

REVIEW OF THE GENUS *DENDRODORIS* EHRENBERG, 1831 (GASTROPODA: NUDIBRANCHIA) IN THE ATLANTIC OCEAN

ÁNGEL VALDÉS, JESÚS ORTEA, CONXITA ÁVILA¹ AND
MANUEL BALLESTEROS²

Departamento de Biología de Organismos y Sistemas, Laboratorio de Zoología, Universidad de Oviedo, 33005 Oviedo, Spain. ¹*Departamento de Ecología Bentónica, Centro de Estudios Avanzados de Blanes, CSIC, 17300 Blanes, Spain.* ²*Departamento de Biología Animal, Facultad de Biología, Universidad de Barcelona, 08028 Barcelona, Spain.*

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ABSTRACT

Six valid species of the nudibranch genus *Dendrodoris* Ehrenberg, 1831 inhabit the Atlantic Ocean, including the Mediterranean and Caribbean Seas. *Dendrodoris lumbata* (Cuvier, 1804), *Dendrodoris grandiflora* (Rapp, 1827), *Dendrodoris nigra* (Stumpson, 1855) (immigrant from the Red Sea), *Dendrodoris krebsi* (Mörch, 1863), *Dendrodoris senegalensis* Bouchet, 1975 and *Dendrodoris warta* Marcus & Gallagher, 1976. Additional data about the biology and geographical distribution of these species are presented. New evidence suggests that other species assigned to the genus *Dendrodoris*, *Dendrodoris racemosa* Pruvot-Fol, 1951 and *Dendrodoris minima* Pruvot-Fol, 1951, must be included in the genus *Doriopsilla* Bergh, 1880. Three new species of *Dendrodoris* are described from the Northeastern Atlantic and West Africa: *Dendrodoris angolensis*, *Dendrodoris guineana* and *Dendrodoris herytra*.

The variable external morphology makes species recognition difficult. Instead, the diagnostic characters utilised to separate species are the shape of the male cirrus hooks, the structure of the reproductive system and features of the egg-mass.

INTRODUCTION

The absence of radula and the variability of colour, makes the previous classification of *Dendrodoris* species highly subjective. A review of the literature revealed considerable confusion regarding the taxonomy of the species of this genus, due primarily to inadequate anatomical study (or none at all) and the indiscriminate use of several characteristics to separate species (mainly external features).

In the Atlantic Ocean (including the Mediterranean and Caribbean Seas), 23 nominal species of *Dendrodoris* have been described,

but most of them are synonyms or belong to another genus. The objectives of this paper are to determine which characteristics of the genus *Dendrodoris* have taxonomic significance, to review all species described in the Atlantic Ocean, and to propose a list of the valid species of this area.

MATERIAL AND METHODS

The specimens studied in this paper were collected during several scientific expeditions around the Atlantic Ocean or were generously provided by a number of colleagues and institutions, with colour slides of living animals.

Most of this material is now conserved in the Laboratorio de Zoología, Departamento de Biología de Organismos y Sistemas, University of Oviedo (abbreviated as LZUO) and in other institutions. Several museums lent us type material for examination or provided information. The following abbreviations are used to denote these institutions: BMNH: The Natural History Museum, London, U.K.; ZMUC: Zoologisk Museum, Københavns Universitet, Copenhagen, Denmark; MNHN: Muséum National d'Histoire Naturelle, Paris, France; FSBC: Florida Marine Research Institute, St. Petersburg, USA; MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain; MCNT: Museo Insular de Ciencias Naturales, Tenerife, Spain. USNM: National Museum of Natural History, Washington D.C., USA; RMNH: Natuurhistorisch Nationaal Museum, Leiden, The Netherlands; IRSN: Institut Royal des Sciences Naturelles de Belgique—Koninklijk Instituut voor Natuurwetenschappen, Brussels, Belgium.

Details of external morphology were described from live specimens and colour slides. The specimens were dissected by dorsal incision. At least one specimen from each locality was dissected. Their internal features were examined and drawn under a binocular dissecting microscope. The male eversible

cirrus of each specimen dissected were isolated and mounted for optical microscopical examination in glycerine. The male cirrus hooks of different levels of the male cirrus (apex, middle region and base) were drawn with the aid of a camera lucida.

SYSTEMATIC DESCRIPTIONS

Family Dendrodorididae O'Donoghue, 1924
Genus *Dendrodoris* Ehrenberg, 1831

Dendrodoris Ehrenberg, 1831: 94. (Type species: *Dendrodoris lugubris* Ehrenberg, 1831; by subsequent designation by Gray, 1847.)

Doridopsis Alder & Hancock, 1864: 124. (Type species: *Doridopsis gemmacea* Alder & Hancock, 1864; by original designation.)

Hanstellodoris Pease, 1871: 300 (new name for *Doridopsis* Alder & Hancock).

Description: Species of the genus *Dendrodoris* generally have a soft body, without spicules; when spicules occur they are minute and isolated. In a few species the notum bears large tubercles. The dorsal colour is very variable, typically dull, but several species show bright colours. The mantle margin is delicate, usually wide and wavy, with radiating striations. Gills are tripinnate and disposed in a circle, closed posteriorly by the anus. The rhinophores have a cylindrical stalk and the club is lamellate. Ventrally, oral tentacles are absent or very reduced.

Internally, *Dendrodoris* species have a pair of ptyaline glands whose ducts join forming a Y shaped duct, which anteriorly connects to the pharyngeal bulb. In the oesophagus there are two circular glands (oesophageal glands) near to the oral ganglion. The intestine has a small gland on its anterior part, which we name the pyloric gland.

The heart connects with the aorta that runs forward to the central nervous system. Anteriorly, the aorta opens laterally into the blood gland.

The reproductive system is characterised by the presence of a glandular prostate. It connects by a duct to the vas deferens. There is a eversible cirrus in the male opening, which has numerous hooks inside, which are variable in number and shape. The gametolytic gland has two ducts, one of them is the vagina, and the other one connects with the seminal receptacle and the female gland. The hermaphrodite gland is usually separated from the digestive gland.

Remarks: Since its original description, the genus *Dendrodoris* has been subject of disagreement, particularly on its relations with the genera *Doriopsis* Pease, 1860, *Doridopsis* Alder & Hancock, 1864 and *Doriopsilla* Bergh, 1880.

The generic name *Dendrodoris* was introduced by Ehrenberg (1831, p. 94) for two species recorded from the Red Sea, including a four-word description. The type species of *Dendrodoris* is *Dendrodoris lugubris* Ehrenberg, 1831 by subsequent designation (Gray 1847, p. 164). Subsequently, Pease (1860, p. 32) described the new genus *Doriopsis* as lacking oral tentacles and the gills disposed in the form of a semicircle. The type species of *Doriopsis* is *Doriopsis granulosa* Pease, 1860 by monotypy.

