PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Fourth Series

Volume 56, No. 20, pp. 213–273, 40 figs. 2 tables, Appendix August 26, 2005

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

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The phylogenetic relationships of *Acanthodoris* Gray, 1850 within the Onchidoridiidae 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. Reproductive differences in the new species include a shorter deferent duct, vaginal duct and receptaculum seminis duct than found in other externally similar species. Radula differences include multifid jaw rodlets 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*. *Acanthoris pilosa* has no jaw rods and 3 flat outer lateral plates. Phylogenetic analyses place the new species in a relatively basal position to the remaining *Acanthodoris* species and closely related to *Acanthodoris falklandica* Eliot, 1907 from South America and *Acanthodoris nanega* Burn, 1969 from South Australia. The species from the West Coast of North America and the North Atlantic, i.e., *A. pilosa*, form a derived clade, separate from the Southern Hemisphere species.

The phylogenetic relationships among the Onchidoridiidae 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* Millen, 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, Goniodorididdae, Polyceridae, Gymnodorididdae, Aegiridae and Onchidorididdae) (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 Onchidorididdae: *Onchidoris, Adalaria, Arctadalaria, Acanthodoris, Doridunculus, Prodoridunculus, Actodoris, Calycidoris, Akiodoris* (as *Aciodoris*) and *Diaphorodoris* (Millen 1987; Rudman and Willan 1998).

However, the most recent phylogeny that includes the Onchidorididdae (Millen and Martynov 2005) shows that the traditional Onchidorididdae is a paraphyletic group that includes *Onchidoris* and no other members of the traditional Goniodorididdae. Millen and Martynov's analysis places the remaining Onchidorididdae in a separate clade that they name the Akiodorididdae. Their analysis also shows that there is one radular character supporting a clade of dorids that includes *Acanthodoris*, along with three other Onchidorididdae 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 Onchidorididdae 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 were 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 Onchidorididdae are included: *Adalaria, Calycidoris, Diaphorodoris* and *Onchidoris*. Members of the family group Goniodorididdae are included for comparison (*Goniodoris, Okenia*).

Species Descriptions

Family Onchidorididdae Gray, 1827

[= Acanthodoridinae P. Fischer, 1881 = Pseudodorididdae Eliot, 1910 (n.a.) = Ancylodorididdae Thiele, 1926 = Lamellidorididdae Pruvot-Fol, 1933 = Villiersiidae Abbott, 1974 (n.a.) = Calycidorididdae 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. Naked rachis. Narrow radula. First pleural tooth very large, hooked, few external lateral 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 [SeaSlug Forum, accessed 2005]), North Pacific (Aleutian Islands south to Central California [Behrens 1991]).

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. 3F for a drawing of the ventral anterior surface of a specimen from Wales.

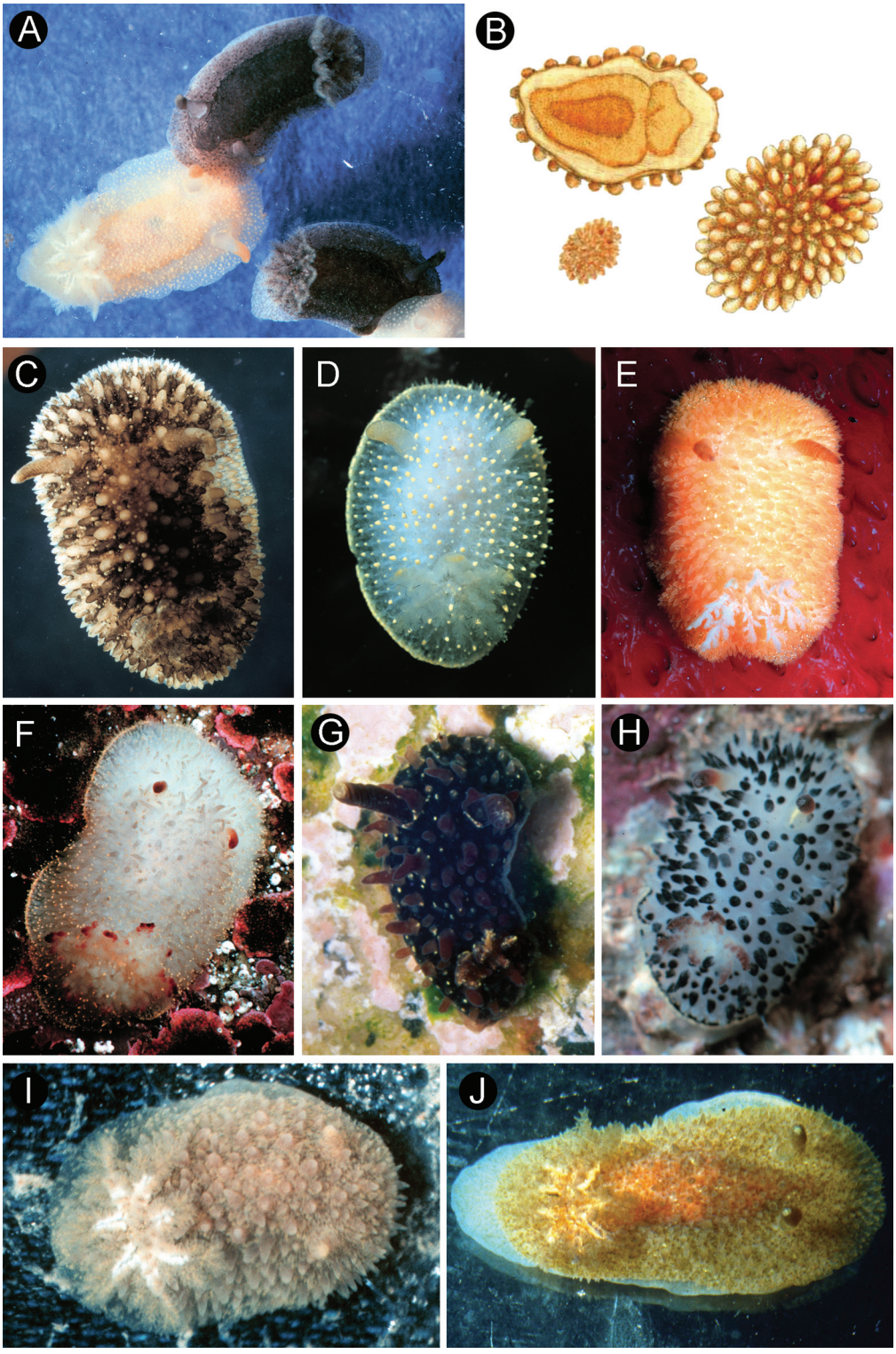
Digestive system.— *Acanthodoris pilosa* shares the same general digestive anatomy as other *Acanthodoris* species (Fig. 3A). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is ovoid, with four large muscles attached, two per side. There are two small salivary 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have multi-tipped, rounded apices (Fig. 2D). The radular formula is $29 \times 3.1.0.1.3$ (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 hermaphroditic duct enters the ampulla terminally. The ampulla is elongate and tubular (Fig. 3C). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 much thinner than the penial sheath. The proximal end widens before terminating into the large round bursa copulatrix. From the bursa a long duct 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 stalked at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and three large pleural nerves and four small pedal 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

Figure 1. Photos of living animals. A. *Acanthodoris pilosa* (Abildgaard in Müller, 1789). Photo by T. Gosliner. B. *Acanthodoris pilosa* original drawing by Abildgaard (1789). C. *Acanthodoris brunnea* MacFarland, 1905. Photo by T. Gosliner. D. *Acanthodoris hudsoni* MacFarland, 1905. Photo by T. Gosliner. E. *Acanthodoris lutea* MacFarland, 1925. Photo by T. Gosliner. F. *Acanthodoris nanaimoensis* O'Donoghue, 1921. Photo by W. Lee. G. *Acanthodoris pina* Marcus and Marcus, 1967. Photo by A. Valdés. H. *Acanthodoris rhodoceras* Cockerell in Cockerell and Eliot, 1905. Photo by R. Ames. I. *Acanthodoris serpentinotus* Williams and Gosliner, 1979. Photo by T. Gosliner. J. *Acanthodoris planca* Fahey and Valdés, 2005. Photo by T. Gosliner.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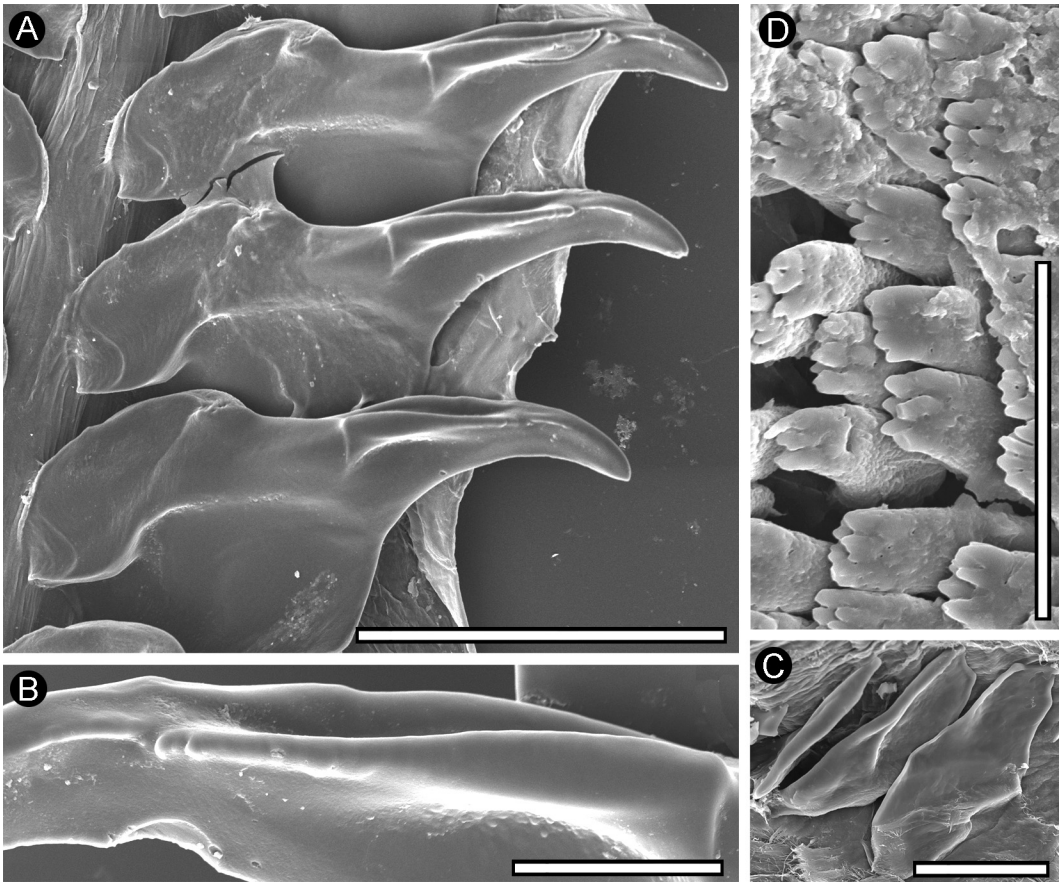

FIGURE 2. *Acanthodoris pilosa* CASIZ 118891. Radular morphology. A First lateral teeth. Scale = 300 µm. B. Close up of denticles. Scale = 50 µm. C. Outer lateral teeth. Scale = 50 µm. D. Jaw rodlets. Scale = 50 µm.

(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 animal 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. This designation stabilizes the name *A. pilosa* with contemporary usage.

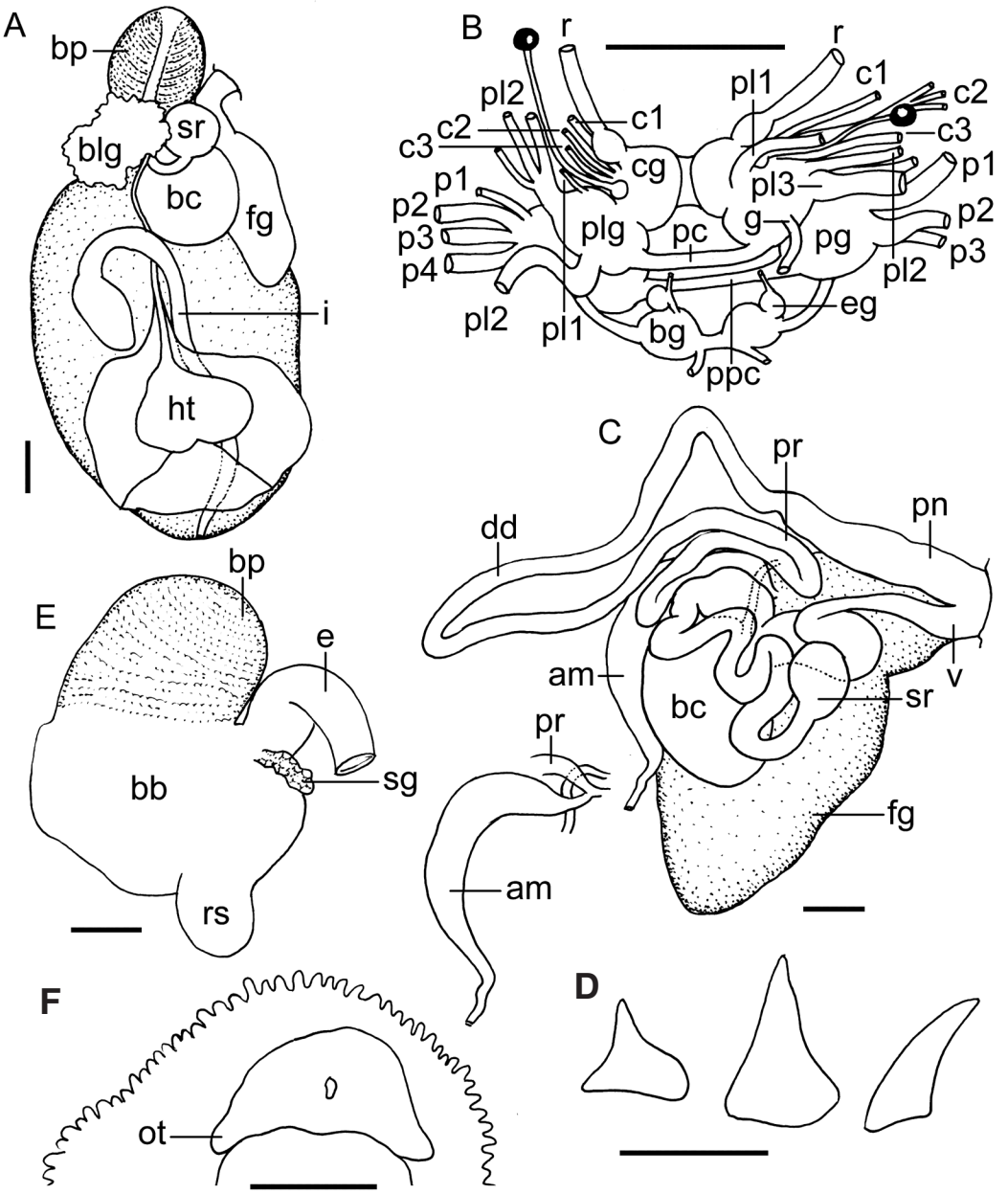

FIGURE 3. *Acanthodoris pilosa* CASIZ 118891. A. Digestive system. B. Cerebro-pleural ganglia. C. Reproductive morphology with detail of oviduct, prostate and ampulla morphology. D. Detail of penial spines. E. Buccal bulb. F. Anterior ventral surface. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bg=buccal ganglion, blg=blood gland, bp=buccal pump, c1–3=cerebral ganglia, cg=cerebral ganglion, dd=deferent duct, e=esophagus, fg=female gland mass, ht=heart, od=oviduct, ot=oral tentacle, pg=pedal ganglion, p1–4=pedal nerves, pc=pedal commissure, pg+plg=pleural ganglion, pl1–3=pleural nerves, ppc=parapedal commissure, pr=prostate, r=rhinonophoral nerves, rs=radular sac, sg=salivary gland, sr=seminal receptacle. Scale bars = 1 mm.

