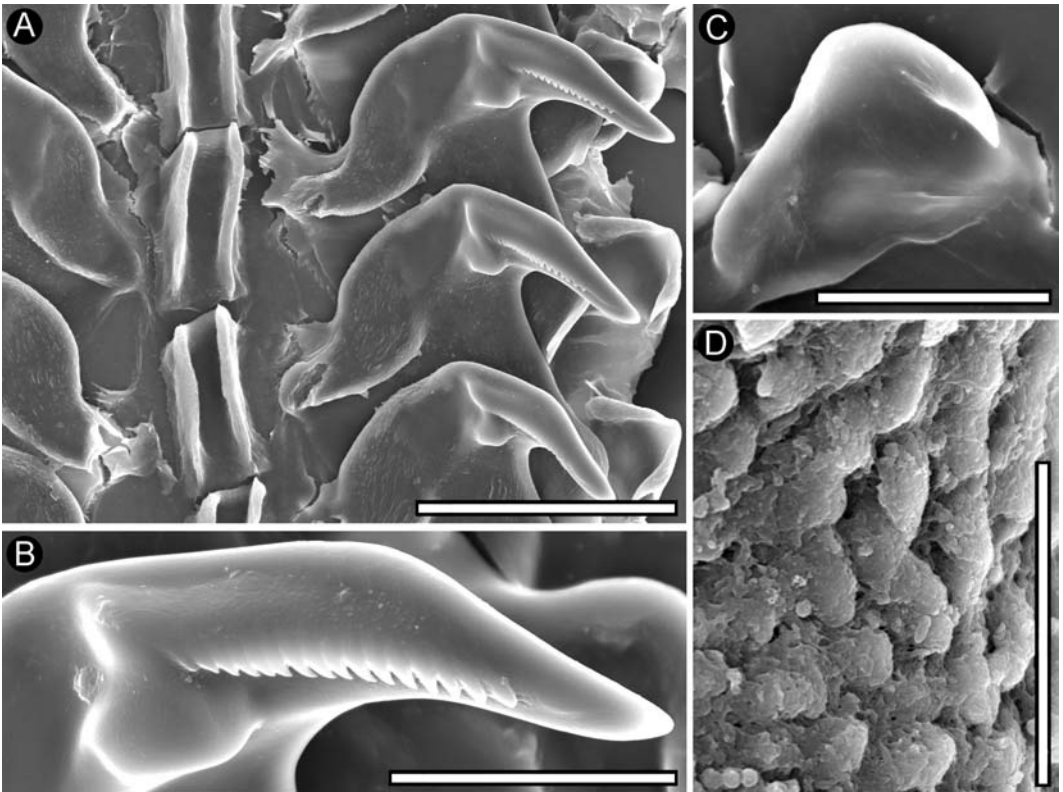


FIGURE 38. *Onchidoris muricata* CASIZ 087251. Radular morphology. A First lateral teeth. Scale = 50 μ m. B. Close up of denticles. Scale = 20 μ m. C. Close up of outer lateral tooth. Scale = 20 μ m. D. Jaw rodlets. Scale = 20 μ m.

the esophagus. There is a prominent buccal bulb that has a longitudinal crease (as found in other *Onchidoris* species). The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with rods at the edge. The rods are very small and rounded (Fig. 38D). The radular formula is 32x1.1.1.1 (CASIZ 087251), with all teeth as described and illustrated by Millen (1985). That is, there is a large rachidian tooth that has parallel distinct edges and the first lateral teeth are all similar in form. The outer lateral tooth is a shallow plate with a thin hook (Figs. 38A–C). The

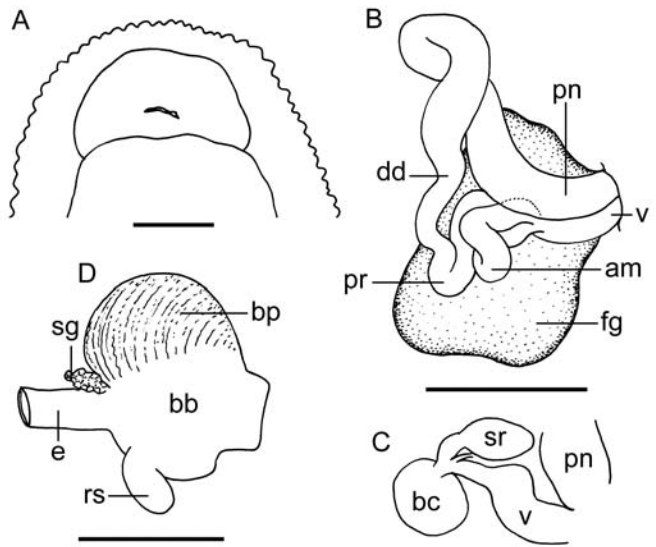


FIGURE 39. *Onchidoris muricata* CASIZ 087251. A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Scale bars = 1 mm.

large first tooth is has a long pointed hook that has up to 16 pointed denticles on the inner border of the hook. There is a curved heel or shoulder at the inner tooth edge that blends into the ridge from which the denticles protrude. The ridge extends to the tip of the hook devoid of denticles. At the base of the ridge there is a rounded protrusion.

REPRODUCTIVE SYSTEM.— The ampulla resembles a curved sausage (Fig. 39B). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is a short tube. It narrows slightly into the short deferent duct, which has one curve before it widens into the penis. The penis is sausage shaped and only slightly wider than the deferent duct. It terminates into the common genital atrium. The penis does not contain penial hooks. The vaginal duct is relatively short and wider than the deferent duct. At the distal end, the vagina slightly widens from the vaginal duct before it joins with the penis at the common genital atrium. The proximal end of the vaginal duct terminates into the small round bursa copulatrix. From the bursa the oviduct connects to the slightly smaller ovoid seminal receptacle. The uterine duct is short and connects at the point where the bursa and receptaculum join.

REMARKS.— Millen (1985) reviewed this species and presented a thorough discussion of the synonymies. The material we examined for the present study closely matches the descriptions and illustrations presented by Millen. Characters for the present phylogenetic analysis are taken from Millen and are corroborated with the specimens examined herein.

Villiersia scutigera Orbigny, 1837:15

REMARKS.— Pruvot-Fol (1954) synonymized *Villiersia* with *Lamellidoris*.

The description of *Villiersia scutigera* Orbigny, 1837 was limited to external characters. Pruvot-Fol (1954) wrote that because of this, the true identity of this species could not be confirmed. Although the illustrations provided by d'Orbigny of the body shape, gill arrangement, notal papillae and ventral surface bear some resemblance to a few species of *Onchidoris*, the coloration of *Villiersia scutigera* most closely matches that of *Onchidoris bouvieri* as described by Schmekel and Portmann (1982).