Later, Alder & Hancock (1864, p. 125) omitted the Ehrenberg and Pease names, and introduced the new genus *Doridopsis* with the same features as *Dendrodoris*: 'cloak large, without spicula or marginal appendages; no oral tentacles; mouth suctorial, without tongue, jaws or collar'. These authors included detailed anatomical data, later completed by Hancock (1866, p. 189). The type species of *Doridopsis* is *Doridopsis gemmacea* Alder & Hancock, 1864 by original designation.

Pease (1871, pp. 229–300) reaffirmed his genus as valid and different from *Doridopsis*. At the same time, he argued that *Doridopsis* was preoccupied by *Doriopsis* and suggested the replacement of *Doridopsis* by the new name *Hanstellodoris* Pease, 1871. However, Bergh (1876, pp. 384–385) regarded *Doriopsis* and *Doridopsis* as synonyms, and accepted *Doriopsis* as the valid name of the genus. This opinion was widely accepted between the years 1876 and 1924. But later, Bergh (1880, pp. 316–317) introduced the new genus *Doriopsilla* which differs from *Doriopsis* by its somewhat rigid and granulated mantle. In this genus, Bergh included the new species *Doriopsilla areolata* Bergh, 1880, and, with a question mark, *Doriopsis granulosa* Pease. Only external features were described. The type species of *Doriopsilla* is *D. areolata* by monotypy.

O'Donoghue (1924, pp. 561–562) considered that Ehrenberg made the name *Dendrodoris* available by providing a brief description, and treated *Doriopsis* and *Doridopsis* as junior subjective synonyms of *Dendrodoris*. Pruvot-Fol (1930, p. 291) adopted the criteria of O'Donoghue, but suggested that *Doriopsis* is not a synonym of *Dendrodoris* and must be included in the family Archidorididae Bergh, 1892 on the bases of its anatomical features,

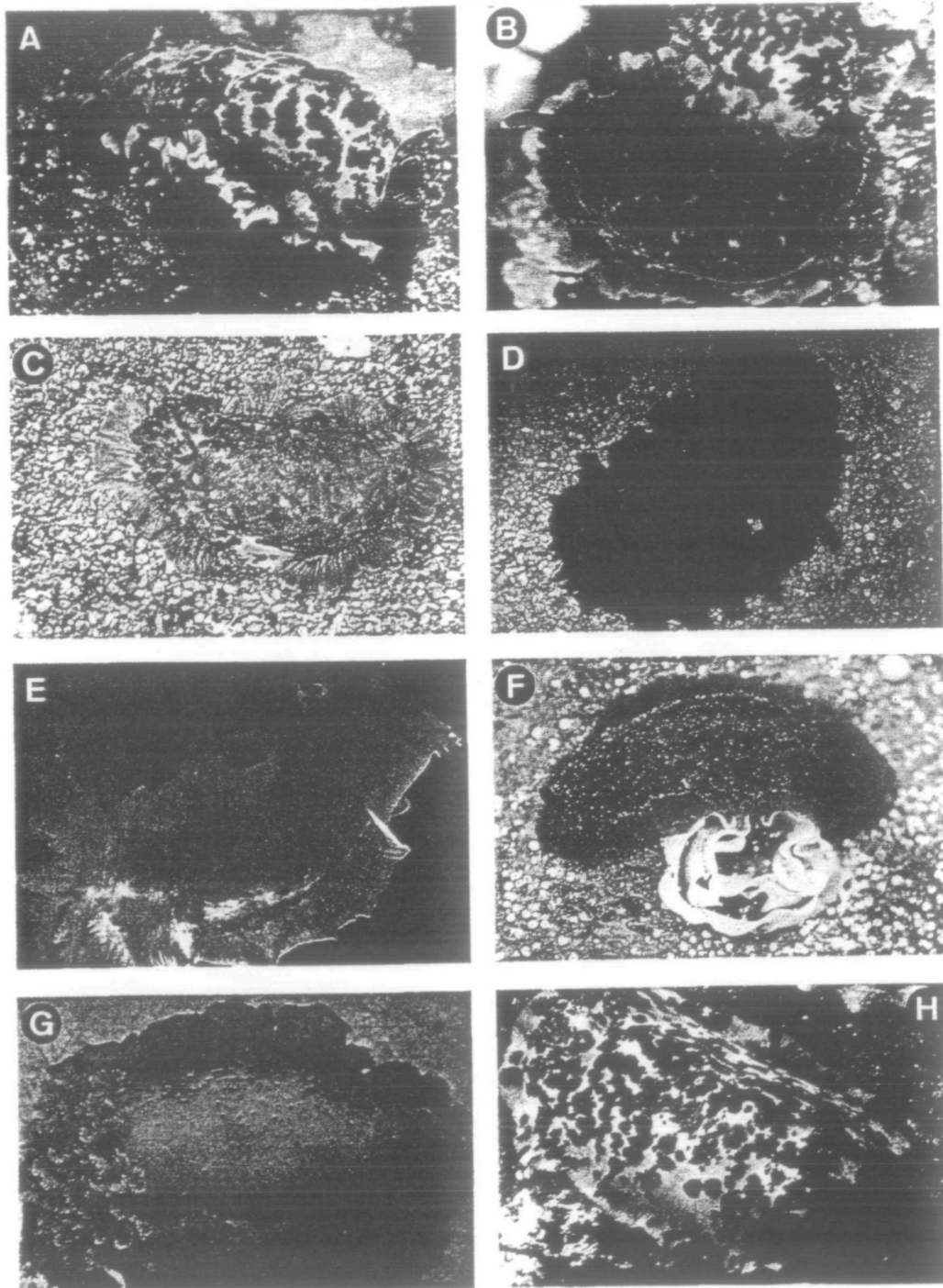


Figure 1. Photographs of living animals showing external features. **A.** *Dendrodoris limbata*, Capo Miseno, Naples, Italy (LZUO 117.48). **B.** *D. limbata*, Port Lligat, Spain, Nov. 1992. **C.** *Dendrodoris grandiflora*, Capo Miseno, Naples, Italy, Mar. 1989. **D.** *D. grandiflora*, Cubellas, Spain. **E.** *D. grandiflora*, Canary Islands, Spain. **F.** *D. grandiflora*, Agadir, Morocco (LZUO 120.06). **G.** *Dendrodoris krebsii*, Cienfuegos, Cuba (BMNH, 1913155). **H.** *D. krebsii*, Mochuma, Venezuela, Nov. 1993.