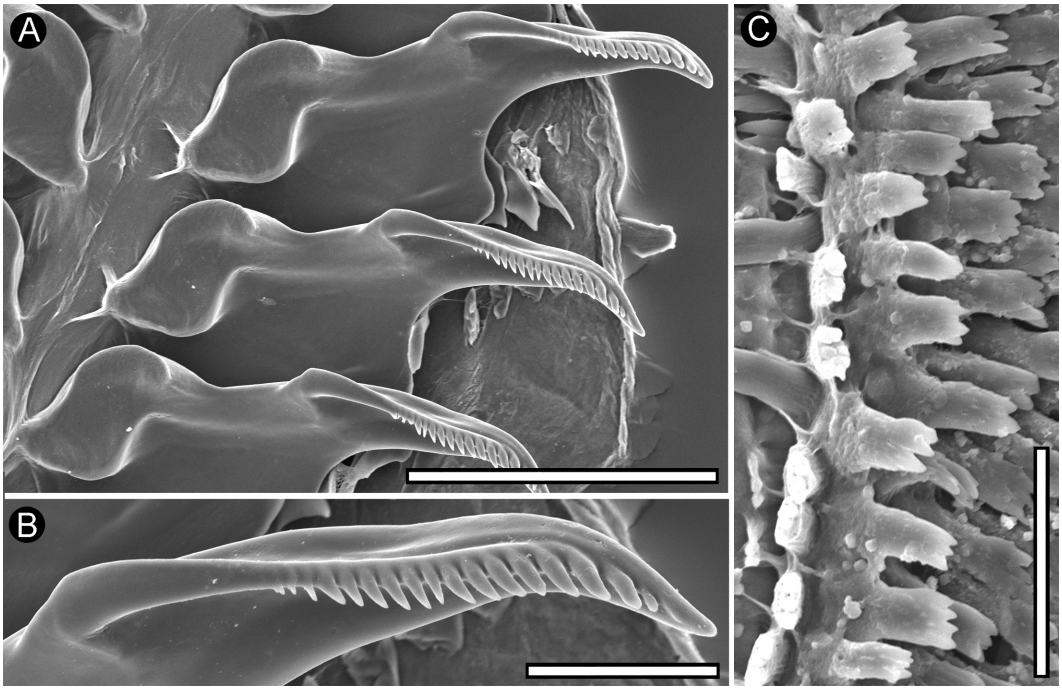

FIGURE 4. *Acanthodoris brunnea* CASIZ 105621. Radular morphology. A First lateral teeth. Scale = 200 µm. B. Close up of denticles. Scale = 50 µm. C. Jaw rodlets. Scale = 30 µm.

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.

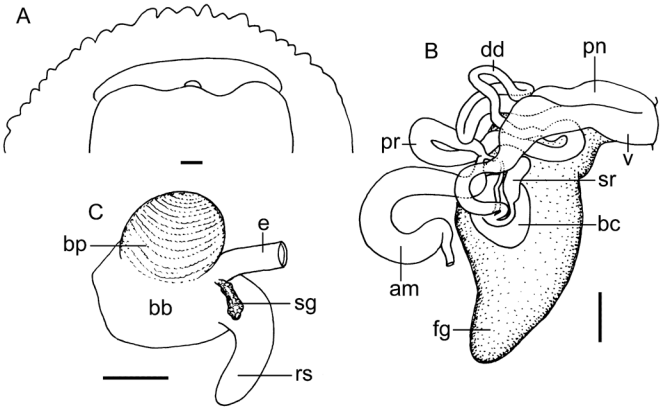

FIGURE 5. *Acanthodoris brunnea* CASIZ 105621. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

DISTRIBUTION.— West coast of North America, from Santa Monica, southern California, USA to Vancouver Island, Canada (MacFarland 1905; O'Donoghue 1921; Behrens 1991, 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 present 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. 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. 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have multi-tipped, pointed apices (Fig. 4C). The radular formula (CASIZ 105621) is $29 \times 4.1.0.1.4$, 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 hermaphroditic duct enters the ampulla terminally. The ampulla is elongate (Fig. 5B). It branches into the oviduct and the tubular prostate. 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 penial sheath 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 penial sheath. The proximal end narrows and terminates into the round bursa copulatrix. From the bursa a short duct 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, Chile. 7 m depth. 3 specimens, 6–7 mm dissected. January 1995, S. Millen.

Distribution.— Falkland Islands (Eliot 1907; Odhner 1926), southern 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 Chile.

Digestive system.— *Acanthodoris falklandica* shares the same general digestive anatomy as

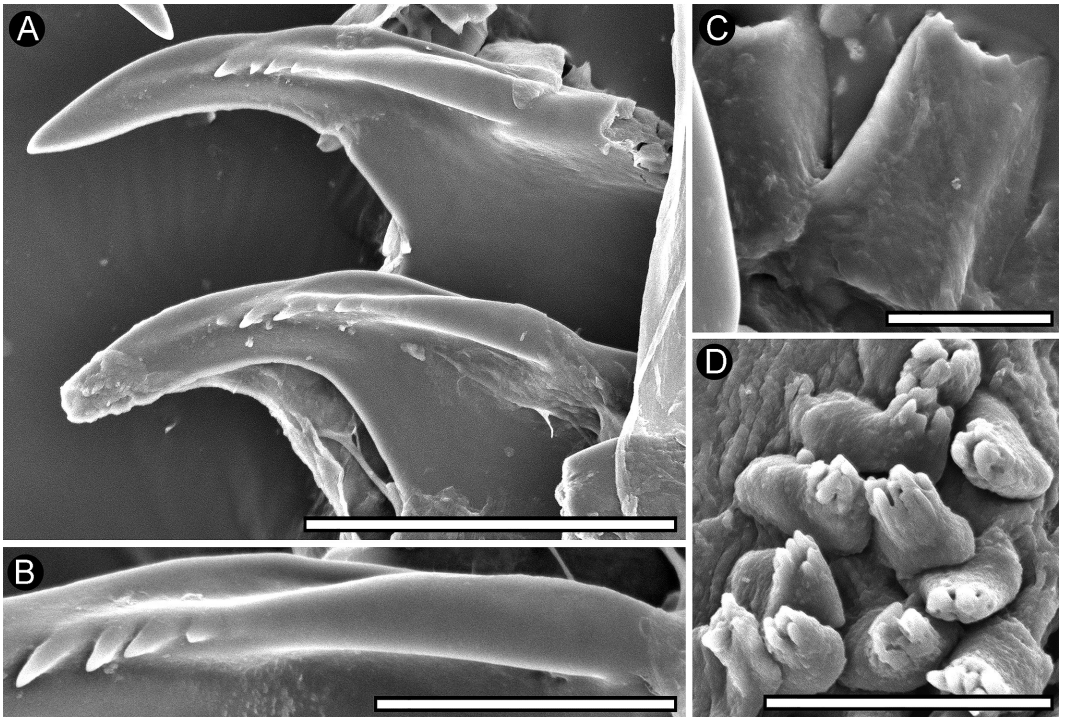

FIGURE 6. *Acanthodoris falklandica* LACM 153981. Radular morphology. A First lateral teeth. Scale = 50 µm. B. Close up of denticles. Scale = 20 µm. C. Outer lateral teeth. Scale = 10 µm. D. Jaw rodlets. Scale = 20 µm.

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 salivary 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 with rodlets at the top of the opening. The rodlets have multitipped, pointed apices (Fig. 6D). The radular formula is

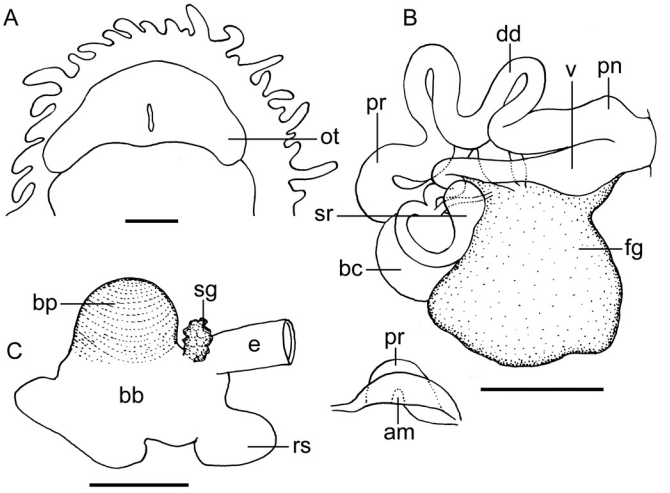

FIGURE 7. *Acanthodoris falklandica* LACM 153981. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 0.5 mm.

23×2.1.0.1.2 (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 hermaphroditic duct enters the ampulla terminally. The ampulla is short and tubular (Fig. 7B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath is wide, elongate and terminates into a common genital atrium. The penis does not contain penial hooks. The 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 penial sheath. At the proximal end, the vaginal duct narrows before terminating into the large, round bursa copulatrix. From the bursa a long duct 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 (1926) and Marcus' (1959) descriptions and illustrations of the radula. The specimen we examined has a formula of 23 × 5.1.0.1.5. Eliot's description of the new species included a radular formula of 33 × 7.1.0.1.7 with up to seven pointed, flattened outer plates. Odhner described a radular formula of 30 × 4.1.0.1.4 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 San Diego, southern California, USA to Vancouver Island, Canada (MacFarland 1905; O'Donoghue 1921; Behrens 1991, 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 salivary 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

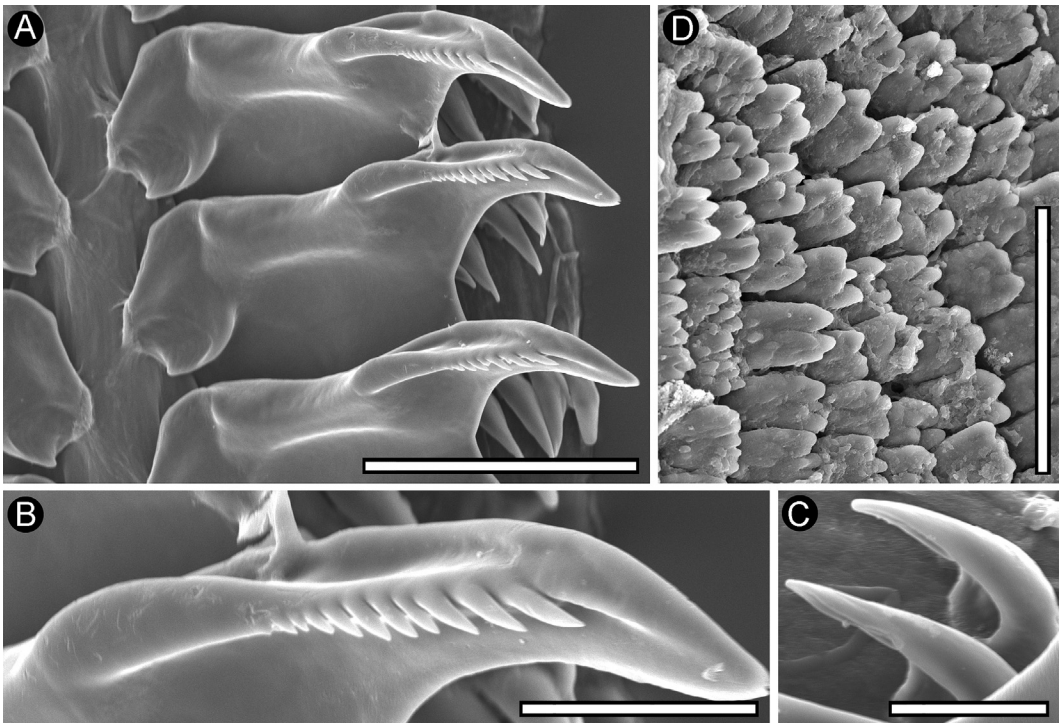

FIGURE 8. *Acanthodoris hudsoni* CASIZ 070785. Radular morphology. A First lateral teeth. Scale = 100 µm. B. Close up of denticles. Scale = 30 µm. C. Outer lateral teeth. Scale = 20 µm. D. Jaw rodlets. Scale = 50 µm.

with a longitudinal crease as described by MacFarland (1905). The labial disk frames the opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have multi-tipped, pointed apices (Fig. 8D). The radular formula is 24 × 5.1.0.1.5 (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.

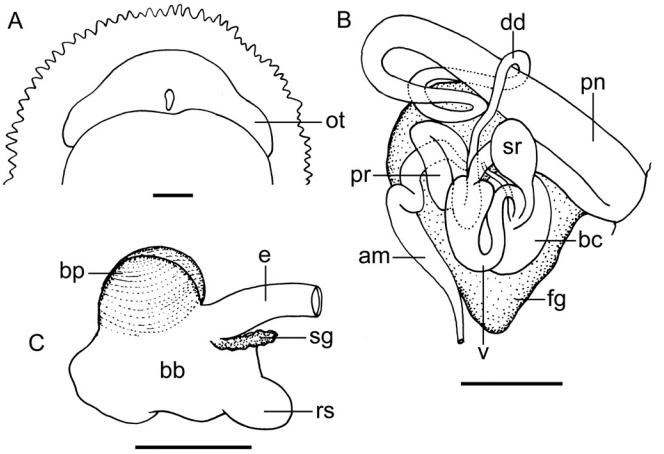

FIGURE 9. *Acanthodoris hudsoni* CASIZ 070785 A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

Reproductive system.— The hermaphroditic duct enters the ampulla terminally. The ampulla is elongate (Fig. 9B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 penial sheath. 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 a duct 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. 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 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, Marin County, northern California to southern Baja California (Cape Colnett) (MacFarland 1925; Behrens 1991, 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 salivary 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have rounded, scalloped apices (Fig. 10D). The radular formula is $34 \times 7.1.0.1.7$ (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,

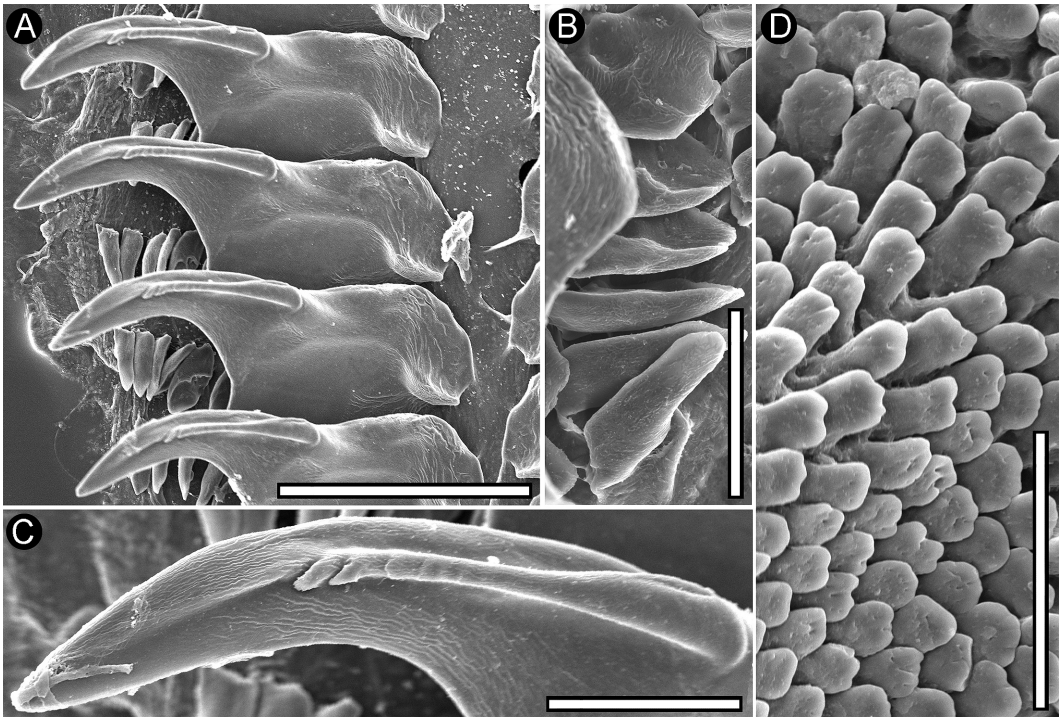

FIGURE 10. *Acanthodoris lutea* CASIZ 070677. Radular morphology. A First lateral teeth. Scale = 200 µm. B. Outer lateral teeth. Scale = 20 µm. C. Close up of denticles. Scale = 50 µm. D. Jaw rodlets. Scale = 50 µm.