PHYLOGENETIC ANALYSIS

Onchidorididae taxa included in the present analysis are *Adalaria jannae* Millen, 1987, *A. loveni* (Alder and Hancock, 1862), *A. proxima* (Alder and Hancock, 1854), *Calycidoris guentheri* Abraham, 1876, *Diaphorodoris lirulatocauda* Millen, 1985, *D. luteocinta* (Sars, 1870), *D. mitsuui* (Baba, 1938), *D. papillata* Portmann and Sandmeier, 1960), *Goniodoris nodosa* (Thompson and Brown, 1984) and *Okenia mediterranea* (Ihering, 1886). Characters were polarized with the outgroup taxa *Bathydoris clavigera* Thiele, 1912, which, according to Valdés (2002), is a basally situated species of *Bathydoris*, the closest sister clade to the Phanerobranchia and Cryptobranchia. Other outgroup taxa included in the present analysis are *Cadlina luteomarginata* MacFarland 1966, a species of the most basal clade of the Chromodorididae (Gosliner and Johnson 1999) and *Akiodoris salacia* Millen and Martynov, 2005, which according to Millen and Martynov (2005) is the most basally situated taxon in the sister clade to the remaining Onchidorididae. Character states were taken from both the literature and from examinations of museum material when available. Table 1 summarizes the information for the outgroup taxa and the Onchidorididae (other than *Acanthodoris*) included in the analysis. Morphological data were organized using MacClade, ver 3 (Maddison and Maddison 2000). Synapomorphies were examined using MacClade and the character-trace option, using the majority rule tree from PAUP analyses.

TABLE 1. Outgroup taxa and Onchidorididae species included in the present analysis, literature source and material examined.

<i>Species</i>	<i>Literature Source</i>	<i>Additional material examined (# specimens)</i>
<i>Bathydoris clavigera</i> Thiele, 1912	Marcus & Marcus 1962; Valdés 2002	
<i>Cadlina luteomarginata</i> MacFarland, 1966	MacFarland 1966	
<i>Akiodoris salacia</i> Millen and Martynov, 2005	Millen & Martynov 2005	
<i>Adalaria jamae</i> Millen, 1987	Millen 1987	CASIZ 142450 (8) LACM 153983 (1)
<i>Adalaria loveni</i> (Alder and Hancock, 1862)	Thompson 1984, Millen 1987	
<i>Adalaria proxima</i> (Alder and Hancock, 1854)	Alder & Hancock 1854, Thompson 1984	CASIZ 087252 (27) CASIZ 087250 (1) CASIZ 070645 (4) LACM 153982 (1) USNM 804963 (1)
<i>Calycidoris güntneri</i> Abraham, 1876	Abraham 1876, 1877; Roginskaya 1972; Valdés 2002	CASIZ 086915 (1) CASIZ 086920 (1)
<i>Diaphorodoris lirulatocauda</i> Millen, 1985	Millen 1985	CASIZ 076203 (2) LACM 153984 (1)
<i>Diaphorodoris luteocinta</i> (Sars, 1870)	Schmekel & Portmann 1982; Pruvot-Fol 1954; Valdés 2002	CASIZ 072580 (6) CASIZ 087443 (7)
<i>Diaphorodoris mitsuui</i> Baba, 1938	Baba 1938	CASIZ 069759 (1)
<i>Diaphorodoris papillata</i> Portmann & Sandmeier, 1960	Portmann & Sandmeier 1960	CASIZ 099115 (2)
<i>Goniodoris nodosa</i> (Thompson & Brown, 1984)	Thompson & Brown 1984	
<i>Okenia mediterranea</i> (Ihering, 1886)	Schmekel & Portmann 1982; Valdés & Ortea 1995	

CHARACTERS.— The following characters were considered for use in the analyses of Aegiridae. The character states are indicated as follows: 0: the presumed plesiomorphic condition; 1,2: apomorphic condition. For character states that are not applicable, “-” is used and for missing data, “?” is used. The distribution of plesiomorphic and apomorphic character states is presented in Table 2. Character states for the taxa examined for the present study can be found in Table 2 (see Appendix A for the full data matrix). “Outgroup taxa” refers to the combination of *Bathydoris clavigera*, *Cadlina luteomarginata* and *Akiodoris salacia*. “Ingroup taxa” refers to all *Acanthodoris* plus *Adalaria*, *Calycidoris*, *Diaphorodoris*, *Onchidoris*, *Goniodoris* and *Okenia*.

1. *Dorsal tubercle length*: The dorsal tubercles are short (0) in *Bathydoris*, *Adalaria*, *Diaphorodoris luteocinta*, *D. mitsuui*, *Goniodoris*, *Onchidoris*, and *Acanthodoris pilosa*. In the remaining taxa, the tubercles are long (1).

TABLE 2. Characters and states examined for the phylogenetic analysis of *Acanthodoris*. 0 = presumed plesiomorphic; 1,2 = apomorphic conditions.

<i>Character</i>	<i>States</i>
Dorsal tubercles	0: elongate; 1: short
Dorsal tubercles	0: pointed; 1: round
Dorsal tubercles	0: dense; 1: sparse
Rhinophores	0: elongate; 1: short
Rhinophore sheaths	0: none; 1: non contractile; 2: contractile
Body shape	0: ovoid; 1: elongate
Head	0: veliform; 1: rounded
Mantle margin	0: none; 1: narrow; 2: wide
Posterior mantle	0: entire; 1: bilobed
Gill protection	0: no pocket; 1: retractile; 2: contractile
Gill notal sculpture	0: absent; 1: present
Mid dorsal crest	0: absent; 1: present
Caudal crest	0: absent; 1: present
Buccal pump	0: absent; 1: present
Peripheral muscles	0: absent; 1: present
Rachidian	0: present; 1: absent
Lip disk	0: labial armature; 1: smooth, thin
Jaw rodlets	0: single apex; 1: multi apices
Number of teeth 1/2 row	0: many; 1: few
Number inner laterals	0: first differs only; 1: more differ from outers
Lateral teeth	0: cusp with or w/o denticles; 1: beak shaped
Denticulation	0: both sides; 1: inner only; 2: absent
Denticles	0: many; 1: few
Outer lateral teeth	0: elongate/hamate; 1: elongate/oval; 2: wide/rectangular
Outer lateral teeth	0: multiple; 1: one
Ampulla	0: elongate/narrow; 1: short/wide
Receptaculum seminis	0: absent; 1: present
RS ducts	0: one duct; 1: two ducts
RS duct insertion	0: on vagina; 1: on uterine duct; 2: base of bursa
Oviduct connection	0: into female gland mass; 1: into receptaculum
Penial spines	0: absent; 1: present
Vagina size	0: narrower than penis; 1: same as penis; 2: wider
Cerebro-pleural ganglia	0: separate; 1: fused
Body color	0: white/yellow; 1: other
Dorsal spots	0: absent; 1: present

2. *Dorsal tubercle shape*: The dorsal tubercles are pointed (0) in nearly all taxa included. But *Adalaria* species, *Onchidoris bilamellata*, *Akiodoris*, *Cadlina* and all *Diaphorodoris* except *D. luteocinta* have rounded tubercles (1).