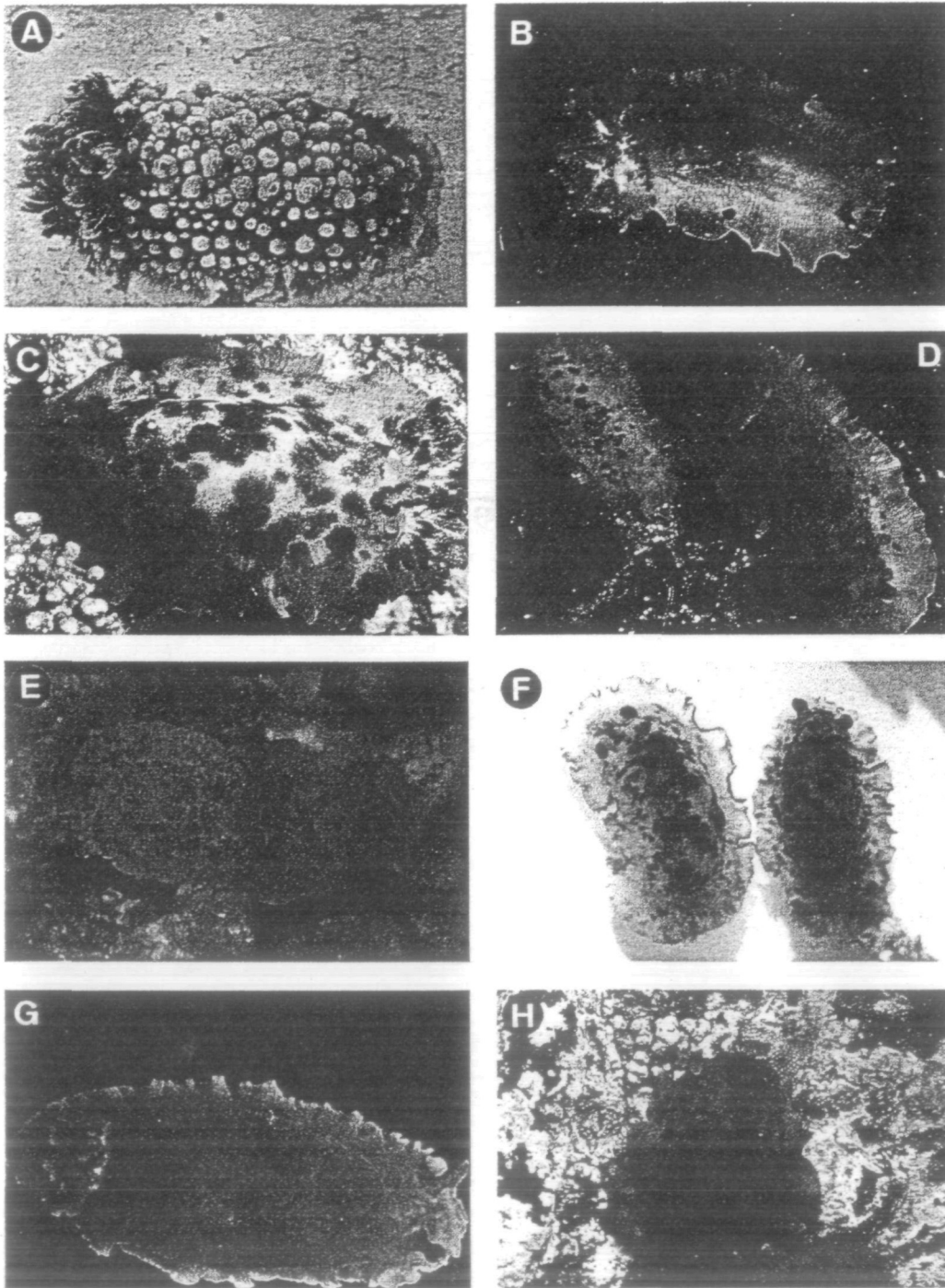


Figure 2. Photographs of living animals showing external features. **A.** *Dendrodoris warty*, U.S.A. (USNM 763414, Source: Slide Archive of USMN; published with permission of *The Veliger*). **B.** *Dendrodoris cf. nigra*, Galapagos, Mar. 1990. **C.** *Dendrodoris senegalensis*, Cape Verde Islands (LZUO 117.16). **D.** *D. senegalensis*, Cape Verde Islands, Aug. 1985. **E.** *Dendrodoris guineana*, Ghana (MNCN 15.05/15830). **F.** *Dendrodoris angolensis*, Santa María, Angola (MNHN). **G.** *Dendrodoris herytra*, North of Spain (LZUO 117.04). **H.** *D. herytra*, Madeira (LZUO 120.18).

including the presence of radula. Steinberg (1961, pp. 58–59) considered *Doriopsilla* a synonym of *Dendrodoris* on the basis of a similar central nervous system. Pruvot-Fol (1954, p. 336), however, retains *Doriopsilla* as valid on the bases of the absence of a ptyaline gland.

At present, Pruvot-Fol's (1930; 1954) criteria are widely accepted and *Dendrodoris* and *Doriopsilla* are considered different and valid genera.

Dendrodoris limbata (Cuvier, 1804)
(Figs. 1A-B, 3, 4A)

Doris limbata Cuvier 1804: 468–469, pl. LXXIV, 3.

Doris nigricans (non Fleming, 1820: 618) Otto 1821: 8.

Doris virescens Risso 1826: 31, pl. II, 11.

Doris setigera Rapp 1827: 521, fig. 8.

Doris lugubris Gravenhorst 1831: 13.

Doris rappu Cantraine 1841: 58–59.

Doris sismondæ Verany 1846: 21.

Doriopsis obscura Abraham 1877: 263.

Dendrodoris languida Pruvot-Fol 1951: 44–46, fig. 30, pl. II, 9.

Type material: The type material of *Doris limbata* is lost; it has not been registered in the book of entries of the collections of MNHN, and no material of this species labelled as collected or identified by Cuvier has been found. Two specimens collected from Marseille, France, and labelled by Pruvot-Fol as '*Dendrodoris limbata*' have been found. There is no evidence that this is the type material of *Doris limbata*, but it comes from the type locality and belongs to this species. For this reason, one of the two specimens (25 mm preserved length) is here designated the neotype of this species.

The type material of *Doris nigricans* is untraceable; the type locality is Villefranche, on the Mediterranean coast of France. The type material of *Doris virescens* is lost (Arnaud, 1977); the type locality is Nice, France. The type material of *Doris setigera* is untraceable, the type locality of this species is Naples, Italy. The type material of *Doris lugubris* is untraceable; the type locality is Trieste, Italy. The type material of *Doris rappu* is presumed lost; it could not be located in RMNH or IRSN; it was collected from Sardinia, Naples and the Dalmatian coast. The type material of *Doris sismondæ* is untraceable; the type locality is Riviera di Ponente, on the Ligurian coast of Italy. *Doriopsis obscura* Syntypes: BMNH 1993086, date and source

unknown, we studied 3 of 5 specimens 26, 28 and 30 mm preserved length (one of them, 28 mm preserved length, was dissected by dorsal incision, the male eversible cirrus was mounted in glycerine). The type material of *Dendrodoris languida* is presumed lost, it could not be located in MNHN; the type locality is Banyuls, France.