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 hermaphroditic duct enters the ampulla terminally. The ampulla is large and bulbous (Fig. 11B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath is tubular, elongate and terminates into a

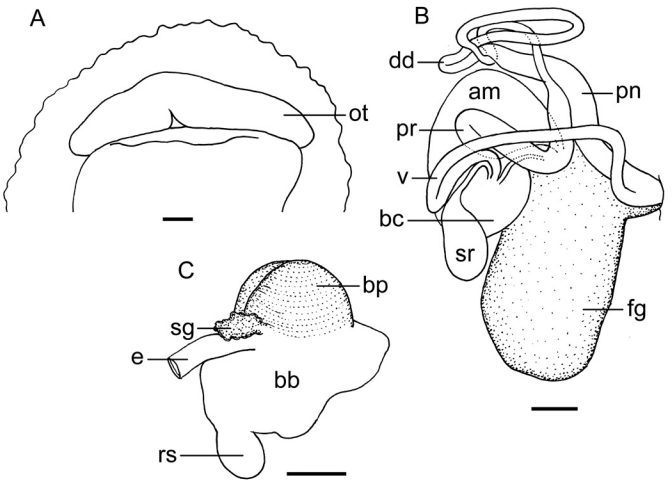

FIGURE 11. *Acanthodoris lutea* CASIZ 070677 A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

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 a short duct 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.

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 and G. Sphon. LACM 72-108 Cape Arano State Park, Oregon. Intertidal. 1 specimen, 20 mm. August 1972, G. Sphon and G. Kennedy. LACM 71-113 Whale Rock, Del Norte County, 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 (Santa Barbara) (MacFarland 1926; Behrens 1991, 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 Figure 13A 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 salivary 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have blunt, deeply scalloped apices (Fig. 12D). The radular formula (LACM 72-103) is $33 \times 3.1.0.1.3$, 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,

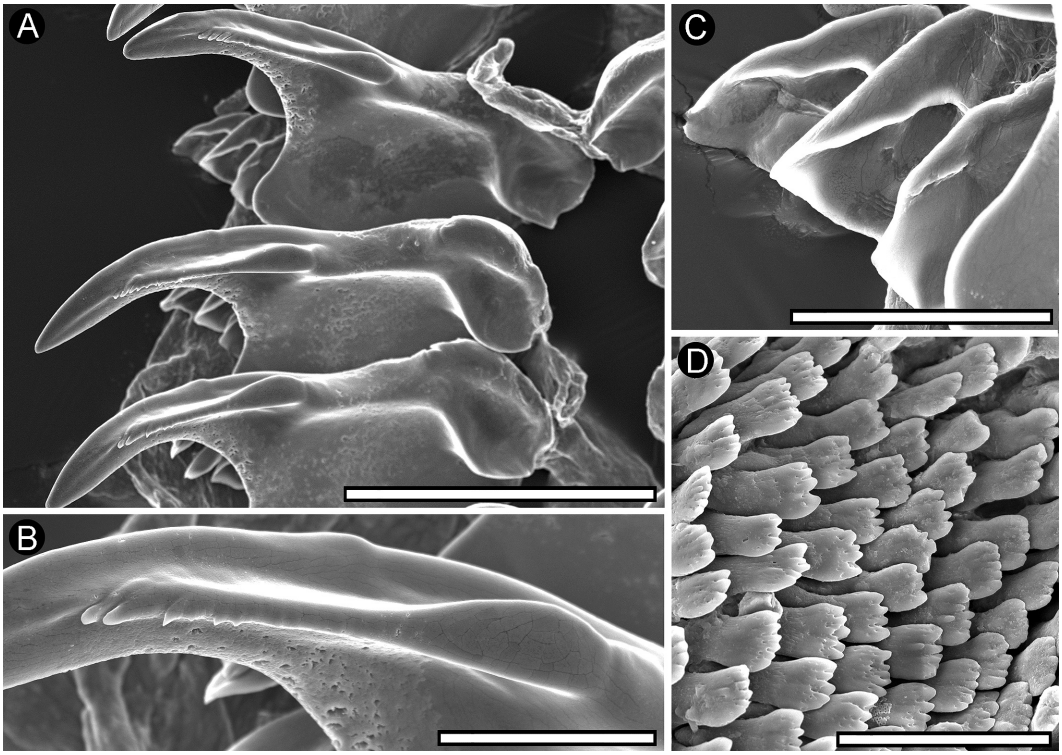

FIGURE 12. *Acanthodoris nanaimoensis* LACM 72-103. Radular morphology. A First lateral teeth. Scale = 200 µm. B. Close up of denticles. Scale = 50 µm. C. Outer lateral teeth. Scale = 50 µm. D. Jaw rodlets. Scale = 50 µm.

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 hermaphroditic duct enters the ampulla terminally. The ampulla is long and thin (Fig. 12B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath is tubular, elongate and terminates into the common genital atrium. The penial sheath does not contain penial hooks. The vaginal duct is very long and wider than the def-

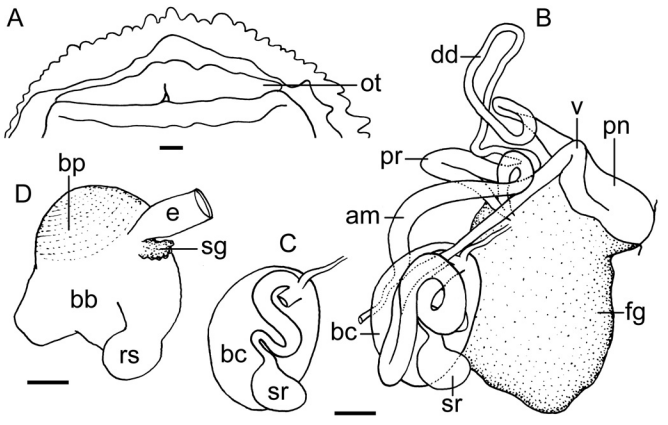

FIGURE 13. *Acanthodoris nanaimoensis* LACM 72-103. A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

erent 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 a long duct 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's (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 31 × 3.1.0.1.3. 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 a long, sub-conical penis, armed with minute hooks. Our specimens match MacFarland's (1926) description of the reproductive organs. O'Donoghue (1921) did not illustrate the reproductive system of his specimens, but only described the penial morphology.

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. Our study suggests that the two species are synonymous, with *A. nanaimoensis* having priority.

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

Acanthodoris nanega Burn, 1969

Figs. 14–15.

Acanthodoris nanega Burn, 1969.

Material Examined.— CASIZ 100574 Victor Harbour, Granite Island, South Australia. 3.6 m depth. 2 specimens, 7–10 mm, 7 mm dissected. August 1994 (no collector identified).

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 salivary glands at the side of the oral tube, near the radular sac (Fig. 15C). 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have blunt, deeply scal-

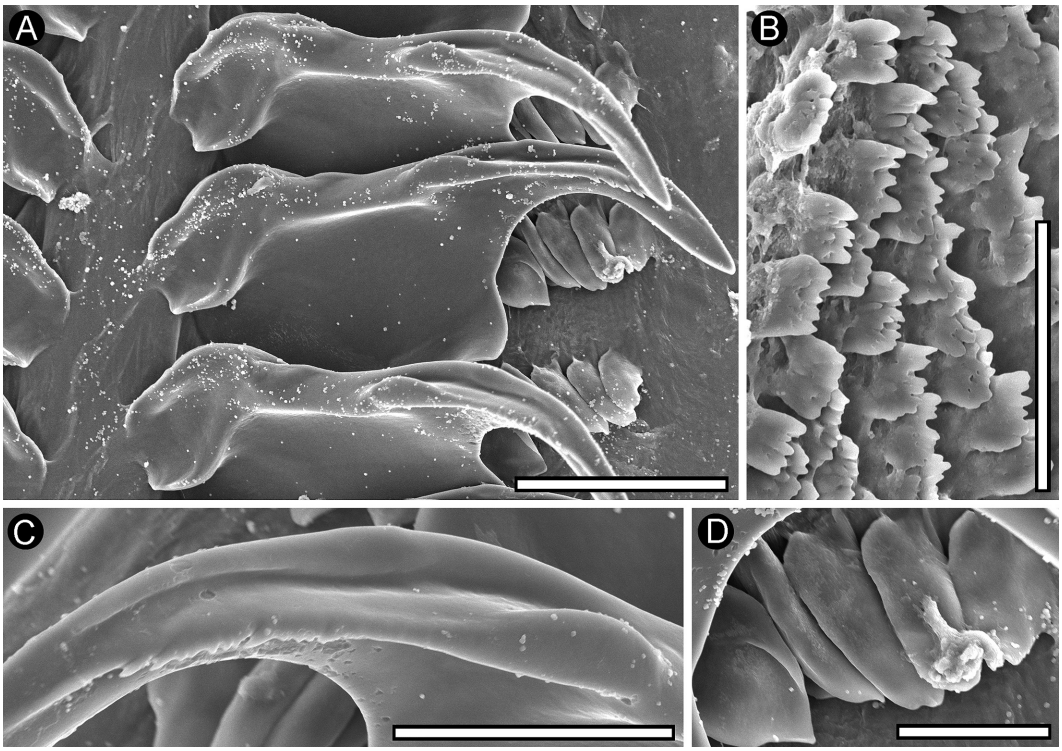

FIGURE 14. *Acanthodoris nanega* CASIZ 100574. Radular morphology. A First lateral teeth. Scale = 100 µm. B. Jaw rodlets. Scale = 50 µm. C. Close up of denticles. Scale = 50 µm. D. Outer lateral teeth. Scale = 30 µm.

loped apices (Fig. 14B). The radular formula is $27 \times 5.1.0.1.5$ (CASIZ 100574), 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.

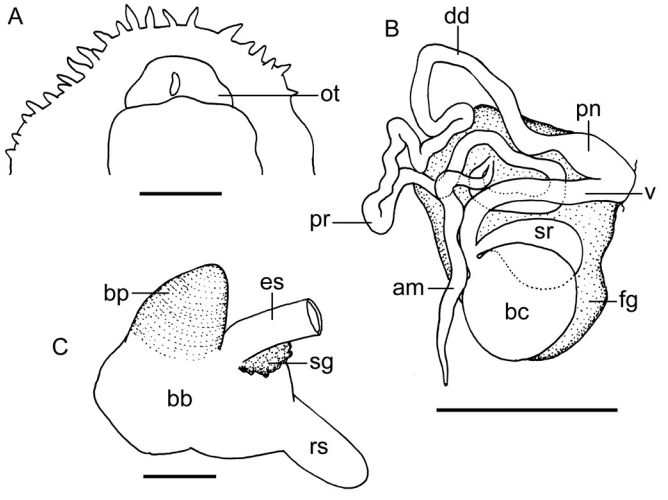

FIGURE 15. *Acanthodoris nanega* CASIZ 100574. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

Reproductive system.— The hermaphroditic duct enters the ampulla terminally. The ampulla is elongate (Fig. 15B). It branches into the oviduct and the tubular prostate. 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 penial sheath is short and bulbous and terminates into the common genital atrium. The penial sheath 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 a duct 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.

Burn (1969) noted the similarities between *A. nanega* and *A. globosa* Abraham, 1877, from New Zealand. However, the only difference he mentioned to distinguish the two species was a broader lateral tooth base in *A. nanega*. It is possible that these two species are synonymous.

Acanthodoris pina Ev. Marcus and Er. Marcus, 1967

Figs. 1G, 16–17.

Acanthodoris pina Marcus and Marcus, 1967:201.
Acanthodoris stohleri Lance 1968:8, pl. 2, figs. 7–11.

Material Examined.— LACM 153100 Bahía de los Ángeles, 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.— Northwest Coast of Mexico, Baja California (Marcus and Marcus 1967, Lance 1968, and present study).

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 salivary 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have blunt, deeply scalloped apices (Fig. 16D). The radular formula is $31 \times 5.1.0.1.5$ (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

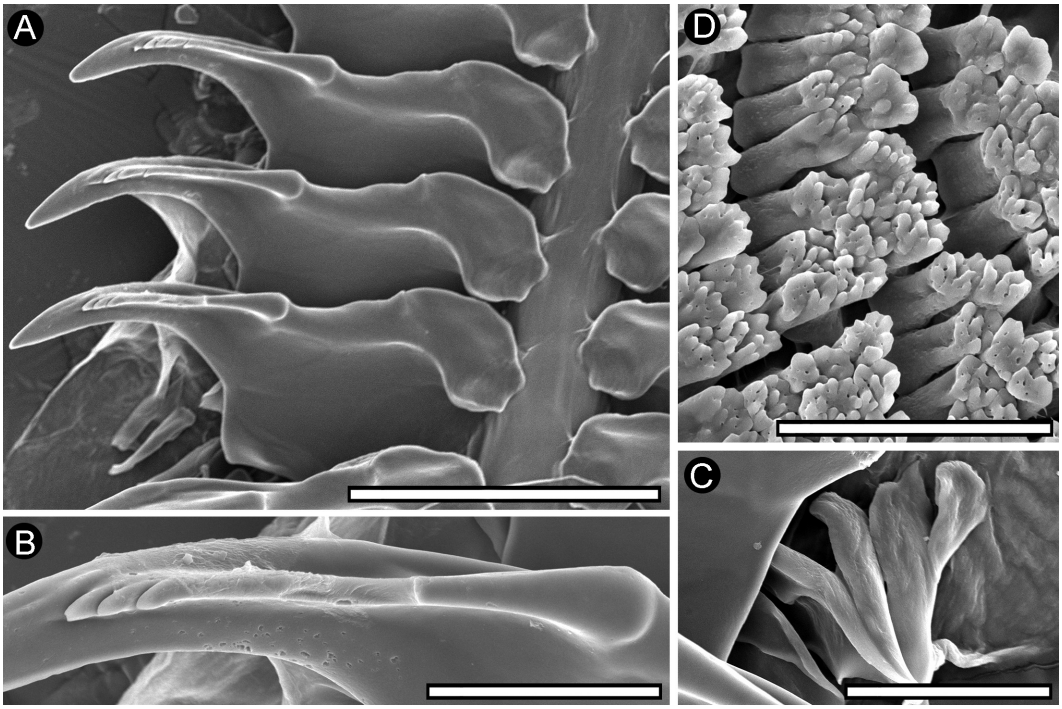

FIGURE 16. *Acanthodoris pina* LACM 153100. Radular morphology. A First lateral teeth. Scale = 200 µm. B. Close up of denticles. Scale = 50 µm. C. Outer lateral teeth. Scale = 50 µm. D. Jaw rodlets. Scale = 50 µm.

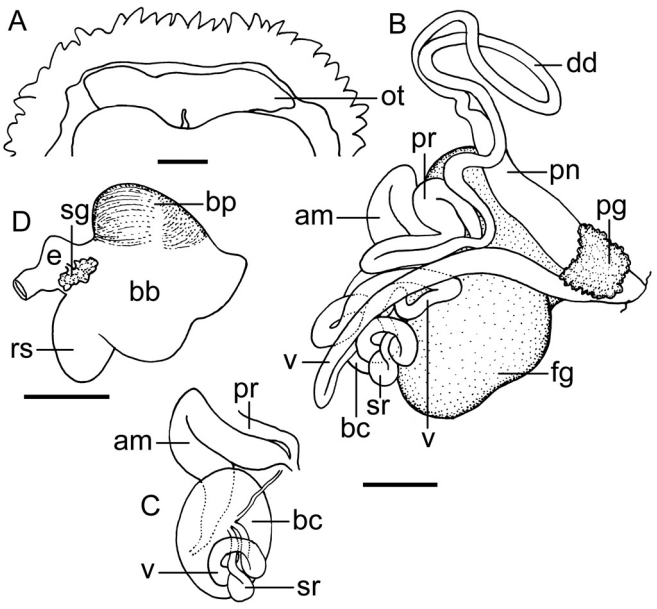

FIGURE 17. *Acanthodoris pina* LACM 153100 A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

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 hermaphroditic duct enters the ampulla terminally. The ampulla is thick and elongate (Fig. 17B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath is elongate and wide and terminates into the common genital atrium. There is a glandular portion of the penis located at the distal end. We did not observe 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 a duct 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 and 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 of *Acanthodoris* collected in Bahía San Luis Gonzaga, Baja California. He did not describe the reproductive system except to note the presence of penial spines. His publication, naming a new species, *Acanthodoris stohleri,* was preceeded 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 and Eliot, 1905:38.
Acanthodoris sp. MacGinitie and MacGinitie, 1949:363.