3. *Dorsal tubercle distribution*: The tubercles are sparsely distributed (0) in two species of *Diaphorodoris*, *Goniodoris*, *Okenia*, *Acanthodoris falklandica*, *A. nanega*, *Bathydoris* and *Akiodoris*. They are densely distributed (1) in the remaining taxa.

4. *Rhinophore length*: In *Bathydoris* and most of the ingroup, the rhinophores are elongate (0). But in the remaining taxa, the rhinophores are short (1).

5. *Rhinophore sheaths*: In *Bathydoris*, *Goniodoris* and *Okenia* there are no rhinophore sheaths (0). In all other taxa the sheaths are not contractile (1). In *Cadlina* the sheaths are contractile (2).

6. *Body Shape*: In all taxa the body is ovoid (0) but in *Cadlina* the body is more elongate than ovoid (1).

7. *Head shape*: In all taxa, the head is veliform (0), but in *Okenia* and *Cadlina* the head is rounded (1).
8. *Mantle margin*: in *Bathydoris*, *Akiodoris* and *Okenia* there is no mantle margin (0). But in *Diaphorodoris* and *Cadlina* the mantle margin is narrow (1) and in the remaining taxa the margin is wide (2).
9. *Posterior mantle*: In most taxa the posterior mantle is not bilobed (0), whereas in *Goniodoris* it is bilobed (1).
10. *Gill protection*: In *Bathydoris*, *Akiodoris* and all species of *Adalaria* there is no gill pocket (0). In *Cadlina* the gill is retractile into a pocket (1) and in the remaining taxa the gill is contractile (2).
11. *Gill notal sculpture*: In *Bathydoris*, *Cadlina*, *Goniodoris*, *Okenia* and all species of *Diaphorodoris* there are no notal structures such as tubercles within the gill ring (0). But in all remaining taxa, there are tubercles or other low structures within the gill circle (1).
12. *Mid dorsal crest*: In *Goniodoris* and *Okenia* there is a mid dorsal crest (1) but in the remaining taxa, this crest is absent (0).
13. *Caudal crest*: In *Diaphorodoris*, *Goniodoris* and *Okenia* the anterior surface of the foot has a crest along the midline (1). This crest is missing on all other taxa (0).
14. *Buccal Pump*: The buccal pump is absent (0) in *Bathydoris* and *Cadlina*. But in the remaining taxa the pump is present (1).
15. *Peripheral muscles*: There is no band of longitudinal muscle on the pharynx (0) of *Bathydoris*, *Akiodoris* or *Cadlina*. The remaining taxa all have a band of muscle (1).
16. *Rachidian*: There is a rachidian present in the outgroup taxa, species of *Adalaria* and *Onchidoris* (0). But the remaining taxa have no rachidian (1).
17. *Lip disk*: In most taxa, the lip disk contains armature (0), but in *Akiodoris* and species of *Adalaria* the lip disk is smooth and thin (1).
18. *Jaw rodlets*: In species with jaw rodlets, some have a single apex (0) such as *Bathydoris*, *Calycidoris*, *Diaphorodoris mitsuii*, *D. papillata*, *Goniodoris*, *Okenia* and *Onchidoris*. In *Acanthodoris* the rodlets have multiple apices (1).
19. *Number of teeth per half row*: In the outgroup taxa there are many teeth in each row (0), but in the remaining taxa there are few teeth (1).
20. *Number of inner lateral teeth*: In *Akiodoris* and *Cadlina* the first lateral tooth is the only tooth with that particular shape (0). In all other taxa, there is more than one inner lateral tooth that differs from the outer lateral teeth (1).
21. *Lateral teeth shape*: In most taxa examined, the innermost lateral tooth is a cusp with or without denticles (1). In the outgroup taxa the tooth is beak-shaped (0).
22. *Tooth denticulation*: In the outgroup taxa both sides of each tooth have denticles (0). In all remaining taxa except *Calycidoris* the teeth are denticulate on the inner side only. *Calycidoris* has no denticles (2). This character was omitted from the final analysis when interspecific variation was noted, seemingly dependent on the maturity of the specimen.
23. *Denticle number*: In the outgroup taxa, *Acanthodoris hudsoni*, *Adalaria jannae*, *Goniodoris*, *Okenia* and *Diaphorodoris* the denticles are numerous (0). However, in all remaining *Acanthodoris* species, *Onchidoris* and *Akiodoris* there are few denticles (1).
24. *Outer lateral teeth shape*: In those species having outer lateral teeth, there are elongate/hamate teeth (0) in *Bathydoris* and *Cadlina*. In all other species except *Akiodoris* there are elongate/oval teeth (1). In *Akiodoris* the outer lateral teeth are wide rectangles (2).
25. *Outer later teeth number*: In the outgroup taxa and most species examined, there are numerous outer lateral teeth (0). But in *Diaphorodoris*, *Okenia*, *Acanthodoris serpentinosus* and *Onchidoris* there is only one outer lateral tooth (1).
26. *Ampulla length*: In the outgroup taxa, *Okenia* and most *Acanthodoris*, the ampulla is elongate/narrow (0). In *Acanthodoris falklandica*, *A. serpentinosus* and *Onchidoris* the remaining taxa it is short/wide (1).
27. *Receptaculum seminis*: In *Bathydoris* the receptaculum is absent (0). But in the remaining taxa the receptaculum is present (1).
28. *Receptaculum duct*: In all outgroup taxa and most other species included, the receptaculum is connected by a single duct (0). But in *Adalaria* and *Onchidoris* there are two ducts (1).
29. *Receptaculum insertion*: In *Adalaria*, *Onchidoris*, *Akiodoris* and *Bathydoris* the receptaculum duct

inserts on the vaginal duct (0). In *Goniodoris*, *Okenia* and *Cadlina* the duct inserts on the uterine duct (1) and in the remaining taxa, the duct inserts at the base of the bursa (1).

30. *Oviduct*: In most taxa examined the oviduct connects to the female gland mass (0). In *Adalaria* and *Onchidoris* the oviduct connects to the receptaculum (1).