External morphology (Fig. 1A-B): The background colour of *D. limbata* can be yellow, grey, dark brown or black. Some specimens show a yellow background coloration, with pale brown and black spots on the dorsum, but these never appear on the mantle edge which is always yellow. Other specimens are predominantly grey, with dark and occasionally white spots, and a yellow line bordering the mantle edge. Others are black or dark brown, and lack spots but have the yellow line on the mantle edge. Only one specimen had the mantle margin edged in white. No relation between size and pigmentation has been observed in adult specimens.

Ventrally, specimens are yellow, with black spots scattered on the foot and the border of the mantle. Gills are usually dark, with the exterior edge in yellow or white. The rhinophores are dark brown or black, with the apex white or yellow. Juvenile specimens are uniformly yellow, except for a black ring which may be present on the rhinophores.

Minute and dispersed spicules sometimes occur on the dorsum. The mantle edge is thin and slightly striated; when the animal moves it is held close to the foot. It is roughly half the width of the foot.

Anatomy (Fig. 3A-D): The oesophagus has five folds. Anteriorly, beside the second fold, there are two oesophageal glands. The intestine has a small pyloric gland. The triangular-shaped heart, connects by the aorta with the blood gland, which covers only a small portion of the reproductive system.

The reproductive system has a granular prostate roughly 1/3 as long as wide. The deferent duct has a very convoluted and narrow proximal region. The ampulla is very large, with 4 folds. The vagina is granular, twice as wide as the deferent duct. There is a differentiated mucus portion in the female gland. The gametolytic gland is 10 times larger than the seminal receptacle, and they are joined by a narrow and folded duct. The male eversible cirrus has large hooks with narrow bases; their shape and variability are shown in Fig. 3D.

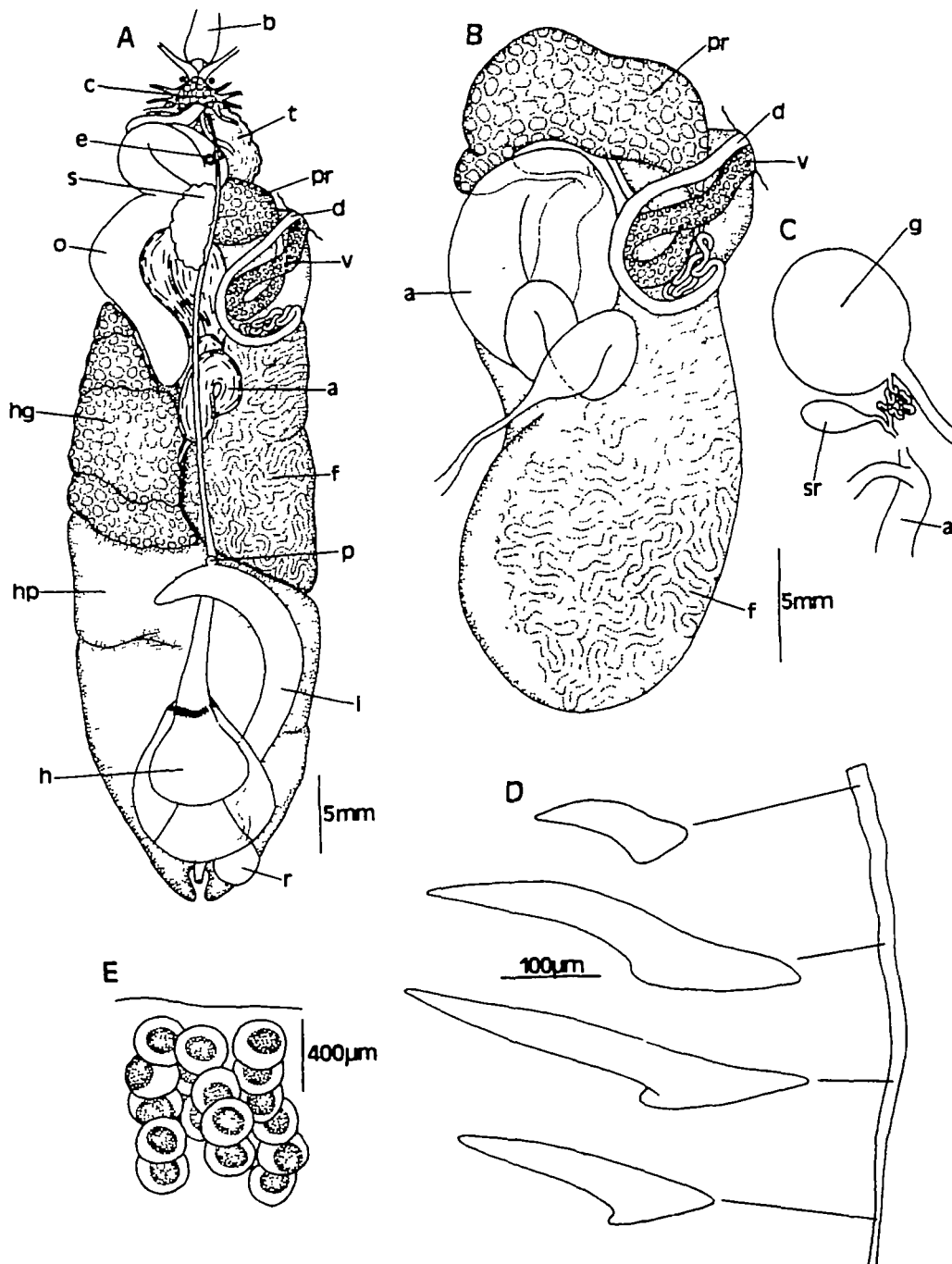


Figure 3. *Dendrodoris limbata* (LZUO 120.09). A. Dorsal view of the internal organs. B. Reproductive system. C. Genital organs previously hidden under the prostate. D. Shape and disposition of the hooks along the male eversible cirrus. E. Detail of the egg mass. Abbreviations: a, ampulla; b, pharyngeal bulb; c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; g, gametolytic gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; o, oesophagus; p, pyloric gland; pr, prostate; r, renal sac; s, blood gland; sr, seminal receptacle; t, ptyaline gland; v, vagina.

Spawn (Fig. 3E): The egg mass is spirally coiled, 10 mm in height. The orange eggs are spherical, arranged in parallel lines and enclosed by a spherical capsule. There are about 22 eggs occupying the whole height of the egg-ribbon. The size of the eggs changes during development; on the first day they are approximately 333 μm long (mean), and the capsules 371 μm . After 39 days, just before hatching, the eggs are 523 μm and the capsules 567 μm long. The veliger larvae are heavy, and in less than 48 hours they fall to the bottom and metamorphose into juveniles approximately 475 μm long.