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 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 Alaska 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.

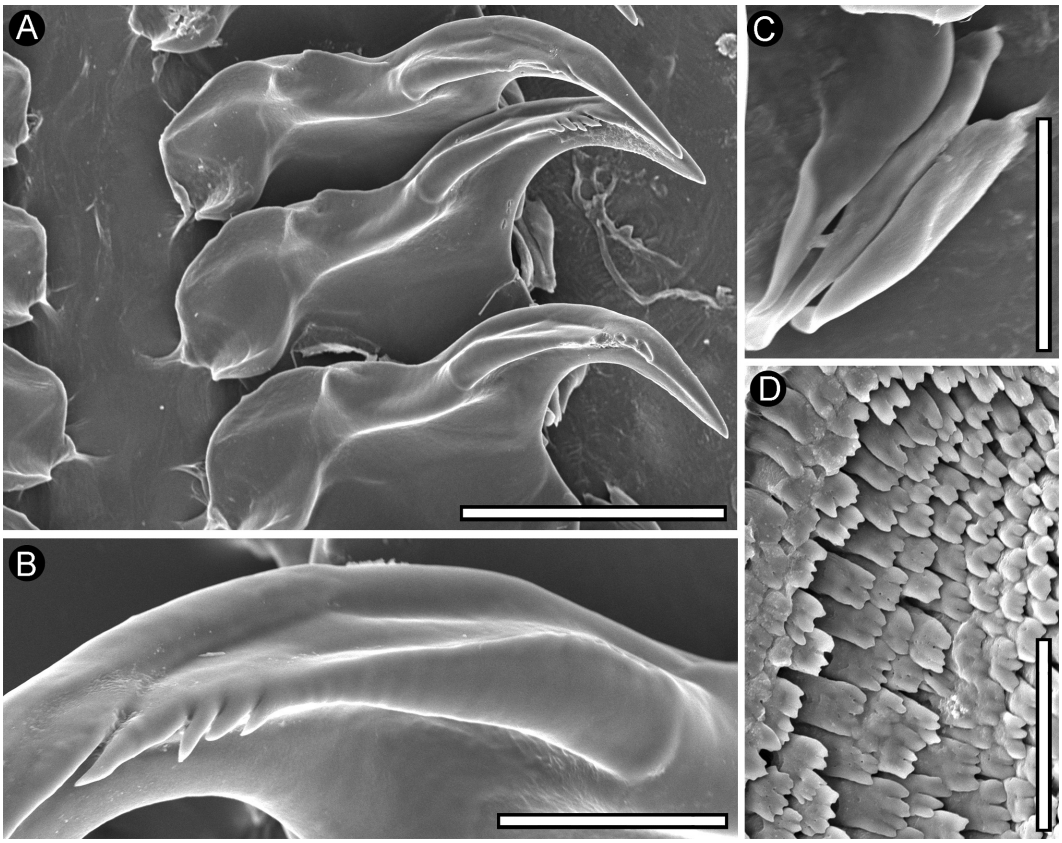

FIGURE 18. *Acanthodoris rhodoceras* CASIZ 068334. Radular morphology. A First lateral teeth. Scale = 200 µm. B. Close up of denticles. Scale = 50 µm. C. Outer lateral teeth. Scale = 30 µm. D. Jaw rodlets. Scale = 50 µm.

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 salivary glands at the side of the oral tube, near the radular sac (Fig. 19C). The radular sac protrudes from the bulb, under the esophagus. There is a large ovoid buccal pump with a longitudinal crease as found in other *Acanthodoris* species. The labial disk frames the opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have pointed, deeply scalloped apices (Fig. 18D). The radular formula is $32 \times 3.1.0.1.3$ (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 hermaphroditic duct enters the ampulla terminally. The ampulla is sausage shaped and elongate (Fig. 19B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 a duct connects to the smaller ovoid seminal receptacle. The long uterine duct connects at the base of the bursa.

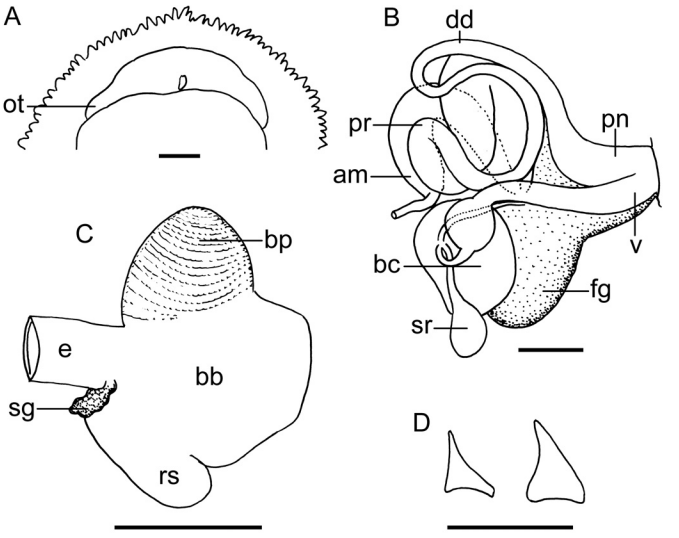

FIGURE 19. *Acanthodoris rhodoceras* CASIZ 068334. A. Anterior ventral surface. Scale bar = 1 mm. B. Reproductive morphology. Scale bar = 1 mm. C. Buccal bulb. Scale bar = 1 mm. D. Sketch of penial spines.Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale = 30 µm.

REMARKS.— The specimens we examined of *A. rhodoceras* match Cockerell'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 serpentinotus Williams and Gosliner, 1979
Fig 1I.

Acanthodoris serpentinotus 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 (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 caerulescens 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. He speculated that *A. globosa* and *A. metulifer* may be synonymous. 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) and Eliot (1907:356) 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 the two species.

Acanthodoris 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*, *A. nanega*, and *A. globosa* causes one to suspect that the four species may be synonymous. However, since the type material of *A. mollicella*, *A. metulifera*, or *A. globosa* could not be located at any of the major natural history museums, no further revision of these species is possible.

Acanthodoris uchidai Baba 1935:119

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 Mabille, 1891:11

Locality.— Cape Horn

Remarks.— This species was only perfunctorily described by Rochebrune and Mabille (Rochebrune and Mabille 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.

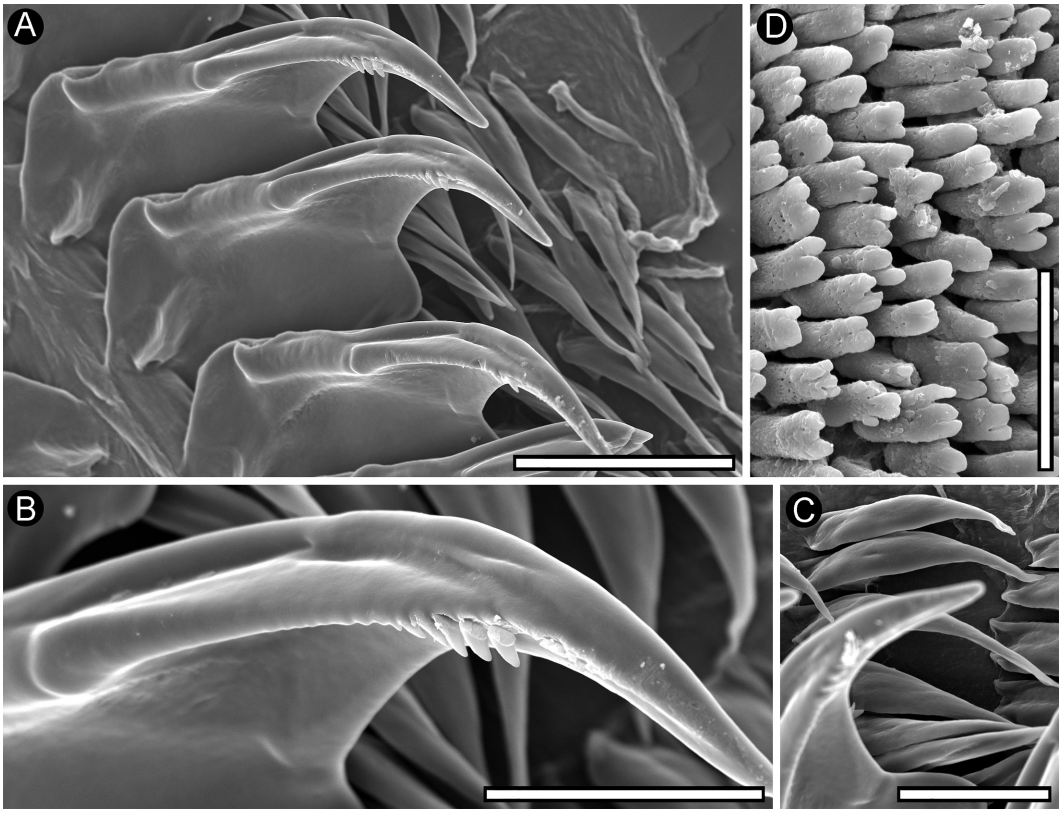

Figure 20. *Acanthodoris planca* CASIZ 171754. Radular morphology. A First lateral teeth. Scale = 100 µm. B. Close up of denticles. Scale = 50 µm. C. Outer lateral teeth. Scale = 50 µm. D. Jaw rodlets. Scale = 30 µm.

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.

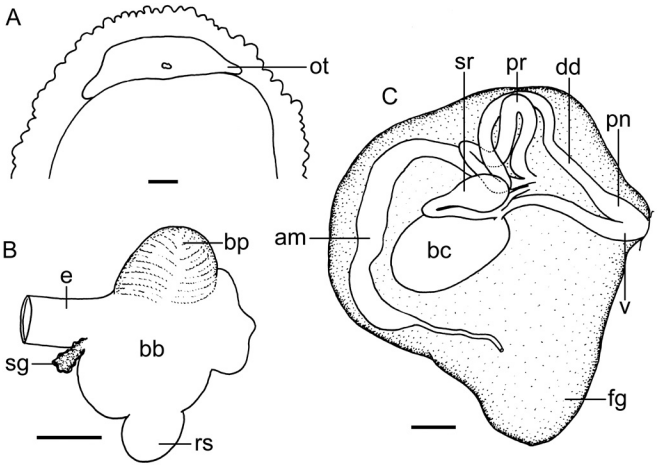

FIGURE 21. *Acanthodoris planca* CASIZ 171754. A. Anterior ventral surface. Scale bar = 1 mm. B. Buccal bulb. C. Reproductive morphology. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

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 salivary 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets are elongate, blunt and have multi-apices (Fig. 20D). The radular formula is $32 \times 6.1.0.1.6$ (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 hermaphroditic duct enters the ampulla terminally. The ampulla is an elongate tube (Fig. 21C). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 a duct 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* 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 (1845) as colorless and by Bergh (1879) as whitish or yellowish.

The radular morphology differs between these species. *Acanthodoris planca* has densely arranged, multifid jaw rodlets and 6–7 elongate, pointed outer lateral teeth. *Acanthodoris lutea* has rounded, scalloped rodlets and 5–6 flattened, triangular plates "with a slight basal thickening"(MacFarland 1925). Verrill (1879) did not report the radular morphology of *A. citrina* but Thompson and Brown (1984) provided scanning electron micrographs of *A. pilosa*. *Acanthodoris pilosa* has three outer lateral teeth that are flattened plates with rounded, multi-tipped labial rodlets.

There are reproductive differences as well. Both the penis and vaginal duct of *Acanthodoris planca* are shorter and thinner than those 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 most 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 (1987) 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.

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

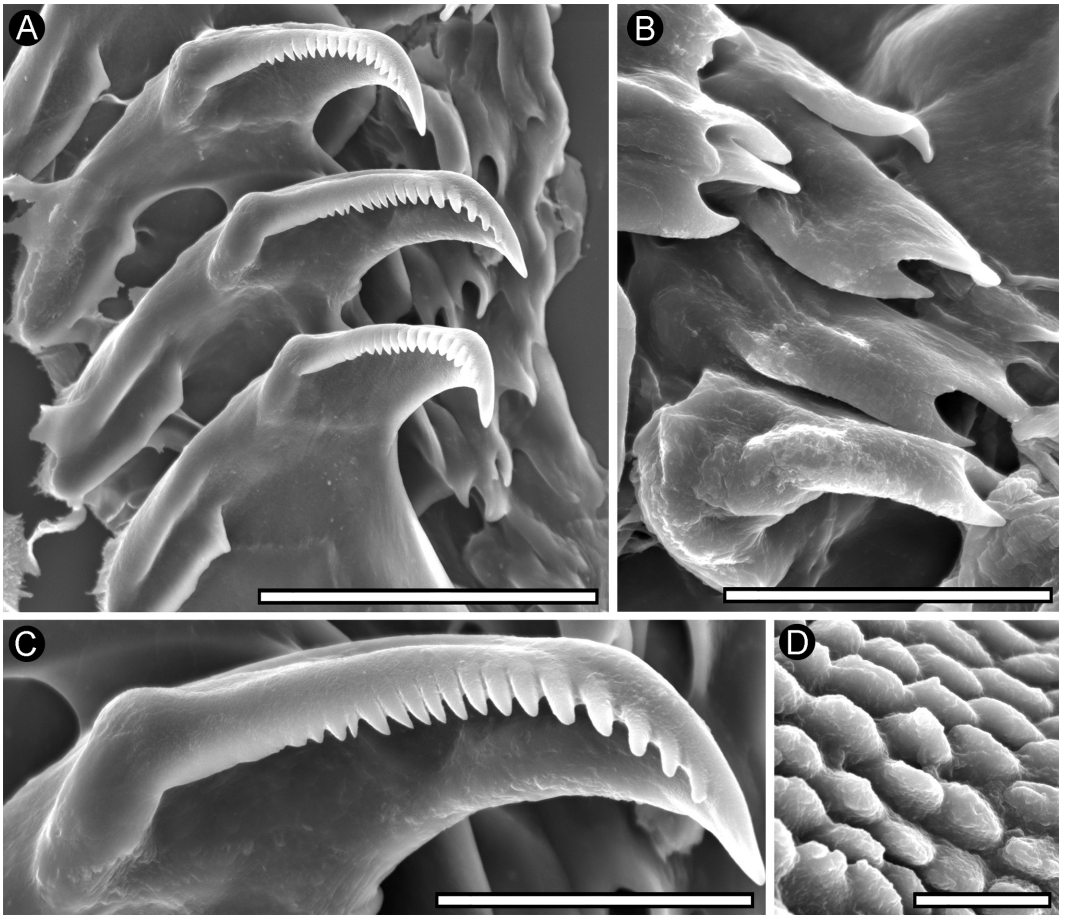

FIGURE 22. *Adalaria jannae* CASIZ 142450. Radular morphology. A First lateral teeth. Scale = 50 µm. B. Close up of outer lateral teeth. Scale = 20 µm. C. Close up of denticles. Scale = 20 µm. D. Jaw rodlets. Scale = 10 µm.

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 Alaska.

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 salivary 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

Onchidoriddidae species. The labial disk frames the opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have blunt, deeply scalloped apices (Fig. 22D). The radular formula is 37 × 4.1.0.1.4 (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 (Figs. 22A–C). 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.