31. *Penial spines*: In *Bathydoris*, *Adalaria* and *Onchidoris*, penial spines are absent (0), but previous authors have observed spines in all other species (1).

32. *Vagina size*: In nearly all taxa examined, the vagina is narrower than the penis (0). In *Diaphorodoris mitsuii*, *Okenia* and *Onchidoris muricata* the penis and vagina are the same width (1). In *Acanthodoris falklandica* the vagina is wider than the penis (2).

33. *Cerebro-pleural ganglia*: In *Bathydoris* and *Adalaria* the ganglia are separate (0). In all other taxa the ganglia are fused (1).

34. *Body color*: In nearly all taxa included in the analysis, the ground color is white or pale yellow (0). But in many *Acanthodoris* species the ground color is not white, but orange or brown or reddish (1).

35. *Dorsum spots*: In most taxa, dorsum pigment spots are absent (0). In *Goniodoris*, *Okenia*, *Acanthodoris brunnea*, *A. lutea* and *A. pina* spots are often found on the dorsum (1).

RESULTS.— One most parsimonious tree was obtained with a length of 95 steps and had a consistency index (CI) of 0.44, a retention index (RI) of 0.68 and a homoplasy index (HI) of 0.56. The tree is shown in Fig. 40A with the character numbers and character reversals. The bold numbers indicate reversals. The trees indicated that *Adalaria*, *Onchidoris*, *Diaphorodoris* and *Acanthodoris* each form a monophyletic clade. Of the outgroup taxa included in the analysis, *Bathydoris clavigera* is most basally situated, with *Cadlina luteomarginata* found as the sister species to the Onchidorididae plus Akiodorididae (Millen and Martynov 2005). *Akiodoris salacia* is sister taxon to the Onchidorididae.

Within the ingroup taxa, the clade containing *Adalaria* and *Onchidoris* is the most basally situated clade, with *Onchidoris* in the more basal position. *Okenia mediterranea* and *Goniodoris nodosa* form a clade that is basally situated to *Diaphorodoris* and *Calycidoris guentheri* is the most basally situated species of this clade. The clade containing all *Acanthodoris* species shows that the most basally situated species are *Acanthodoris planca*, *A. nanega* and *A. nanaimoensis*, all from the Southern Hemisphere. The remaining species found in the Northern Hemisphere form a separate clade.

Bremer support values (shown in Fig. 40A, numbers below the branches) show poor support for most of the clades with the exception of the outgroups and the clade containing *Adalaria* plus *Onchidoris* and the clade of *Goniodoris* plus *Okenia*.

Analyses were also performed using different outgroup taxa such as including *Okenia* and *Goniodoris* with *Bathydoris*, *Cadlina* and *Akiodoris*. *Okenia* and *Goniodoris* were also used as the only outgroup taxa, with *Bathydoris*, *Cadlina* and *Akiodoris* included in the ingroup. Results from both these trials produced the same single most parsimonious tree with the topology as shown in Fig. 40B. The tree scores were the same in all trials.

In the single tree that was produced by the outgroup trials, *Bathydoris*, *Cadlina* and *Akiodoris* group together in a derived sister clade to *Adalaria* and *Onchidoris*. The clade that contains these groups form the sister clade to *Acanthodoris*. *Calycidoris* is basally situated to both clades and *Diaphorodoris* forms a clade at the base of all these taxa.

DISCUSSION

Results from the phylogenetic analysis support the monophyly of *Acanthodoris*, *Onchidoris*, *Adalaria* and *Diaphorodoris*. Additionally, the placement of *Adalaria* and *Onchidoris* in a sister clade to *Acanthodoris*, *Diaphorodoris*, *Goniodoris* and *Calycidoris* agrees with the findings of