Distribution (Fig. 4A): *Dendrodoris limbata* occurs throughout the Mediterranean Sea, from Israel (Barash & Danin, 1971) to the Strait of Gibraltar (García-Gómez, 1983). We have found several Mediterranean records in Vayssière (1913) and Cervera, Templado, García-Gómez, Ballesteros, Ortea, García, Ros & Luque (1988). The records of Nobre (1938–40) from the South of Portugal and Pruvot-Fol (1953) from the Atlantic North Africa, both outside the Mediterranean, probably belong to this species.

Remarks: Cuvier (1804) described *Doris limbata* from Marseille and the specimens he studied were black with a yellow line around the mantle. Von Ihering (1880) included this species in the genus *Doriopsis*, and considered five Mediterranean species (*Doris nigricans* Otto, 1821, *Doris virescens* Risso, 1826, *Doris setigera* Rapp, 1827, *Doris lugubris* Gravenhorst, 1831 and *Doris susmondae* Verany, 1846) as synonyms of *D. limbata*. External features of these nominal species (see Otto, 1823; Risso, 1826; Rapp, 1827; Gravenhorst, 1831 and Verany, 1846) are very similar to those described by Cuvier (1804) for *D. limbata*; only *Doris setigera* differs having large spicules on the dorsum, considered by some authors as bristles of annelids implanted into its skin (Bergh, 1880; Pruvot-Fol, 1954). Von Ihering (1880) and Bergh (1880) also described the anatomical features of *D. limbata*. Pruvot-Fol (1934) included this species in the genus *Dendrodoris* and suggested that *Doris rappii* Cantraine, 1841 could be another synonym (Pruvot-Fol, 1954). Specimens described by Cantraine (1941) show identical features to *D. limbata* and also, Cantraine considered his species identical to *D. setigera*, but without the dorsal bristles described by Rapp (1827).

Abraham (1877) described *Doriopsis obscura*

Abraham, 1877 from the Mediterranean Sea, based on one preserved specimen with no anatomical description. Examination of the holotype shows that this species has identical anatomical features to our material of *Dendrodoris limbata*.

Pruvot-Fol (1951) described *Dendrodoris languida* from four preserved specimens collected from the Mediterranean coast of France. In a latter paper, Pruvot-Fol (1954) redescribed this species with a drawing of the anatomy showing identical features to *Dendrodoris limbata*.

Dendrodoris limbata is clearly separable by its internal features from *Dendrodoris grandiflora* and other Atlantic species. The wide prostate, the shape of the male cirrus hooks and the granular vagina are characteristic of *D. limbata*. Externally, *D. limbata* is characterised by the yellow line around the mantle edge and the dark spots on its ventral side. No other Atlantic species have both of these features.

Material examined: FRANCE—Marseille (43°20'N, 5°26'W), date unknown, 1 specimen 25 mm preserved length (MNHN), NEOTYPE of *Dendrodoris limbata*. ITALY—Naples (40°36'N, 14°20'E) 27 Oct. 1988, 1 specimen 23 mm preserved length (LZUO 117.47); 27 Oct. 1988, 1 specimen 22 mm preserved length (LZUO 117.46); 20 Jan. 1989, 1 specimen 30 mm preserved length (LZUO 117.48); 27 Mar. 1989, 1 specimen 40 mm preserved length (LZUO 120.14). Taranto (40°28'N, 17°14'E) 11 Oct. 1988, 2 specimens 23–26 mm preserved length (LZUO 117.01). Acitrezza, Sicily (37°36'N, 15°11'E), 3 May 1990, 1 specimen 53 mm preserved length (LZUO 120.17). SPAIN—Blanes (41°40'N, 2°47'E), 16 Feb. 1979, 1 specimen 11 mm preserved length (LZUO 117.45); Sept. 1986, 1 specimen 40 mm preserved length (LZUO 120.09); 14 Nov. 1986, 5 specimens 18–27 mm preserved length (LZUO 120.08); May 1991, 1 specimen 39 mm preserved length (LZUO 120.01). Cadaqués (42°17'N, 3°16'E), Feb. 1985, 2 specimens 13–15 mm preserved length (LZUO 117.08); 5 May 1988, 1 specimen 20 mm preserved length (LZUO 120.05). Cubellas (41°12'N, 1°41'E), 3 Mar. 1976, 3 specimens 10–19 mm preserved length (LZUO 117.51). Creus Cape (42°19'N, 3°18'E), 26 Jan. 1980, 1 specimen 23 mm preserved length (LZUO 120.13). La Planassa (41°43'N, 2°56'E), Mar. 1986, 2 specimens 35–39 mm preserved length (BMNH 1993158); Mar. 1986, 2 specimens 42–43 mm preserved length (LZUO 120.19). Botafoch Cape (38°55'N, 1°28'E), Ibiza Island, 2 specimens 13–15 mm preserved length (LZUO 117.60). Formentera Island (39°16'N, 1°27'E), 9 Nov. 1979, 1 specimen 12 mm preserved length (LZUO 117.44). Alborán Sea (36°08'N, 6°01'W), 20 Jul. 1989, 1 specimen 5 mm preserved length (LZUO 111.01). UNKNOWN—3 specimens, 26–30 mm preserved length (BMNH 1993086), SYNTYPES of *Doriopsis obscura*.