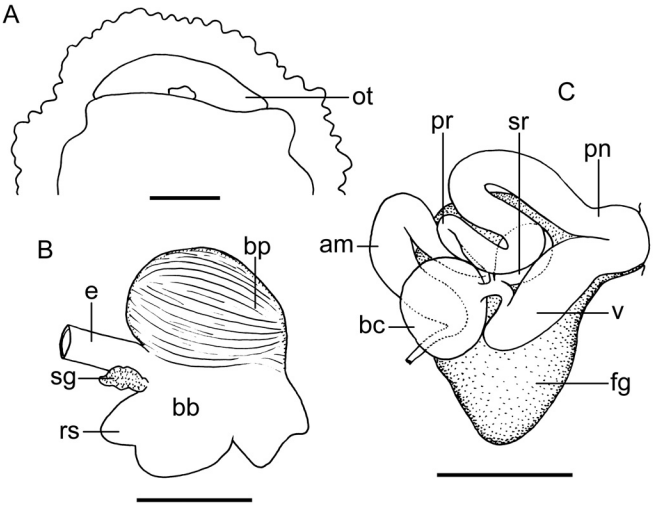

FIGURE 23 (right). *Adalaria jannae* CASIZ 142450. A. Anterior ventral surface. Scale bar = 1 mm. B. Buccal bulb. Scale bar = 0.5 mm. C. Reproductive morphology. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bar = 1 mm.

REPRODUCTIVE SYSTEM.— The hermaphroditic duct enters the ampulla terminally. The ampulla is an elongate tube (Fig. 23C). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 a duct 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 Onchidoriddidae.

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. 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.

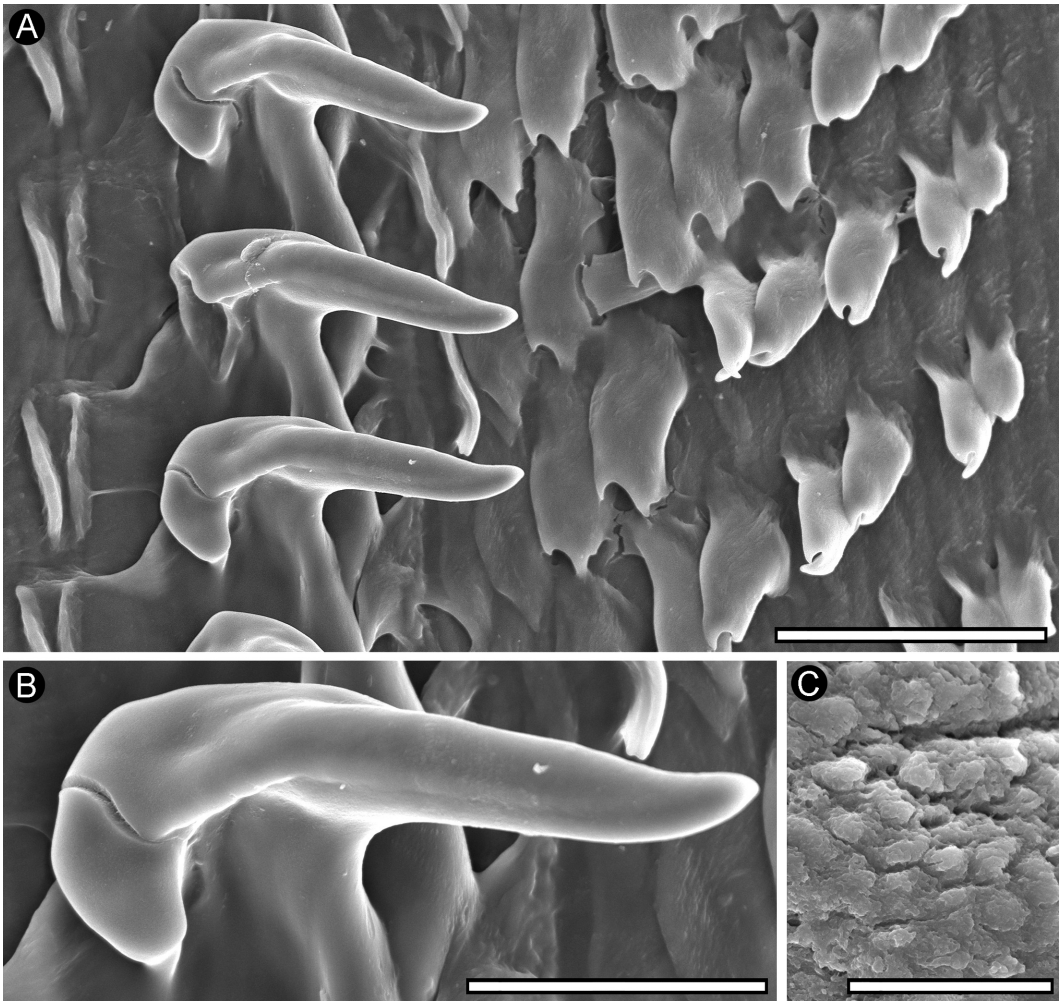

FIGURE 24. *Adalaria proxima* CASIZ 087252. Radular morphology. A. First and outer lateral teeth. Scale = 50 µm. B. Close up of first lateral tooth. Scale = 30 µm. C. Jaw rodlets. Scale = 20 µm.

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.

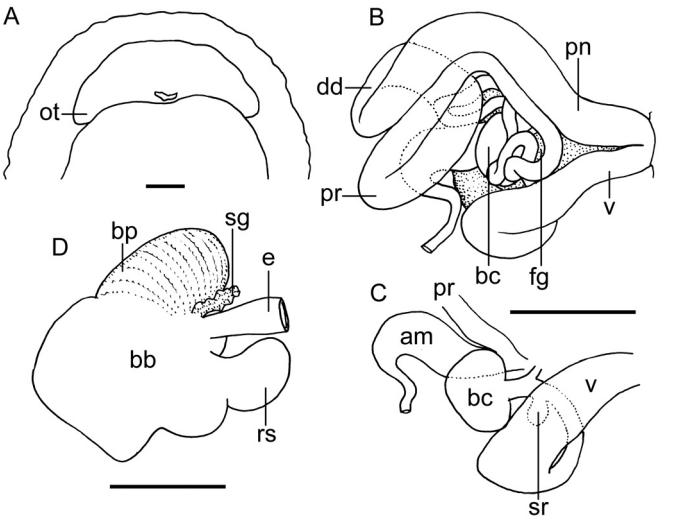

FIGURE 25. *Adalaria proxima* CASIZ 087252. A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

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 salivary 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets are very small, blunt and have rounded tops (Fig. 24C). The radular formula is $43 \times 9.1.1.1.9$ (CASIZ 087252) with all teeth as described by Bergh (1880) and Thompson (1984). 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 hermaphroditic duct enters the ampulla terminally. The ampulla is sausage shaped (Fig. 25B and C). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath is long and as wide as the deferent duct and it terminates into the common genital atrium. No penial armature was observed. 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 copulatrix. 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 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, 1876:133

Figs. 26–27.

Doris sibirica Aurivillius, 1887:372.

MATERIAL EXAMINED.— CASIZ 086915 Wainwright, Alaska. 10 m depth. 1 specimen, 25 mm dis-

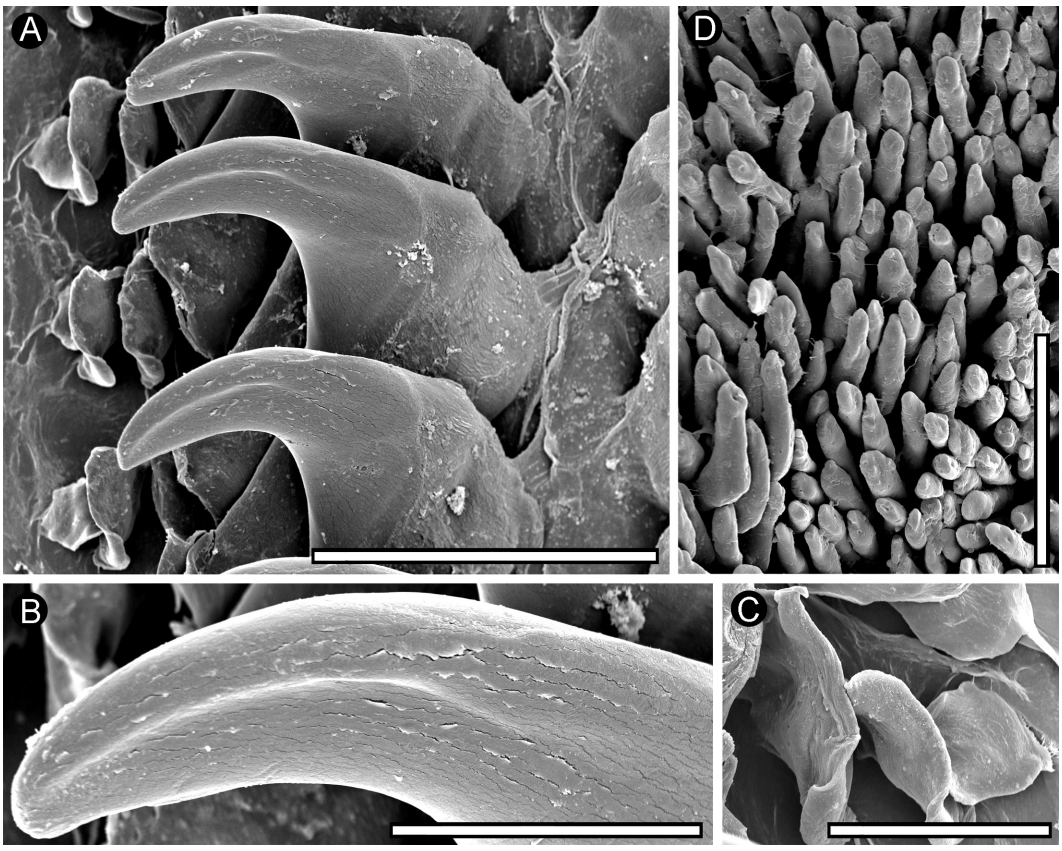

FIGURE 26. *Calycidoris guentheri* CASIZ 086915. Radular morphology. A First lateral teeth. Scale = 300 µm. B. Close up of first lateral tooth. Scale = 100 µm. C. Close up of outer lateral teeth. Scale = 100 µm. D. Jaw rodlets. Scale = 50 µm.

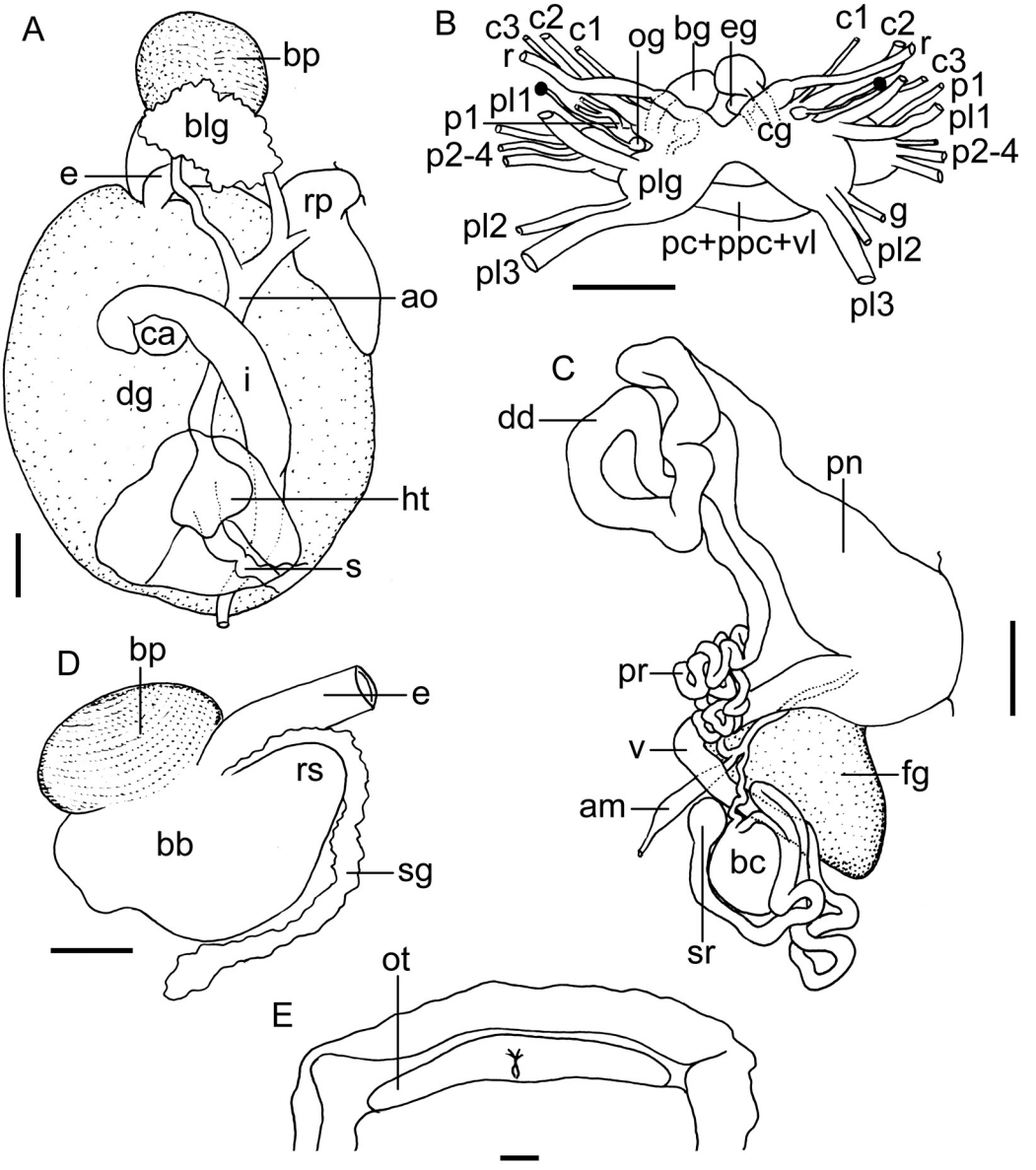

FIGURE 27. *Calycidoris guentheri* CASIZ 086915. A. Digestive system. B. Central nervous system. C. Reproductive morphology. D. Buccal bulb. E. Anterior ventral surface. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bg=buccal ganglion, blg=blood gland, bp=buccal pump, c1–3=cerebral ganglia, cg=cerebral ganglion, dd=deferent duct, e=esophagus, fg=female gland mass, ht=heart, od=oviduct, ot=oral tentacle, pg=pedal ganglion, p1–4=pedal nerves, pc=pedal commissure, pg+plg=pleural ganglion, pl1–3=pleural nerves, ppc=parapedal commissure, pr=prostate, r=rhinonophoral nerves, rs=radular sac, sg=salivary gland, sr=seminal receptacle. Scale bars = 1 mm.

sected. 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets are elongate and have mostly blunt tips (Fig. 26D). The radular formula (CASIZ 086915) is 29 × 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 hermaphroditic duct enters the ampulla terminally. The ampulla is an elongate tube (Fig. 27C). It branches into the oviduct and the tubular prostate. The oviduct enters the large female gland mass. The prostate is a convoluted, thickened tube. It does not narrow into the deferent duct, which is straight and wider, then it further widens into the penial sheath. The penial sheath 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 a thick and very elongate duct 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-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 stalked at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and three large pleural nerves and four small pedal 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 (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 1960:182.
Diaphorodoris luteocincta var. *reticulata* Portmann and Sandmeier 1960:181.