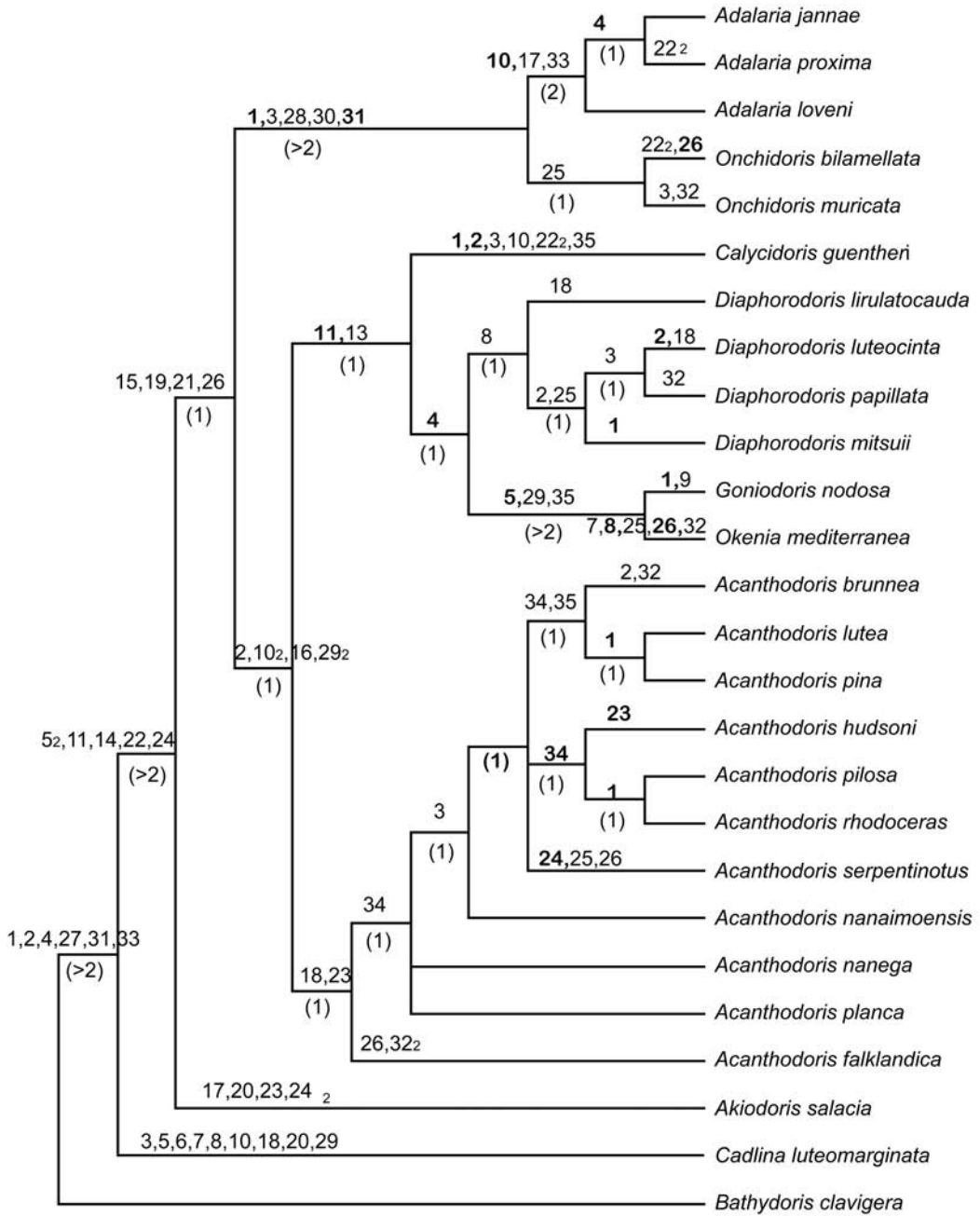


FIGURE 40. Phylogeny of *Acanthodoris*. Single most parsimonious tree, 95 steps. Numbers below the branches are Bremer decay values. Numbers shown above the branches are character numbers from Table 2. The bold numbers indicate reversals.

The tree is derived from three outgroup taxa, *Bathydoris*, *Cadlina* and *Akiodoris*.

Millen and Martynov (2005). Our findings also agree with Millen and Martynov's results showing *Cadlina* in a basal position relative to *Akiodoris*.

The synapomorphies for *Acanthodoris* are (18) jaw rodlets with multi-apices and (23) few denticles on the lateral teeth. Characters that unite members of the traditional Goniodorididae include (5) a contractile rhinophore sheath, (11) presence of notal sculpture within the gill circle, (14) presence of a buccal pump, (22) denticles on the inner side of the lateral teeth and (24) elongate/hamate outer lateral teeth.

Our results support the findings of Millen (1985) with regard to the relationship between *Diaphorodoris* and *Calycidoris*, *Acanthodoris* and *Akiodoris*. Millen demonstrated that based on reproductive characters, these four genera are more closely aligned to each other than to *Onchidoris*. This same result is shown in our phylogenetic analysis (Fig. 40A). *Onchidoris* is in a sister clade to the clade containing *Diaphorodoris*, *Calycidoris* and *Acanthodoris*. In addition, Millen demonstrated that external and radular characters clearly separate *Onchidoris* and *Diaphorodoris* as separate genera. Our analysis also found radular characters to support the two genera (#25, outer lateral teeth and #17, lip disk).

The results of the present analysis differ in some aspects from the phylogeny of the Nudibranchia reconstructed by molecular markers (Wollscheid-Lengeling *et al.* 2001). In that analysis, the tree constructed by combining three genes (16S, 18S and COI, p. 251) shows *Goniodoris nodosa* and *Diaphorodoris luteocincta* as basally situated to *Cadlina luteomarginata*. In our analysis (Fig. 41) *Cadlina* is more basal to *Goniodoris* and *Diaphorodoris*. However, in their tree constructed from a single gene (COI, maximum likelihood tree, p. 250) *Cadlina* and *Diaphorodoris* appear in sister clades, with *Bathydoris clavigera* in a clade basal to both. The placement of *Bathydoris* is consistent with our findings. In their tree derived from partial sequences of 16S (maximum likelihood tree, p. 249), *Acanthodoris* and *Onchidoris* group together in a basally situated clade to *Cadlina* with *Diaphorodoris* more derived than any of these groupings. Our phylogeny also shows *Diaphorodoris* as more derived than either *Acanthodoris* or *Onchidoris*.

In the present analyses, as noted above, the selection of outgroups affected the placement of the major clades. If five outgroups were selected (*Bathydoris*, *Akiodoris*, *Cadlina*, *Goniodoris* and *Okenia*) a single most parsimonious tree resulted (Fig. 40B) with the same tree scores as obtained by using the three outgroups noted above. There was no difference in this second tree structure however, if only *Goniodoris* and *Okenia* were selected as outgroups. In the single tree produced, *Okenia* and *Goniodoris* are the most basally situated taxa and *Diaphorodoris* is a monophyletic clade basal to the remainder of taxa. Interestingly, *Bathydoris*, *Cadlina* and *Akiodoris* cluster in a clade more derived than the monophyletic clade of *Acanthodoris*. This tree agrees in some aspects with the tree derived from the partial sequence of 16S (Wollscheid-Lengeling *et al.* 2001). In that tree, *Goniodoris* is the most basally situated taxon and *Diaphorodoris* is basally situated to *Cadlina*, *Onchidoris*, *Goniodoris* and *Acanthodoris*. The placement of these taxa in Wollscheid-Lengeling *et al.*'s analysis agrees with our morphology based tree when we use either *Goniodoris* plus *Okenia* as the outgroups, or by using five outgroups as described above.

The present phylogeny of *Acanthodoris* (Fig. 40) contains one conspicuous clade of *Acanthodoris*, including species found in the Northern Hemisphere. Basally situated to this clade are three species found exclusively in the Southern Hemisphere: *Acanthodoris falklandica*, *A. planca* and *A. nanega*. This hypothesis suggests that *Acanthodoris* from the northern hemisphere have a common ancestor. It is also remarkable that species from the eastern Pacific are much more diverse than species from either the Atlantic or the southern hemisphere. The southern hemisphere species form a grade at the base of the more derived northern hemisphere clade. There are two most likely scenarios for this tree structure. One possibility is that there could have been a mass extinc-

tion of Atlantic, western Pacific or Southern Hemisphere species. Another possibility is that the dispersal scenario for *Acanthodoris* is similar to the findings of Fahey and Gosliner (2004) for Aegiridae. In that study, the distribution pattern indicated a possible dispersal scenario from the Antarctic, north along both coasts of Australia, then into the tropical Indo-Pacific. The topology of the present tree indicates that a similar scenario could have occurred for *Acanthodoris*. The difference is that *Acanthodoris* could have dispersed from the Southern Hemisphere and then into the Eastern Pacific Ocean, where most *Acanthodoris* are found.

However, as with the case of Aegiridae (Fahey and Gosliner 2004), it is likely that not all species of Onchidorididae have been described. It is possible that there may be other undescribed species that will enable a more thorough analysis of biogeographical relationships among this clade of nudibranchs.