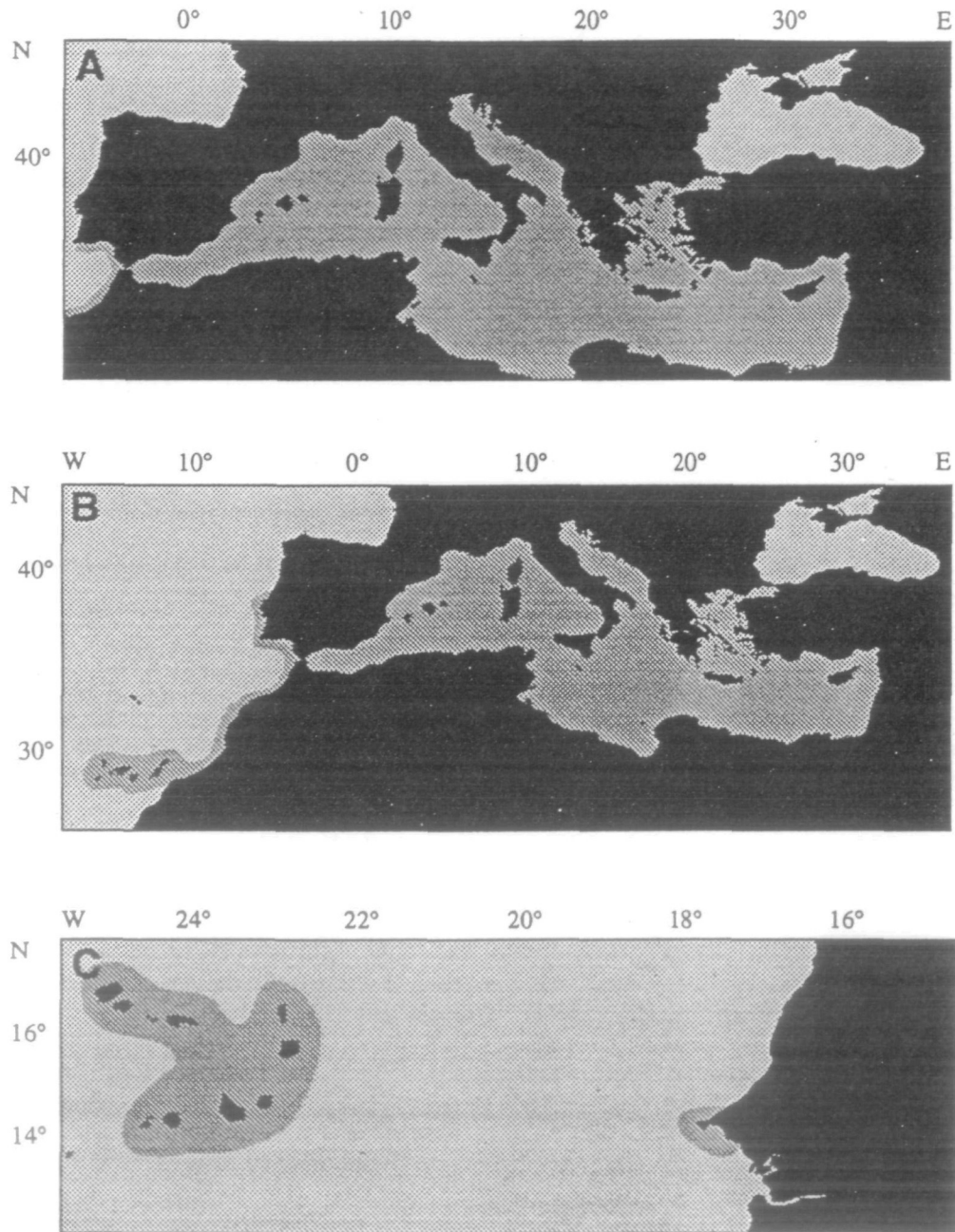


Figure 4. Maps of the known distribution of the Eastern Atlantic described species of the genus *Dendrodoris*. **A.** *Dendrodoris limbata*. **B.** *Dendrodoris grandiflora*. **C.** *Dendrodoris senegalensis*.

***Dendrodoris grandiflora* (Rapp, 1827)**
(Figs 1C-F, 4B, 5, 6)

- Doris guttata* Risso 1826: 33.
Doris grandiflora Rapp 1827: 520–521, fig. 3.
Dendrodoris sp White 1955: 183–184
 ? *Dendrodoris longula* Pruvot-Fol 1951 46–47,
 fig. 31
 ? *Dendrodoris pseudorubra* Pruvot-Fol 1951:
 44, fig. 31, pl. II, 11–12
Dendrodoris temarana Pruvot-Fol 1953: 87–88,
 fig. 31, pl. III, 55.

Type material: The type material of *Doris guttata* is lost (Arnaud, 1977), it was collected in Southern Europe

The type material of *Doris grandiflora* is untraceable; the type locality is Naples, Italy Neotype (here designated): Straits of Gibraltar, 20 Jul. 1989, 24 mm preserved length (MNHN). The holotypes of *Dendrodoris longula* and *Dendrodoris pseudorubra* collected from the Mediterranean coast of Spain, and the holotype of *Dendrodoris temarana*, type locality of Temara, Morocco, are all presumed lost and could not be located in MNHN.

External morphology (Fig. 1C-F): The body colour is very variable. The background colour of specimens from the Mediterranean Sea is grey, cream, pale green, pale brown or light red, with brown or black spots on the dorsum. In Portugal, most specimens studied have a yellow background colour, with dark spots (brown or black). These spots are variable in size, and in some specimens cover all the dorsum. One specimen from the South of Portugal is uniformly yellow with no spots. The specimens from North Africa and Canary Islands are usually red or orange and most of them have dark spots on the dorsum. In all cases, the number and size of the spots bear no relation to the size of the animal.

Ventrally, specimens have the same colour as the dorsum and there are no dark spots. The rhinophores and gills usually have the same colour as the body, with the apex (of the rhinophores) and the exterior border (of the gills) white. Juvenile specimens are uniformly red.

No spicules are present in the notum. The mantle margin is slightly striated and usually as wide as the foot.

Anatomy (Figs 5A-B, 6): The oesophagus has three folds. On its anterior portion, just beside the second fold, there are two oesophageal

glands. The intestine has a conspicuous pyloric gland. The heart connects by the aorta with the blood gland, which covers a small portion of the reproductive system.

The reproductive system has a long, folded and granular prostate which is several times longer than it is wide. The deferent duct has a narrow, long and folded proximal region, about 1/2 of the distal region length. The deferent duct is wider and is of similar length to the vagina. The vagina decreases in diameter as it approaches the gametolytic gland. The ampulla has only one fold. There is a differentiated mucus portion in the female gland. The gametolytic gland is three times larger than the seminal receptacle, and they are connected by a duct broader than the distal portion of the vagina. A little variability has been observed between the reproductive systems of specimens from different areas (Fig 6A-E), but the former description can be applied to all of them. The male eversible cirrus has numerous small hooks with elongated bases, their variable shape is shown in Figure 5B.

Spawn (Fig 5C): The egg mass is spirally coiled, 6 mm in height and 0.5 mm in width. The yellow eggs are oval arranged in parallel lines, and enclosed in a much larger spherical capsule. Eggs measured 60–100 µm (mean: 80 µm). Capsules measured 140–190 µm (mean: 160 µm).

Distribution (Fig. 4B) This species inhabits the Mediterranean Sea, from Turkey (Swennen, 1961) and Israel (Barash & Danin, 1971) to the Strait of Gibraltar (García-Gómez, 1983). We have found other Mediterranean records in Vayssière (1913) and Cervera *et al.* (1988). In the Atlantic Ocean, it has been recorded from Portugal (Fez, 1974) to Canary Islands (Odhner, 1932; Pérez, Bacallado & Ortea, 1991) and the Sahara (White, 1955). The present paper gives the most southerly record of this species, from Mauritania.

Remarks: The species *Doris guttata* was described by Risso (1826) as being transparent grey with black spots. One year later, Rapp (1827) described *Doris grandiflora* from the Gulf of Naples with the same features. Following the Principle of Priority the valid name of this species is *D. guttata* (the oldest name applied to it). However, the name *D. guttata* has not been used as valid since its original description, whereas *D. grandiflora* has been widely and continuously used. Ortea & Valdés

(1994) successfully argued that for nomenclatural stability, the currently accepted name *grandiflora* (in the binomen *Dendrodoris grandiflora*) be placed on the Official List of the Specific Names in Zoology, and recommended suppression of the specific name *guttata*. This

proposal was endorsed by the International Commission on Zoological Nomenclature in Opinion 2886.