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 exam-

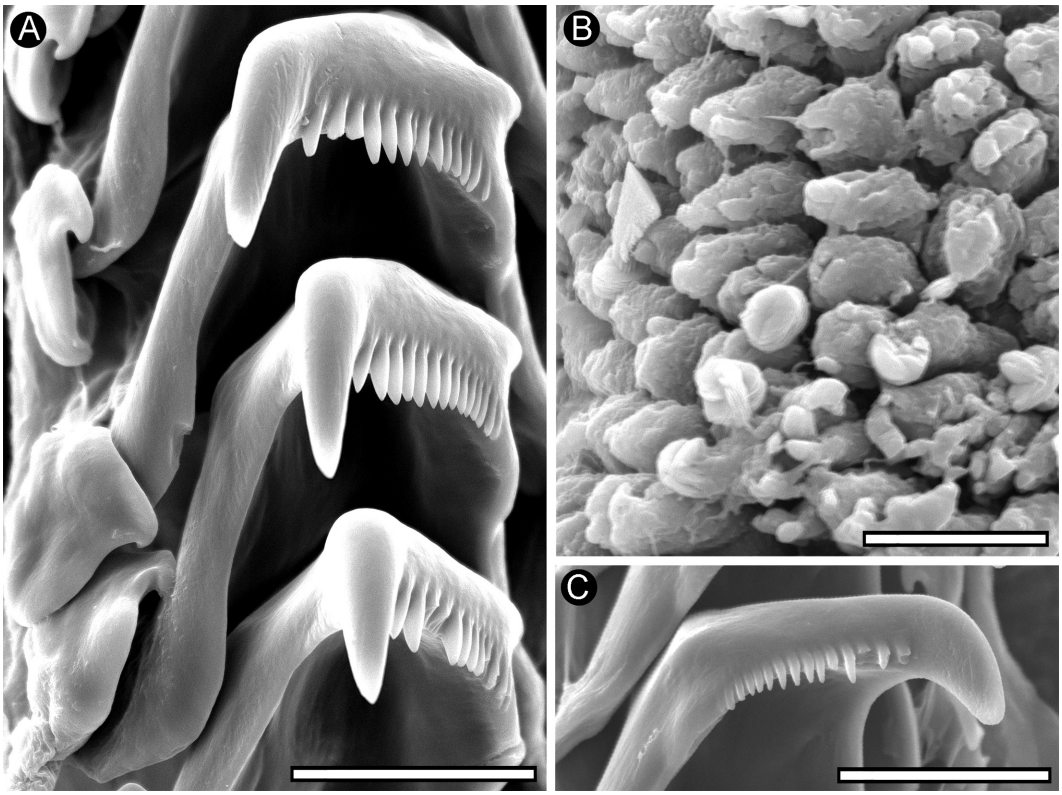

Figure 28. *Diaphorodoris luteocinta* CASIZ 087443. Radular morphology. A First lateral teeth. Scale = 20 µm. B. Jaw rodlets. Scale = 10 µm. C. Close up of denticles. Scale = 25 µm.

ined 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 luteocinta* 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 salivary glands at the side of the oral tube, near the radular sac (Fig. 29C). The trapezoidal radular sac

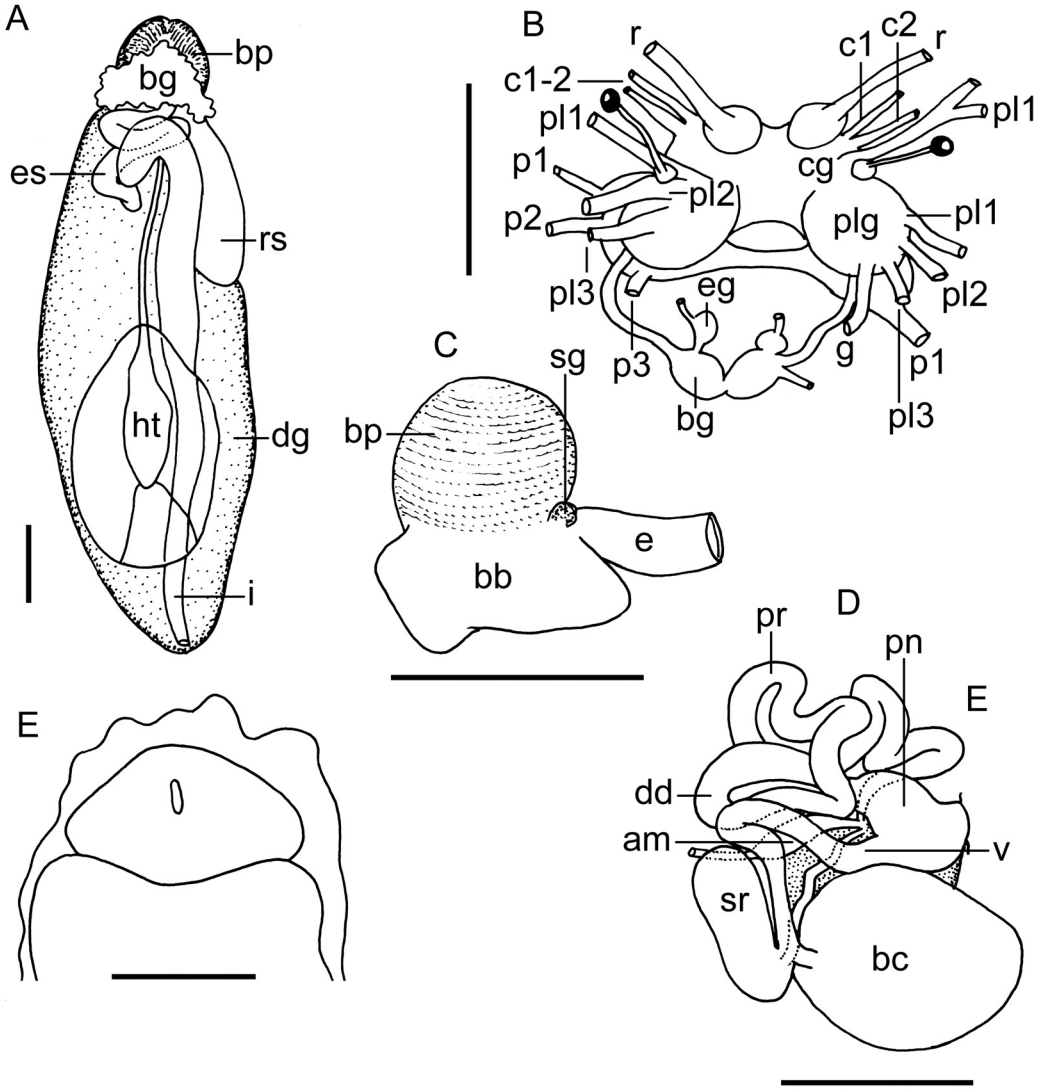

FIGURE 29. *Diaphorodoris luteocinta* CASIZ 087443. A. Digestive system. B. Cerebro-pleural ganglia. C. Buccal bulb. D. Reproductive morphology. E. Anterior ventral surface. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bg=buccal ganglion, blg=blood gland, bp=buccal pump, c1–3=cerebral ganglia, cg=cerebral ganglion, dd=deferent duct, e=esophagus, fg=female gland mass, ht=heart, od=oviduct, pg=pedal ganglion, p1–4=pedal nerves, pc=pedal commissure, pg+plg=pleural ganglion, pl1–3=pleural nerves, ppc=parapedal commissure, pr=prostate, r=rhinonophoral nerves, rs=radular sac, sg=salivary gland, sr=seminal receptacle. Scale bars = 1 mm.

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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have multi-tipped apices that are blunt (Fig. 28B). The radular formula (CASIZ 087443) is $28 \times 1.1.0.1.1$, 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 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 hermaphroditic duct enters the ampulla terminally. The ampulla is elongate and tubular (Fig. 29D). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 a duct 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 stalked at the cerebro-pleural juncture. There are three cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, three large pleural nerves, and three small pedal 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.— 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 Alaska to San Luis Obispo County, 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 anato-

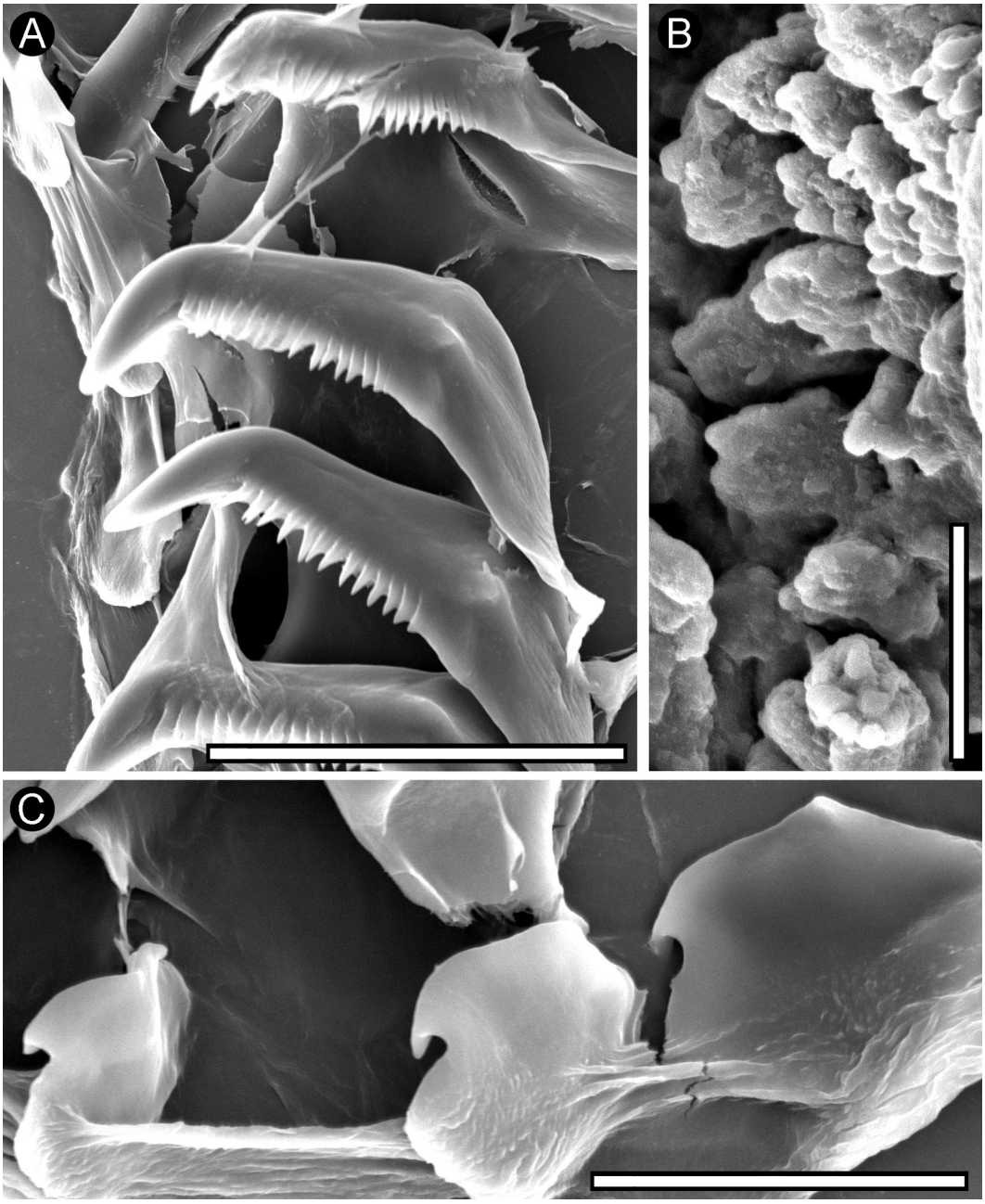

FIGURE 30. *Diaphorodoris lirulatocauda* CASIZ 076203. Radular morphology. A First lateral teeth. Scale = 50 µm. B. Jaw rodlets. Scale = 10 µm. C. Close up of outer lateral teeth. Scale = 20 µm.

my 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets have blunt, scalloped apices, some which look like open flowers (Fig. 30B). The radular formula (CASIZ 076203) is 20 × 1.1.0.1.1, 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.

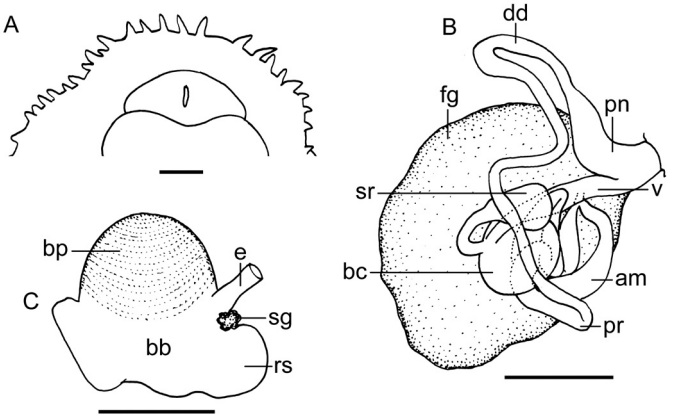

FIGURE 31. *Diaphorodoris lirulatocauda* CASIZ 076203. A. Anterior ventral surface. B. Reproductive morphology. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 0.5 mm.

REPRODUCTIVE SYSTEM.— The hermaphroditic duct enters the ampulla terminally. The ampulla is a thick sausage shape (Fig. 31B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 a short duct 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 mitsuii (Baba, 1938)

Figs. 32–33.

Lamellidoridella mitsuii Baba, 1938:130.
Diaphorodoris sp. Gosliner, 1987:92.

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), South Africa (Gosliner 1987), Australia (Willan and Coleman 1984), and Papua New Guinea (present study).

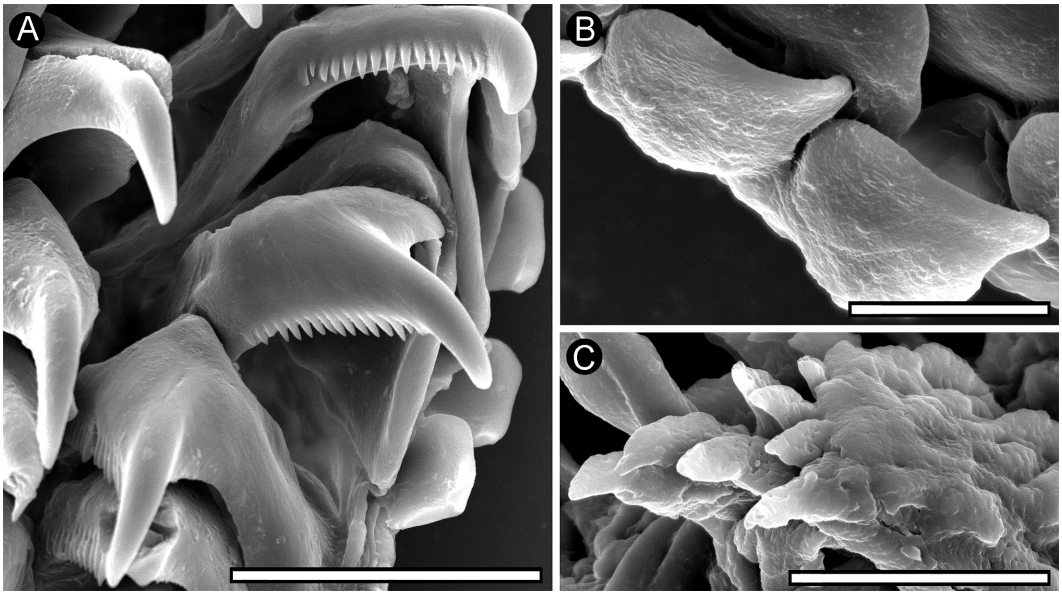

FIGURE 32. *Diaphorodoris mitsuii* CASIZ 069759. Radular morphology. A First lateral teeth. Scale = 30 µm. B. Jaw rodlets. Scale = 10 µm. C. Close up of denticles. Scale = 20 µm.