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LITERATURE CITED

- ABILDGAARD, P.C. 1789. Nudibranchia. Page 7, pl. 8.5 in O. Müller, ed., *Zoologia Danica sev animalium Daniae et Norvegiae rariorum ac minus notorum descriptiones et historia*. 3rd edition. N. Mølleri, Havniae, Denmark.
- ABRAHAM, P.S. 1876. Notes on some genera of nudibranchiate Mollusca, with notices of a new genus and some hitherto undescribed species in the collection of the British Museum. *Annals and Magazine of Natural History*, ser. 6, 7:132–146, 4 pls.
- ABRAHAM, P.S. 1877. Revision of the anthobranchiate nudibranchiate Mollusca, with descriptions or notices of forty-one hitherto undescribed species. *Proceedings of the Zoological Society of London*:196–269, pls 27–30.
- AGASSIZ, L. 1846. *Onchidoris* de Blainville 1816. in H.S. Scudder, ed. *Nomenclator Zoologicus*. Government Printing Office, Washington, USA. 340 pp.
- AGASSIZ, L. 1850. Notes in minutes of Nov. 7, 1849 meeting of Boston Society of Natural History drawings of *Doris diademata*, *D. coronata*, *D. tenella*, *D. pallida*, all new Agassiz species exhibited and *Meliboea arbuscula* reported from Gay Head, Mass. *Proceedings of the Boston Society of Natural History* 3:191.
- ALDER, J., AND A. HANCOCK. 1842. Descriptions of several new species of nudibranchious Mollusca found on the coast of Northumberland. *Annals and Magazine of Natural History* 9:31–36.
- ALDER, J., AND A. HANCOCK. 1845. Notice of a new genus and several new species of nudibranchiate Mollusca. *Annals and Magazine of Natural History* 16:311–316.
- ALDER, J., AND A. HANCOCK. 1845–1855. *A monograph of the British nudibranchiate Mollusca: with figures of all the species*, vol. 1, pts. 1–7. The Ray Society. London, UK. 54 pp., 8 pls.
- ALDER, J., AND A. HANCOCK. 1862. Descriptions of a new genus and some new species of naked Molluscs. *Annals and Magazine of Natural History* 10:261–265.
- AURIVILLIUS, C. 1887. Placophora och Gastropoda, Ofersicht öfver de af Vega-expeditionen insamlade arkiska hafsmollusker. *Kongelige Svenska Vetenskaps-Akademiens Handlingar* 2:313–383.
- BABA, K. 1935. The fauna of Akkeshi Bay Part I Opisthobranchia. *Journal of the Faculty of Science Hokkaido University* (6) Zoology 4:115–125, pls. 7–8.

- BABA, K. 1938. Three new nudibranchs from Izu, Middle Japan. *Annotationes Zoologicae Japonenses, Tokyo* 17:130–133.
- BABA, K. 1949. *Opisthobranchs of Sagami Bay*. Iwanami Shoten, Tokyo. 194 pp. 50 pls.
- BECK, H. 1842. *Doris literata*. Page 78 in H. Möller, ed., *Index Molluscorum Groenlandiae, Naturhistorie Tidsskrift*, vol. 4(1). Kjöbenhavn, Denmark.
- BEHRENS, D.W. 1980. *Pacific Coast Nudibranchs. A Guide to the Opisthobranchs of the Northeastern Pacific*. Sea Challengers. Los Osos, California, USA. 112 pp.
- BEHRENS, D.W. 1991. *Pacific Coast Nudibranchs: A Guide to the Opisthobranchs Alaska to Baja California*. Sea Challengers. Monterey, California, USA. 107 pp.
- BERGH, R. 1878. Malacologische Untersuchungen. Pages 547–601, pls. 62–65 in C. Semper ed., *Reisen im Archipel der Philippinen*, Theil 2, Heft 13. Kreidel, Wiesbaden, Germany.
- BERGH, R. 1880. On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska, Part 2. *Proceedings of the National Academy of Sciences, Philadelphia* 40–127, pls. 9–16.
- BERGH, R. 1905. Die Opisthobranchiata der Siboga-Expedition. Pages 1–248, pls 1–20, in M. Weber, ed., *Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch Gebied verzameld in Nederlandsch Oost-Indië 1899–1900 aan boord H. M. Siboga onder commando van Luitenant ter zee 1^e kl. G. F. Tydeman*, vol. 50. Brill, Leiden, Netherlands.
- BLAINVILLE, H.D. 1816. Quartrième mémoire sur les mollusques, de l'ordre des cyclobranches. *Bulletin des Sciences par la Société Philomathique. Paris*, ser. 3, (1–3):93–97.
- BURN, R. 1969. A memorial report on the Tom Crawford Collection of Victorian Opisthobranchia. *Journal of the Malacological Society of Australia* 12:64–106.
- COCKERELL, T.D., AND C. ELIOT. 1905. Notes on a collection of Californian nudibranchs. *Journal of Malacology* 12:31–53, pls. 7–8.
- CUVIER, G.L. 1830. Les nudibranches (3). *Le règne Animaux Nouvelle* 2:50–58.
- D'ORBIGNY, A. 1837. Mémoire sur les espèces et sur des genres nouveaux de l'ordre des nudibranches, observés sur les côtes de France. *Magasin de Zoologie*, 7 Class, 5:1–16, pls. 102–109.
- DALL, W. 1871. Descriptions of sixty new forms of mollusks from the West Coast of North America and the North Pacific Ocean, with notes on others already described. *American Journal of Conchology* 7:93–160.
- DESMAREST, E. 1858. *Onchidorus*. Page 142 in J. Chenu, ed., *Encyclopédia Histoire Naturelle*, vol. 4, *Crustacés. Mollusques. Zoophytes*. Marescq et cie, Paris. 22 vols.
- DYBOWSKI, W. 1900. Beschreibung einer Hinterkiemer-Schnecke aus dem Baikalsee. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* 32:143–152.
- ELIOT, C. 1907. Nudibranchs from New Zealand and the Falkland Islands. *Proceedings of the Malacological Society London* 7:327–361.
- ELIOT, C. 1910. *A Monograph of the British Nudibranchiate Mollusca*. Part 8 (Supplement). The Ray Society. London. 198 pp.
- FABRICIUS, O. 1780. *Fauna Groenlandica*. I.G. Rothe, Hafniae et Lipsiae, Denmark. 452 pp.
- FAHEY, S.J., AND T.M. GOSLINER. 2004. A phylogenetic analysis of the Aegiridae Fischer, 1883 (Mollusca, Nudibranchia, Phanerobranchia) with descriptions of eight new species and a reassessment of Phanerobranch relationships. *Proceedings of the California Academy of Sciences*, ser. 4, 55:613–689.
- FARRAN, G.P. 1903. The nudibranchiate molluscs of Ballynakill and Bofin Harbours, Co. Galway. *Report on the Sea and Inland Fisheries of Ireland for 1901*, Part 2:123–132.
- FÉRUSSAC, A. 1922. Tableaux systématiques des animaux mollusques. *Suivis d'un Prodrôme Général* I–XLVII:1–110.
- FLEMING, J. 1820. *Doris nigricans*. *Brewster's Edinburgh Encyclopedia* 14:618.
- FORBES, E. 1838. *Malacologia Monensis, A Catalogue of the Mollusca Inhabiting the Isle of Man and the Neighboring Sea*. J. Carfrae and Son, Edinburgh, Scotland. 63 pp.
- GISTEL, J. 1848. *Villiersia* D'Orbigny, A. 1837. *Naturgeschichte des thierreichs für höhere Schulen*. Hoffman'sche Verlags-Buchhandlung, Stuttgart, Germany. 216 pp., 32 pls.
- GMELIN, J. 1791. In C. Linnaeus, ed., *Systema Naturae*, ed. 3, 1(6): 3103–3107, 3147–3148.
- GODDARD, J. 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary

- of benthic opisthobranchs known from Oregon. *The Veliger* 27:143–163.
- GOSLINER, T., AND R. JOHNSON. 1999. Phylogeny of *Hypselodoris* (Nudibranchia: Chromodorididae) with a review of the monophyletic clade of Indo-Pacific species, including descriptions of twelve new species. *Zoological Journal of the Linnean Society* 125:1–114.
- GRAY, J.E. 1842–1857. *Figures of Molluscous Animals, Selected from Various Authors*. Longman, Brown, Green and Longmans, London, UK. Vol. 4, 123 pp; Vol. 5, 112 pls.
- HERRMANNSEN, A. 1852. *Indicis generum Malacozoorum, supplementa et Corrigenda*. Theodori Fischer, Cassellis, Germany. 140 pp.
- IREDALE, T., AND C. O'DONOGHUE. 1923. List of British nudibranchiate Mollusca. *Proceedings of the Malacological Society of London* 15:115–226.
- JAECKLE, W. 1984. The opisthobranch molluscs of Humboldt County, California. *The Veliger* 26:207–213.
- JEFFREYS, J. 1869. *British Conchology or an Account of the Mollusca Which Now Inhabit the British Isles and the Surrounding Seas*. J. van Voorst, London, UK. 5 Vols.
- JUST, H., AND M. EDMUNDS. 1985. North Atlantic Nudibranchs (Mollusca) seen by Henning Lemche. *Ophelia* Supplement 2:170.
- KEEN, A. M. 1971. *Sea Shells of Tropical West America: Marine Mollusks from Baja California to Peru*. Stanford University Press. Stanford, California, USA. 624 pp.
- LANCE, J. 1968. New Panamic nudibranchs (Gastropoda; Opisthobranchia) from the Gulf of California. *Transactions of the San Diego Society of Natural History* 15:1–13.
- LEACH, W. 1847. The classification of the British Mollusca. *Annals and Magazine of Natural History* 20:267–273.
- LINNAEUS, C. 1767. *Systema Naturae*. 12. Salvii, Holmiae, Sweden. 1384 pp.
- LOVÉN, S. 1846. Index molluscorum litora Scandinaviae Occidentalia habitantium. *Öfversigt af Kongl Vetenskaps Akademiens Förhandlingar Stockholm* 3:135–160.
- MACFARLAND, F. 1905. Opisthobranchiate Mollusca from Monterey Bay, California, and vicinity. *Bulletin of the United States Bureau of Fisheries* 25:109–151, pls. 18–31.
- MACFARLAND, F. 1925. The Acanthodorididae of the California Coast. *Nautilus* 39:49–65, pls. 2–3.
- MACFARLAND, F. 1926. The Acanthodorididae of the Californian Coast. *Nautilus* 39:94–103, pls. 2–3.
- MACGINITIE, G., AND N. MACGINITIE. 1949. *Natural History of Marine Animals*. McGraw-Hill, New York, USA. 523 pp.
- MADDISON, W.P., AND D.R. MADDISON. 2000. *MacClade*. Sinauer Associates, Cambridge, Massachusetts, USA.
- MARCUS, E. 1959. Lamellariacea und Opisthobranchia. reports from the Lund University Chili Expedition 1948–49. *Lunds Universitets Arsskrift* 36:89–261.
- MARCUS, E., AND E. MARCUS. 1967. *American Opisthobranch Mollusks*. University of Miami Institute of Marine Sciences. Miami, Florida, USA. 256 pp.
- MCDONALD, G. 1975. Key D: Sacoglossa and Nudibranchia in R.I. Smith and J.T. Carlton eds., *Light's Manual, Intertidal Invertebrates of the Central California Coast*. University of California Press, Berkeley, California, USA. 716 pp.
- MCDONALD, G. 1983. A review of the nudibranchs of the California coast. *Malacologia* 24:114–276.
- MCDONALD, G., AND J. NYBAKKEN. 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. *The Veliger* 21:110–119.
- MCDONALD, G., AND J. NYBAKKEN. 1980. *Guide to the Nudibranchs of California, Including Most Species Found from Alaska to Oregon*. American Malacologists Inc., Melbourne, Florida, USA. 72 pp.
- MILLEN, S. 1985. The nudibranch genera *Onchidoris* and *Diaphorodoris* (Mollusca, Opisthobranchia) in the northeastern Pacific. *The Veliger* 28:80–93.
- MILLEN, S., AND A. MARTYNOV. 2005. Redescriptions of the nudibranch genera *Akiodoris* Bergh, 1879 and *Armodoris* Minichev, 1972 (Suborder Doridacea), with a new species of *Akiodoris* and a new family Akiodorididae. *Proceedings of the California Academy of Sciences*, ser. 4, 56(1):1–22.
- MILLEN, S.V. 1987. The nudibranch *Adalaria*, with a description of a new species from the northeastern Pacific. *Canadian Journal of Zoology* 65:2696–2702.
- MÖLLER, H. 1842. Index Molluscorum Groenlandiae. *Naturhistorisk Tidsskrift* 1842:76–94.