Pruvot-Fol's Mediterranean species *Dendrodoris pseudorubra* and *Dendrodoris longula* seem to be very similar to juvenile specimens

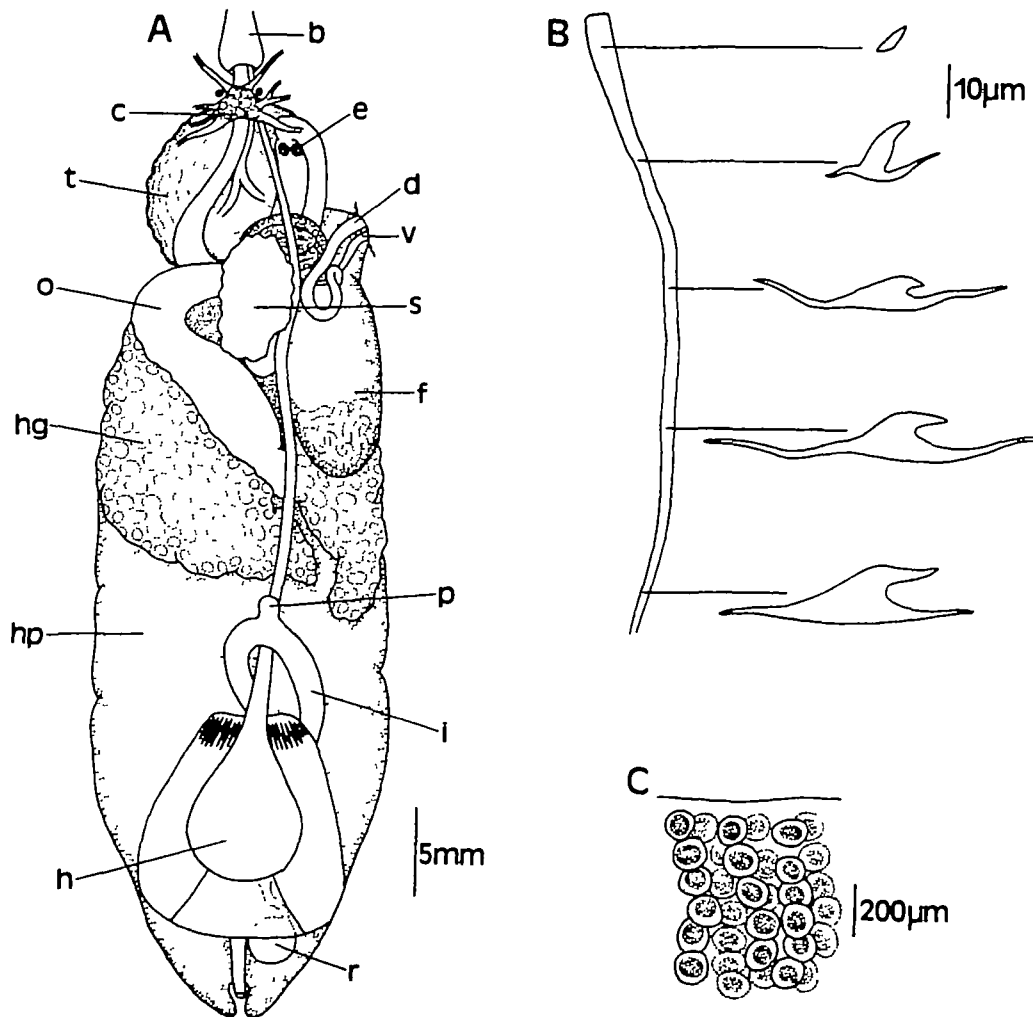
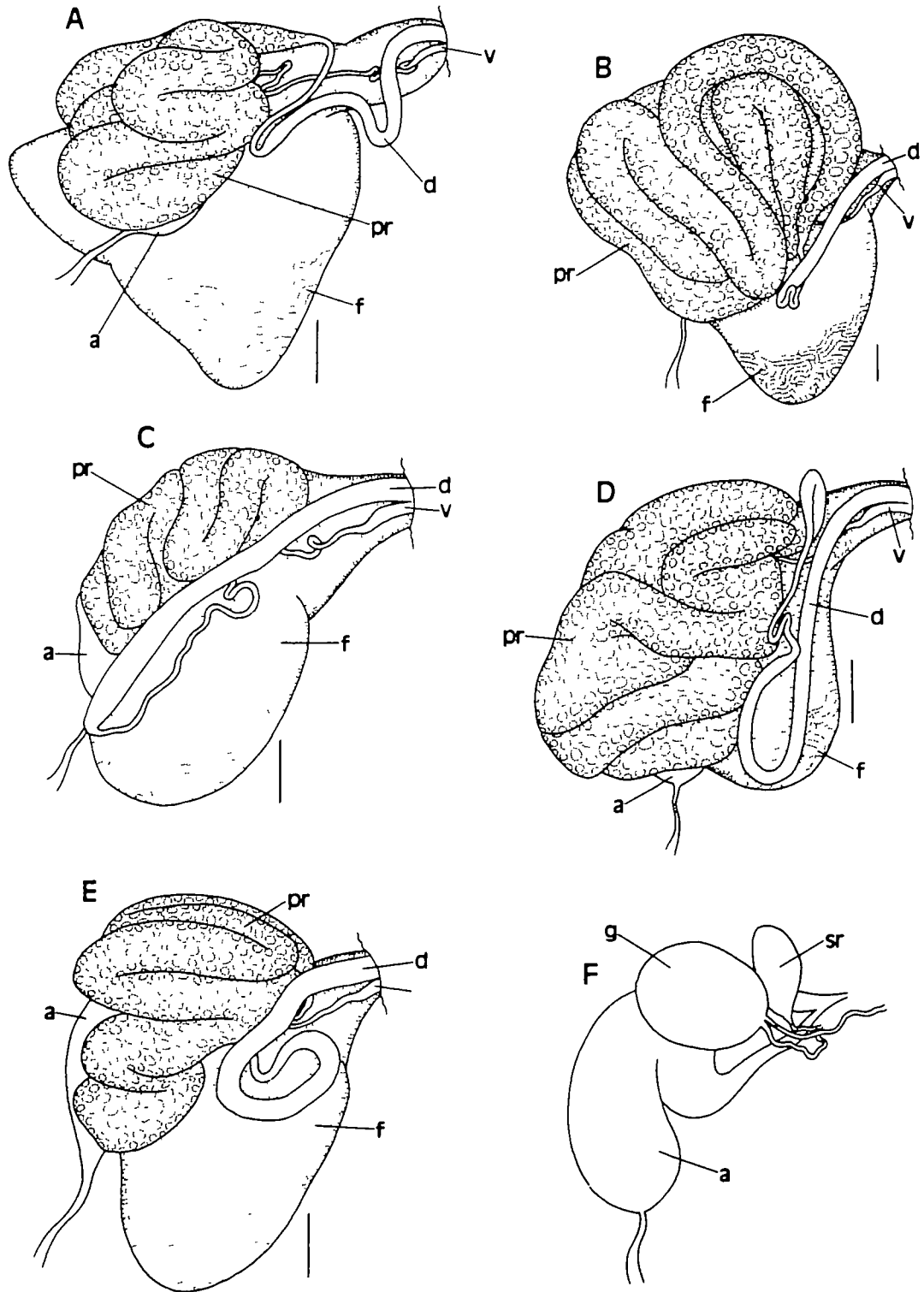