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 mitsuii* 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 salivary 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

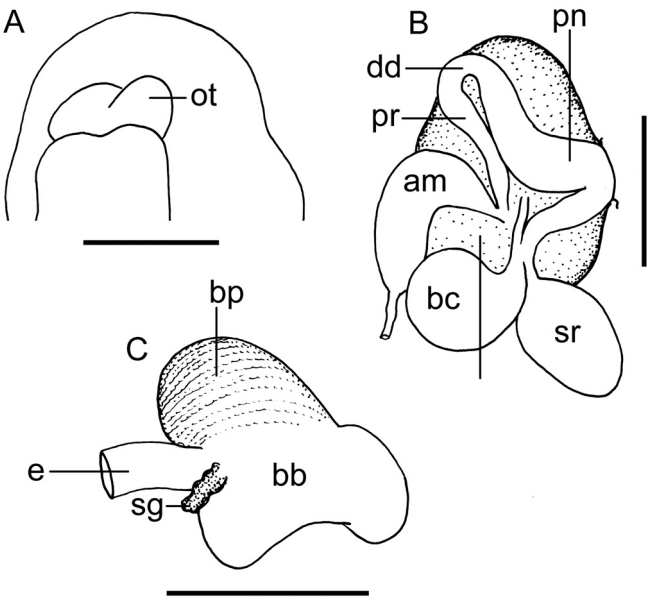

FIGURE 33. *Diaphorodoris mitsuii* CASIZ 069759. A. Anterior ventral surface. Scale bar = 1 mm. B. Reproductive morphology. Scale bar = 0.5 mm. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bar = 0.5 mm.

with a longitudinal crease as found in other *Diaphorodoris* species. The labial disk frames the opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets are pointed with a single apex (Fig. 32C). The radular formula (CASIZ 069759) is 20 × 1.1.0.1.1 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 hermaphroditic duct enters the ampulla terminally. The ampulla is sausage-shaped (Fig. 33B). It branches into the oviduct and the tubular prostate. The thin

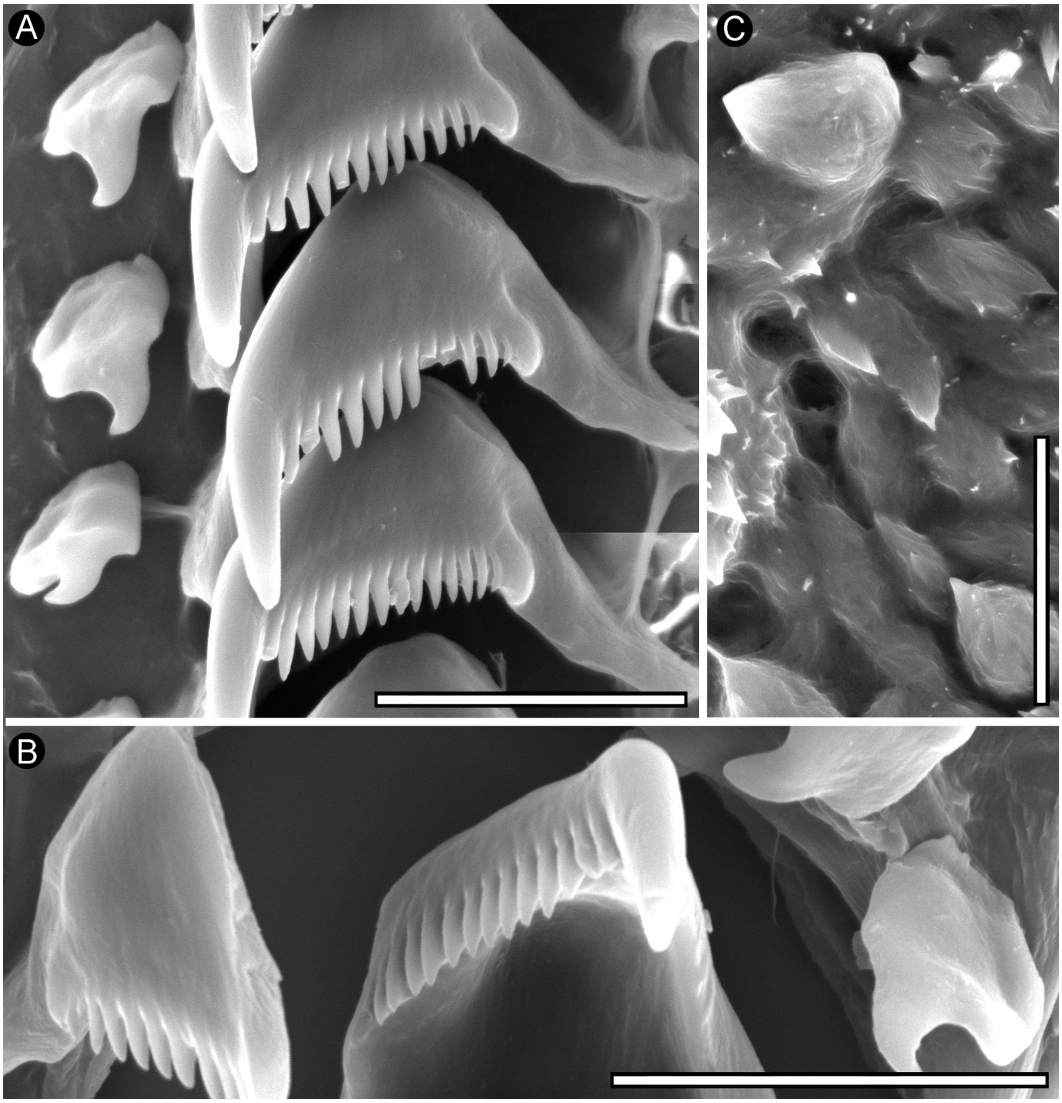

FIGURE 34. *Diaphorodoris papillata* CASIZ 099115. Radular morphology. A First lateral teeth. Scale = 20 µm. B. Close up of denticles. Scale = 20 µm. C. Jaw rodlets. Scale = 10 µm.

oviduct enters the large female gland mass. The prostate is a short tube. It does not narrow appreciably into the short deferent duct, which widens into the penial sheath. The penial sheath is short and wide and terminates into the common genital atrium. Penial armature was not observed. 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 a duct connects to the ovoid seminal receptacle that is the same size as the bursa. The uterine duct connects at the base of the bursa.

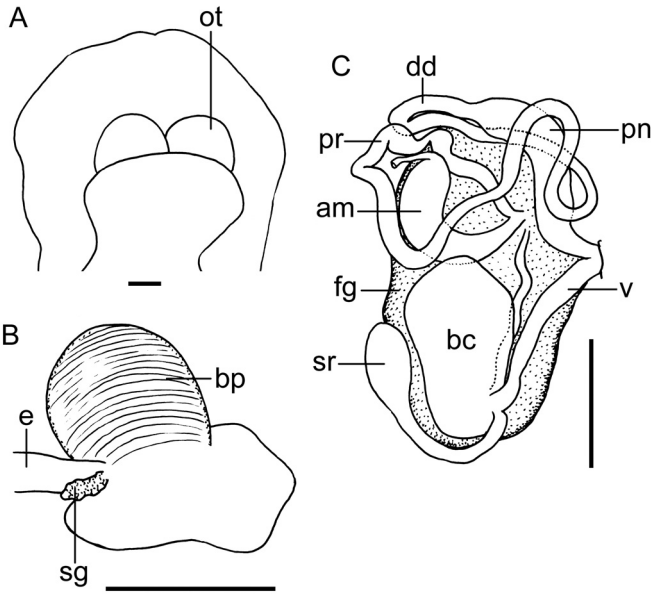

FIGURE 35. *Diaphorodoris papillata* CASIZ 099115. A. Anterior ventral surface. Scale bar = 1 mm. B. Reproductive morphology. Scale bar = 0.5 mm. C. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, ot=oral tentacles, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bar = 0.5 mm.

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.

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.

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 salivary 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 opening to the buccal bulb and is lined with a thick cuticle.

There is a thick plate with rodlets at the top of the opening. The rodlets have pointed apices, some which look like spiked stars (Fig. 34C). The radular formula is 26 × 1.1.0.1.1 (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 hermaphroditic duct enters the ampulla terminally. The ampulla is sausage shaped (Fig. 35C). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 a long duct 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.

Genus *Onchidoris* Blainville, 1816

Type 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.
Proctaporia Mörch, 1857:6 (Type species: *Proctaporia fusca* [Fabricius, 1780] Mörch = *Doris pallida*).
Onchidora Desmarest, 1858:142.
Onchidiorus 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 elfortiania de Blainville, 1816:95.

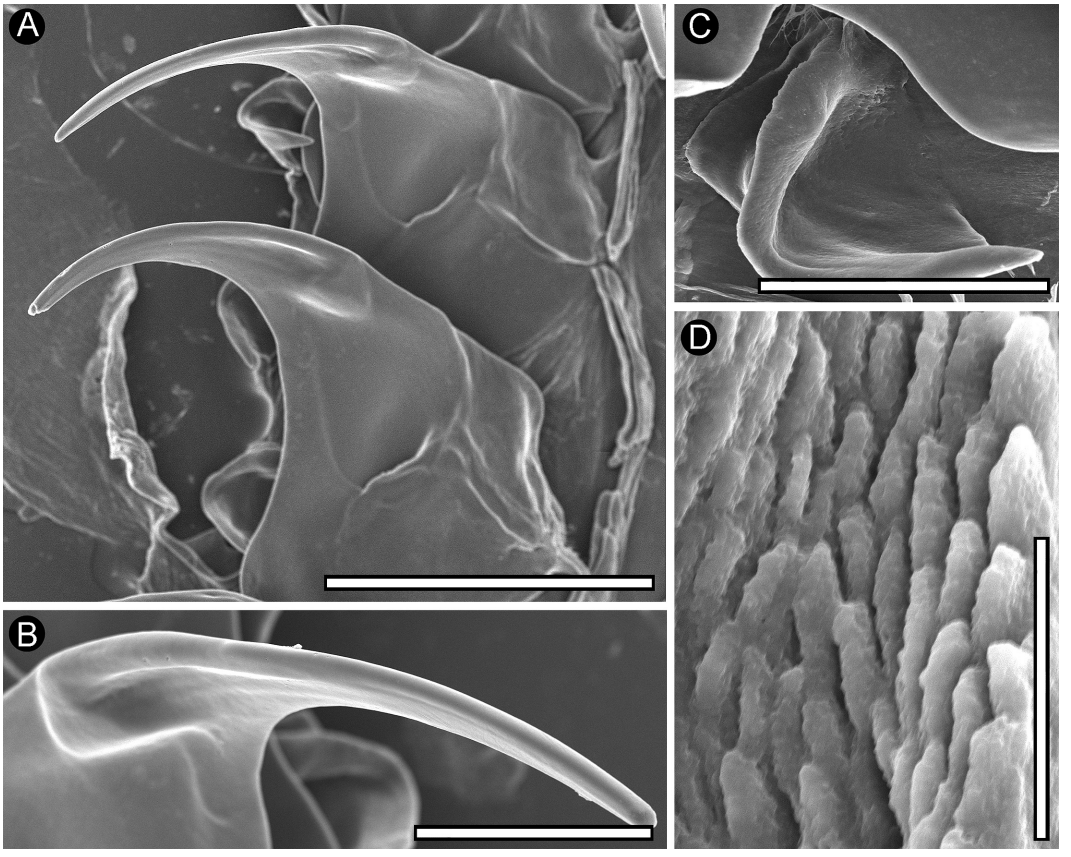

FIGURE 36. *Onchidoris bilamellata* CASIZ 068343. Radular morphology. A First lateral teeth. Scale = 300 µm. B. Close up of first lateral tooth. Scale = 100 µm. C. Close up of outer lateral tooth. Scale = 100 µm. D. Jaw rodlets. Scale = 20 µm.

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).

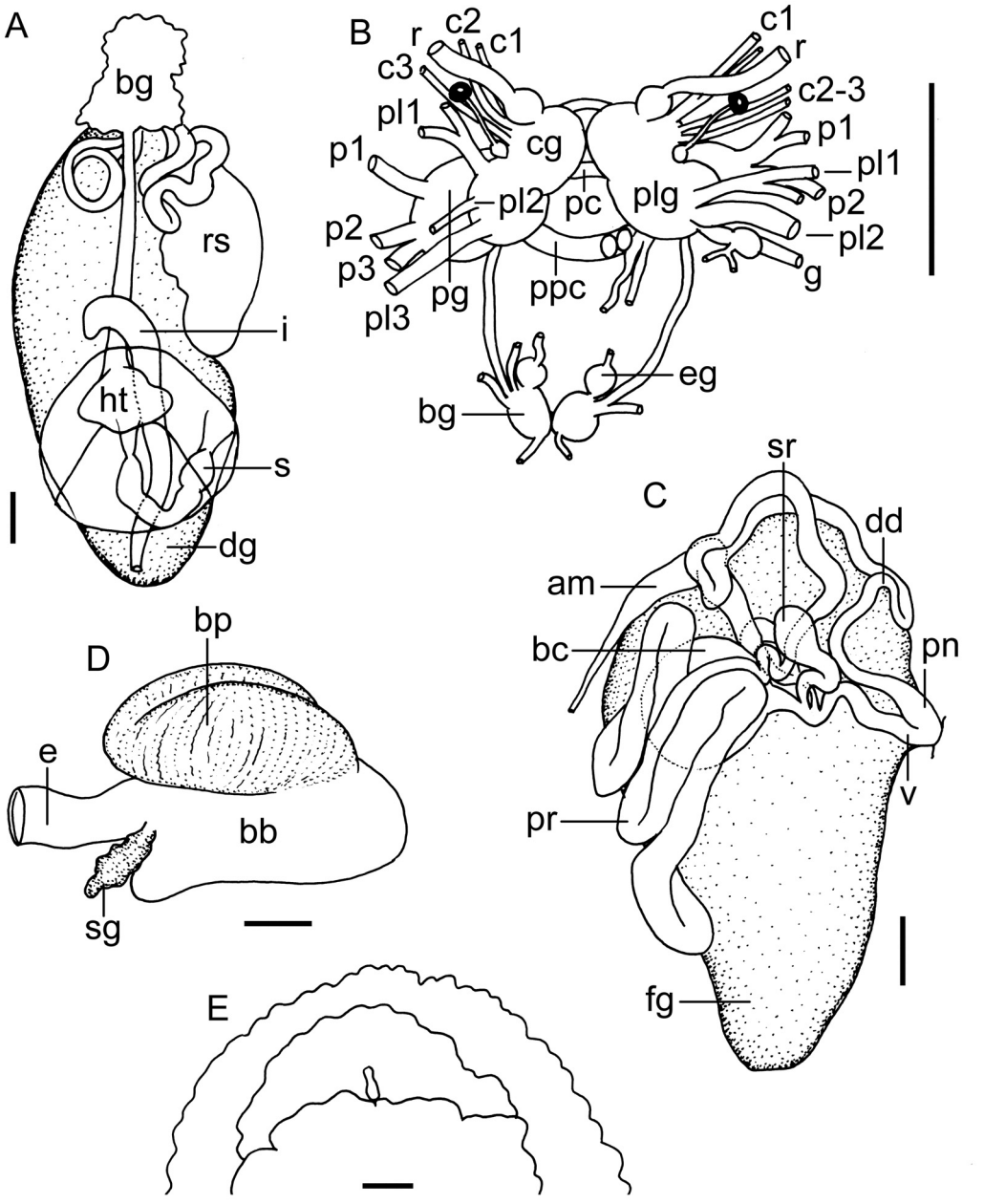

FIGURE 37. *Onchidoris bilamellata* CASIZ 068343. A. Digestive system. B. Cerebro-pleural ganglia. C. Reproductive morphology. D. Buccal bulb. E. Anterior ventral surface. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bg=buccal ganglion, blg=blood gland, bp=buccal pump, c1–3=cerebral ganglia, cg=cerebral ganglion, dd=deferent duct, e=esophagus, fg=female gland mass, ht=heart, od=oviduct, ot=oral tentacle, pg=pedal ganglion, p1–4=pedal nerves, pc=pedal commissure, pg+plg=pleural ganglion, pl1–3=pleural nerves, ppc=parapedal commissure, pr=prostate, r=rhinonophoral nerves, rs=radular sac, sg=salivary gland, sr=seminal receptacle. Scale bars = 1 mm.

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 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 opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets are elongate with single apices (Fig. 36D). The radular formula is $23 \times 1.1.1.1$ (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 *Onchidoris*.

Reproductive system.— The hermaphroditic duct enters the ampulla terminally. The ampulla is elongate (Fig. 37C). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath is 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 a duct 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 stalked at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and three large pleural nerves and three small pedal 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.