- MÖRCH, O. 1857. Pages 11–13, Part 4. Mollusks. Prodrömus faunae molluscorum Grönlandiae. Fortegnelse over Grönlands Blöddyr in H.J. Rink, ed., *Grönland geographisk og statistisk beskrevet*, 1–28.
- MÖRCH, O. 1868. Faunula molluscorum Islandiae. Översigt over Island Blöddyr. *Videnskabelige Meddeleser fra Dansk Naturhistorisk* 11–13:185–227.
- MÜLLER, O. 1776. *Zoologiae Danicae, Prodrömus seu animalium Daniae et Norvegiae ingenarum characteres, nomina, et synonyma imprimis popularium*. N. Mölleri et filii, Havniae, Denmark. 282 pp., 32 pls.
- NYBAKKEN, J. 1978. Abundance, diversity and temporal variability in a California intertidal nudibranch assemblage. *Marine Biology* 45:129–146.
- O'DONOGHUE, C. 1921. Nudibranchiate Mollusca from the Vancouver Island Region. *Transactions of the Royal Canadian Institute* 13:147–209.
- O'DONOGHUE, C. 1927. Notes on the nudibranchiate Mollusca from the Vancouver Island Region. 5. *Transactions of the Royal Canadian Institute* 16:1–12, pl. 1.
- ODHNER, N. 1926. Die Opisthobranchien. Pages 1–100, Vol. 2 in N. Odhner, ed., *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 under the direction of Dr. Otto Nordenskjöld*. Norstedt and Söner, Stockholm, Sweden.
- ORTEA, J., AND M. BALLESTEROS. 1982. Sobre algunos *Onchidoris* Blainville, 1816 (Mollusca, Opisthobranchia, Doridacea) del litoral ibérico. *Investigación Pesquera* 46:239–254.
- PORTMANN, A., AND E. SANDMEIER. 1960. Zur kenntnis von *Diaphorodoris* (Gastropoda, Nudibranchia) und ihrer mediterranen Formen. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 71:174–183.
- PRUVOT-FOL, A. 1951. Études des nudibranches de la Méditerranée (2 Partie). *Archives de Zoologie Expérimentale et Générale* 88:1–80, pls. 1–4.
- PRUVOT-FOL, A. 1954. *Mollusques Opisthobranches*. Office Central de Faunistique. Paris, France. 460 pp.
- ROCHEBRUNE, A., AND J. MABILLE. 1891. *Mollusques*. Gauthier-Villars et fils, Paris, France. 143 pp.
- ROGINSKAYA, I. 1972. *Calycidoris guentheri* (Gastropoda, Nudibranchia) taxonomy and geographical range. *Zoological Journal, Institute of Oceanology, Moscow* 6:913–918.
- ROLLER, R., AND S. LONG. 1969. An annotated list of opisthobranchs from San Luis Obispo County, California, USA. *The Veliger* 11:424–430.
- RUDMAN, W. 2004. Further species of the opisthobranch genus *Okenia* (Nudibranchia: Goniadorididae) from the Indo-West Pacific. *Zootaxa* 695:1–70.
- RUDMAN, W.B. (accessed 2004). SeaSlug Forum. Vol. 2003 <http://www.seaslugforum.net>
- RUDMAN, W.B., AND R. WILLAN. 1998. Opisthobranchia. Pages 915–942 in P.L. Beesley, G.J.B. Ross, A. Wells, eds., *Mollusca: The Southern Synthesis. Fauna of Australia*, vol. 5, pt. B. CSIRO Publishing, Melbourne, Australia. 1234 pp.
- SARS, G. 1870. Bidrag til Kundskab om Christianiafjordens Fauna 2. *NYT Magazin for Naturvidenskaberne* 17:113–232. Nudibranchia 186–194.
- SAUVAGE, H. 1873. Catalogue des nudibranches des Côtes du Boulonnais, dressé, d'après les notes de Bouchard-Chantreaux. *Journal de Conchyliologie* 3:25–36.
- SCHMEKEL, L. 1968. Ascoglossa, Notaspidea und Nudibranchia im Litoral des Golfes von Neapel. *Revue Suisse de Zoologie* 75:103–155.
- SCHMEKEL, L., AND A. PORTMANN. 1982. *Opisthobranchia des Mittelmeeres. Nudibranchia und Saccoglossa*. Springer-Verlag, Berlin, Germany. 410 pp.
- SCHRÖDL, M. 1996. Nudibranchia y Sacoglossa de Chile: Morfología exterior y distribución. *Gayana Zoologia* 60:17–62.
- SCHRÖDL, M. 1997. Range extension of Magellanic nudibranchs (Opisthobranchia) into the Peruvian faunal province. *The Veliger* 40:38–42.
- SCHRÖDL, M. 2003. *Sea Slugs of Southern South America*. Conch Books. Hackenheim, Germany. 165 pp.
- STEINBERG, J. 1963. Notes on the Opisthobranchs of the west coast of North America III. Further nomenclatorial changes in the Order Nudibranchia. *The Veliger* 6:63–67.
- THOMPSON, T.E. 1958. Observations on the radula of *Adalaria proxima* (A. & H.) (Gastropoda Opisthobranchia). *Proceedings of the Malacological Society London* 33:49–56.
- THOMPSON, T.E., AND G.H. BROWN. 1984. *Biology of Opisthobranch Molluscs*, vol. 2. The Ray Society, London, UK. 280 pp.

- THOMPSON, W. 1840. Contributions towards a knowledge of the Mollusca Nudibranchia and Mollusca Tunicata of Ireland, with descriptions of some apparently new species of Invertebrata. *Annals and Magazine of Natural History* 5:84–102.
- THOMPSON, W. 1845. Additions to the fauna of Ireland including descriptions of some apparently new species of Invertebrata. *Annals and Magazine of Natural History* 15:308–322.
- VALDÉS, A. 2002. A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). *Zoological Journal of the Linnean Society, London* 136:535–636.
- VALLÈS, Y. 2002. *Taxonomy and phylogeny of Kaloplocamus and Plocamopherus and their relationships with other phanerobranchs*. Masters thesis. San Francisco State University. San Francisco, California, USA. 266 pp.
- VAYSSIÈRE, A. 1919. Recherches zoologiques et anatomiques sur les mollusques Opithobranches du Golfe de Marseille, 2me Supplément. *Annales de la Museum Histoire Natural Marseille* 17:53–92.
- VERRILL, A. 1870. Contributions to zoology from the Museum of Yale College. No. 8. Descriptions of some New England Nudibranchiata. *American Journal of the Sciences and Arts* 2:405–408.
- VERRILL, A. 1879. Notice of recent additions to the marine fauna of the east coast of North America. No. 4. *American Journal of Science* (3)17:309–315.
- WÄGELE, H. AND R.C. WILLAN. 2000. Phylogeny of the Nudibranchia. *Zoological Journal of the Linnean Society* 130:83–181.
- WILLIAMS, G.C. AND T.M. GOSLINER. 1979. Two new species of nudibranchiate molluscs from the west coast of North America, with a revision of the family Cuthonidae. *Zoological Journal of The Linnean Society* 67:203–223.
- WOLLSCHIED-LENGELING, E. AND J. BOORE, AND W. BROWN, AND H. WÄGELE. 2001. The phylogeny of Nudibranchia (Opisthobranchia, Gastropoda, Mollusca) reconstructed by three molecular markers. *Organisms Diversity & Evolution* 1:241–256.