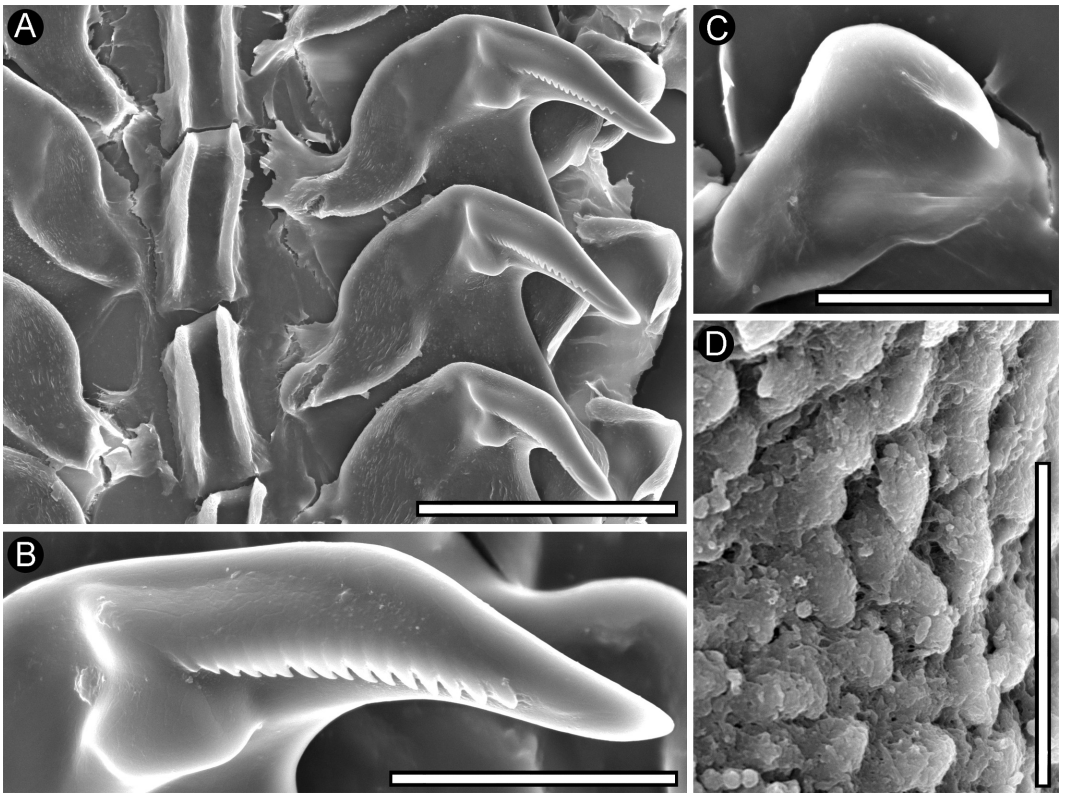

FIGURE 38. *Onchidoris muricata* CASIZ 087251. Radular morphology. A First lateral teeth. Scale = 50 µm. B. Close up of denticles. Scale = 20 µm. C. Close up of outer lateral tooth. Scale = 20 µm. D. Jaw rodlets. Scale = 20 µm.

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. 39A for a drawing of the ventral anterior surface of a specimen from Maine.

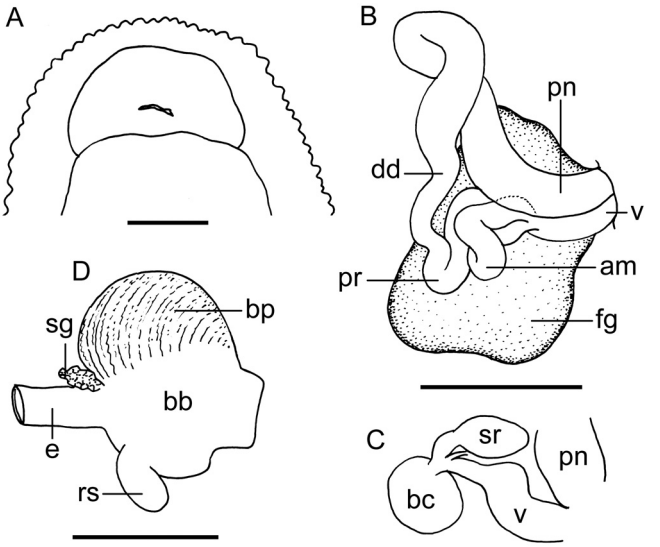

FIGURE 39. *Onchidoris muricata* CASIZ 087251. A. Anterior ventral surface. B. Reproductive morphology. C. Detail of reproductive system duct connections. D. Buccal bulb. Abbreviations: am=ampulla, bb=buccal bulb, bc=bursa copulatrix, bp=buccal pump, dd=deferent duct, e=esophagus, fg=female gland mass, pn=penial sheath, pr=prostate, rs=radula sac, sg=salivary glands, sr=seminal receptacle, v=vagina. Scale bars = 1 mm.

DIGESTIVE SYSTEM.— *Onchidoris muricata* shares the same general digestive anatomy as other Onchidoriddidae (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 salivary glands at the side of the oral tube, near the radular sac (Fig. 37D). The radular sac protrudes noticeably from the bulb, under the esophagus. There is a prominent buccal bulb that has a longitudinal crease (as found in other *Onchidoris* species). The labial disk frames the opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate with rodlets at the top of the opening. The rodlets are very small and rounded (Fig. 38D). The radular formula is $32 \times 1.1.1.1$ (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 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 hermaphroditic duct enters the ampulla terminally. The ampulla resembles a curved sausage (Fig. 39B). It branches into the oviduct and the tubular prostate. 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 penial sheath. The penial sheath 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 a duct 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* d'Orbigny, 1837:15**

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

The description of *Villiersia scutigera* d'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

Onchidoridid 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. mitsuii* (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 Chromodoridid ae (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 Onchidoridid ae. 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 Onchidoridid ae (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.

Characters.— The following characters were considered for use in the analyses of Onchidoridid ae. 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. mitsuii, Goniodoris, Onchidoris*, and *Acanthodoris pilosa.* In the remaining taxa, the tubercles are long (1).

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. luteocincta* 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.

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

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

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* and *Okenia* there is no mantle margin (0). But in *Akiodoris, 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* and all species of *Adalaria* there is no single gill pocket (0). In *Cadlina* the gill is retractile into a pocket (1) and in the remaining taxa the gill is contractile but not retractile into an opening (2).

11. *Gill notal sculpture*: In *Bathydoris, Cadlina, Goniodoris, Okenia* and all species of *Diaphorodoris*

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

Character	*States*
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 penial sheath; 1: same as penial sheath; 2: wider
Cerebro-pleural ganglia	0: separate; 1: fused
Body color	0: white/yellow; 1: other
Dorsal spots	0: absent; 1: present

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 tooth 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 serpentinotus* 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. serpentinotus* 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 penial sheath (0). In *Diaphorodoris mitsuii, Okenia* and *Onchidoris muricata* the penial sheath and vagina are the same width (1). In *Acanthodoris falklandica* the vagina is wider than the penial sheath (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 94 steps and had a consistency index (CI) of 0.45, a retention index (RI) of 0.68 and a homoplasy index (HI) of 0.55. The tree is shown in Fig. 40 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. falklandica,* all from the Southern Hemisphere. The remaining species found in the Northern Hemisphere form a separate clade.

Bremer support values (shown in Fig. 40, 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 (tree not shown). 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 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 Onchidoridae 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 among *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. 40). *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. 40), *Cadlina* is more basal to *Goniodoris* and *Diaphorodoris.* However, in

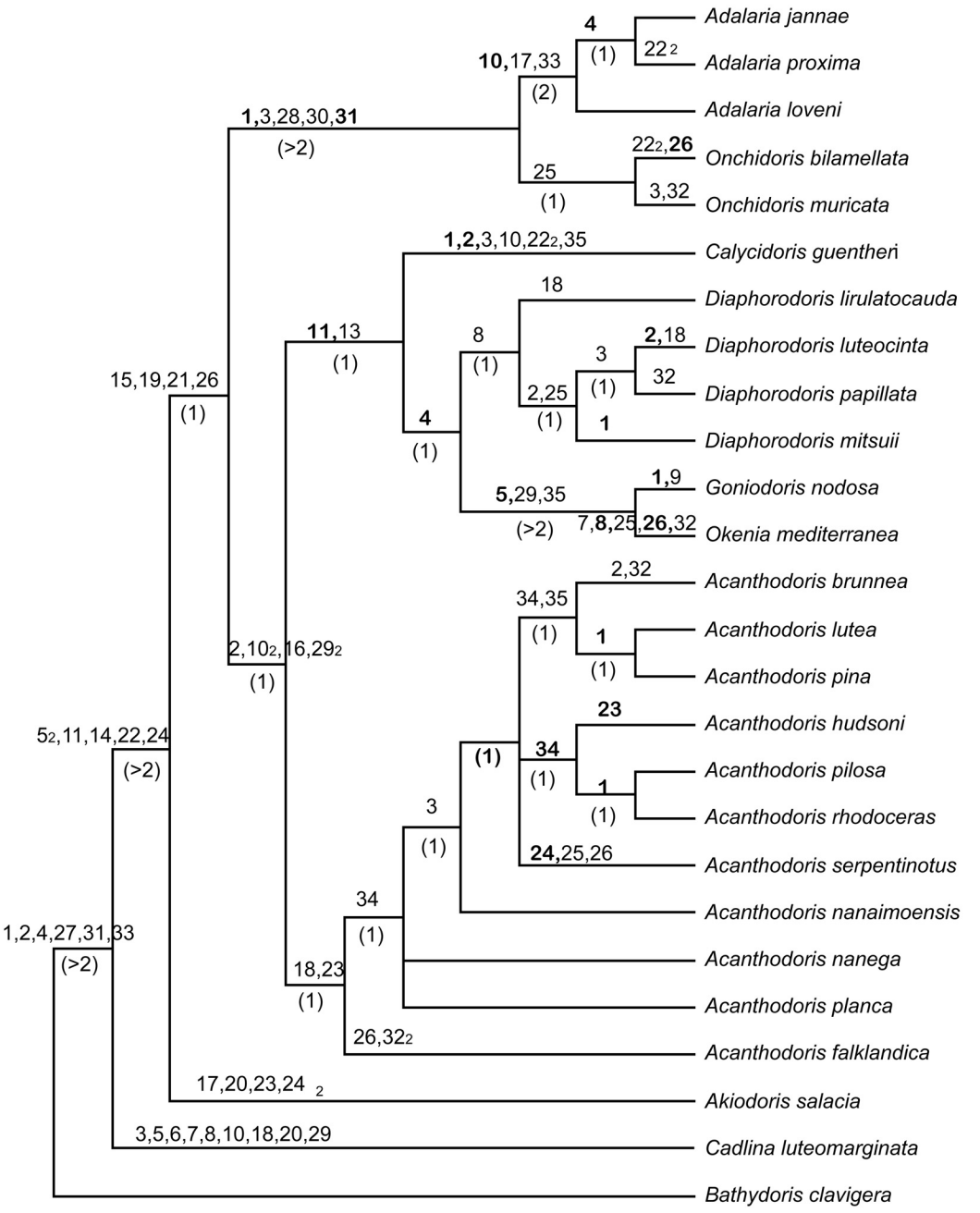

FIGURE 40. Phylogeny of *Acanthodoris*. Single most parsimonious tree, 94 steps. Numbers below the branches are Bremer decay values. Numbers shown above the branches are character numbers from Table 2. The bold numbers indicate reversals.

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

their tree constructed from a single gene (CO1, 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 of16S (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 (tree not shown) 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 extinction 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.

ACKNOWLEDGEMENTS

We thank Sandra Millen for sharing her unpublished data on *Adalaria*, *Akiodoris* and *Armodoris*. Specimens were provided by the Smithsonian National Museum of Natural History, Museo Nacional de Ciencias Naturales, Madrid, Zoologisk Museum Københavns Universitet, Copenhagen and Sandra Millen, University of British Columbia. Thanks to Hans Bertsch who thoroughly researched the status of *Acanthodoris stohleri* syn. nov. And last but not least, thanks to Dr. Michele Aldrich who read proof and saved the authors from an embarrassment of "hidden" errors.

This project was funded by the National Science Foundation PEET grant DEB 9978155 "Phylogenetic Systematics of Dorid Nudibranchs" to T. Gosliner.

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Appendix A

Data matrix for the taxa included in the phylogenetic analysis.

AcanthodMatrix83	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1	Dor	DTt	DTt	Rhi	Rhi	Bod	Hea	Mar	Pos	Gill	Gill	Mid	Cau	Bud	Peri	Rad	Lip	Jaw	Nur	Nur	Lat	Der	Der	Out	Out	Am	Red	RSh	RSh	Ovi	Pen	Vad	Cer	Bod	Dor
1	Adalaria jannae	0	1	1	0	1	0	0	2	0	2	1	0	0	1	1	0	1	–	1	0	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0
2	Adalaria loveni	0	1	1	1	1	0	0	2	0	2	1	0	0	1	1	0	1	–	1	0	1	1	?	1	0	1	1	1	0	1	0	0	0	0	0
3	Adalaria proxima	0	1	1	0	1	0	0	2	0	2	1	0	0	1	1	0	1	–	1	0	1	2	–	1	0	1	1	1	0	1	0	0	0	0	0
4	Calycidoris guentheri	0	0	1	1	1	0	0	2	0	1	0	0	0	1	1	1	0	0	1	0	1	2	–	1	0	1	1	0	2	0	1	0	1	0	1
5	Diaphorodoris lirulatocauda	1	1	0	0	1	0	0	1	0	2	0	0	1	1	1	1	0	1	1	0	1	1	0	1	0	1	1	0	2	0	1	0	1	0	0
6	Diaphorodoris luteocincta	1	0	1	0	1	0	0	1	0	2	0	0	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	0	2	0	1	0	1	0	0
7	Diaphorodoris mitsuii	0	1	0	0	1	0	0	1	0	2	0	0	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	2	0	1	0	1	0	0
8	Diaphorodoris papillata	1	1	1	0	1	0	0	1	0	2	0	0	1	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	2	0	1	1	1	0	0
9	Goniodoris nodosa	0	0	0	0	0	0	0	2	1	0	0	1	1	1	1	1	0	0	1	0	1	1	0	1	0	1	1	0	1	0	1	?	1	0	1
10	Okenia mediterranea	1	0	0	0	0	0	1	0	0	2	0	1	1	1	1	1	0	0	1	0	1	1	0	1	1	0	1	0	1	0	1	1	1	0	1
11	Acanthodoris brunnea	1	1	1	0	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	1	1	1	1
12	Acanthodoris falklandica	1	0	0	1	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	1	1	0	2	0	1	2	1	0	0
13	Acanthodoris hudsoni	1	0	1	0	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	0	1	0	0	1	0	2	0	1	0	1	0	0
14	Acanthodoris lutea	0	0	1	0	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	0	1	1	1
15	Acanthodoris nanaimoensis	1	0	1	1	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	0	1	1	0
16	Acanthodoris nanega	1	0	0	1	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	0	1	1	0
17	Acanthodoris pilosa	0	0	1	1	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	0	1	0	0
18	Acanthodoris pina	0	0	1	0	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	0	1	1	1
19	Acanthodoris rhodoceras	0	0	1	0	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	0	1	0	0
20	Acanthodoris serpentinotus	1	0	1	0	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	2	0	1	0	1	1	0
21	Acanthodoris planca	1	0	0	1	1	0	0	2	0	2	1	0	0	1	1	1	0	1	1	0	1	1	1	0	1	1	1	0	2	0	1	0	1	1	0
22	Onchidoris bilamellata	0	1	1	1	1	0	0	2	0	2	1	0	0	1	1	0	0	0	1	0	1	2	–	1	1	0	1	1	0	1	0	0	1	0	0
23	Onchidoris muricata	0	0	1	1	1	0	0	2	0	2	1	0	0	1	1	0	0	0	1	0	1	1	0	1	1	1	1	1	0	1	0	1	1	0	0
24	Bathydoris clavigera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	Akiodoris salacia	1	1	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	–	0	1	0	1	1	2	0	0	1	0	0	0	1	0	1	0	0
26	Cadlina luteomarginata	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0