Figure 5. *Dendrodoris grandiflora* (LZUO 107.73). A. Dorsal view of the internal organs. B. Shape and disposition of the hooks along the male eversible cirrus. C. Detail of the egg mass. Abbreviations: b, pharyngeal bulb; c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; o, oesophagus; p, pyloric gland; r, renal sac; s, blood gland; t, ptyaline gland; v, vagina.

Figure 6. *Dendrodoris grandiflora*, variability of the reproductive system. A. Specimen from Portugal (LZUO 106.03). B. Specimen from Morocco (LZUO 120.06). C. Specimen from the Mediterranean Sea (LZUO 120.04). D. Specimen from Canary Islands. E. Specimen from the Gibraltar Strait (LZUO 106.11). F. Genital organs previously hidden under the prostate. Abbreviations: a, ampulla; d, deferent duct; f, female gland; g, gametolytic gland; pr, prostate; sr, seminal receptacle; v, vagina.



of *Dendrodoris grandiflora*. The red coloration of *D. pseudorubra* (see Pruvot-Fol, 1951, p. 44) and the shape of the male cirrus hooks of *D. longula* (see Pruvot-Fol, 1951, fig. 31G) resemble those of *D. grandiflora*. Nevertheless the incomplete original description of both species does not permit its definitive identification, and confirmation of synonymy requires fuller anatomical study. Unfortunately, the type material of *D. pseudorubra* and *D. longula* is lost. The evidence indicates that *D. pseudorubra* and *D. longula* should be regarded as *nomina dubia*.

On the other hand, *Dendrodoris temarana* Pruvot-Fol, 1953 from the coast of Morocco, has been fully described. The external features of this species are very close to those of our specimens from North Africa. Also, the reproductive systems of *D. temarana* (see Pruvot-Fol, 1953) and *Dendrodoris grandiflora* are identical.

Dendrodoris grandiflora is clearly separable from other Atlantic species mainly by its internal features. The shape of the male cirrus hooks and the disposition of the reproductive organs are very characteristic of this species.

Material examined: ITALY—Naples (40°36'N, 14°20'E), 1 specimen, 27 Mar. 1989. IBERIAN PENINSULA—Blanes (41°40'N, 2°47'E), Sep. 1978, 1 specimen 17 mm preserved length (LZUO 117.23); 16 Aug. 1979, 1 specimen 14 mm preserved length (LZUO 117.40); 14 Nov. 1986, 5 specimens 18–27 mm preserved length (LZUO 120.08). Cubellas (41°12'N, 1°41'E), 25 Feb. 1976, 2 specimens 15–18 mm preserved length (LZUO 117.49), 31 Dec. 1977, 1 specimen 10 mm preserved length (LZUO 117.41); 4 Mar. 1979, 2 specimens 9 mm preserved length (LZUO 117.43); 9 Aug. 1986, 2 specimens 14–15 mm preserved length (LZUO 117.52); 22 Aug. 1987, 3 specimens 19–25 mm preserved length (LZUO 120.04). Palos Cape (37°38'N, 1°21'E), 22 Aug. 1984, 1 specimen 22 mm preserved length, coll. Templado (LZUO 120.11). Fuengirola (36°35'N, 4°37'W), 2 specimens 4–16 mm preserved length (LZUO 117.62). Gibraltar Straits (36°09'N, 6°09'W), 20 Jul. 1989, 1 specimen 24 mm preserved length (MNHN), NEOTYPE of *Dendrodoris grandiflora*; 20 Jul. 1989, 4 specimens 17–27 mm preserved length (LZUO 106.11). Formentera Island (39°16'N, 1°27'E), 9 Feb. 1976, 3 specimens 14–16 mm preserved length (LZUO 117.42). San Antonio, Ibiza Island (38°59'N, 1°19'E), 4 specimens 10–24 mm preserved length (LZUO 120.02); 3 specimens 13–22 mm preserved length (BMNH 1993153). Sagres (37°00'N, 8°55'W), 11 May 1988, 1 specimen 25 mm preserved length (LZUO 106.03). Setubal (38°31'N, 8°53'W), Mar. 1987, 2 specimens 18–21 mm preserved length, coll. Burnay (LZUO 117.17); 7 specimens 13–24 mm pre-

served length, coll. Burnay (LZUO 120.12). NORTH AFRICA—Temara (31°02'N, 9°49'W), 17 Nov. 1991, 1 specimen 32 mm preserved length, coll. Templado (LZUO 107.73). Agadir (30°23'N, 9°36'W), 6 specimens 10–26 mm preserved length (LZUO 120.06). Baie de l'Etoile, Mauritania, 1 specimen 70 mm preserved length (MNHN). ATLANTIC ISLANDS—Espiga de la Caleta, Tenerife Island, Spain (27°14'N, 43°05'W), 19 Mar. 1979, 1 specimen, coll. Cruz.

Dendrodoris nigra (Stimpson, 1855)
(Fig. 2B)

Doris nigra Stimpson, 1855: 380.

Remarks: This species has been reported by Barash & Danin (1986) as a Lessepsian immigrant to the Israel coast. We were unable to examine this material (deposited in the Tel-Aviv University), and in the absence of a description of the specimens in their paper the identification of this material must remain in doubt.

On the other hand, we assigned to this species material collected from the Galapagos Islands and the Pacific coast of Mexico, which are included in this paper only to clarify the status of the Caribbean nominal species of *Dendrodoris* (see remarks of *Dendrodoris krebsii*). Small specimens from Galapagos are uniformly red (Fig. 2B), but large specimens are black with a red line around the mantle margin, as those described by Stimpson (1855) for *Dendrodoris nigra*. However, the obscure status of most of the Indo-Pacific species and the absence of comparative material does not permit us to be sure about the species to which this material belongs. Brodie (personal communication) considers that there are anatomical differences between our material from the Pacific coast of America and *D. nigra* (see Brodie, 1991).

A future review of the genus *Dendrodoris* in the Indo-Pacific will clarify the status of the North-west American species and the possible candidates of immigration from the Red Sea into the Eastern Mediterranean.

Dendrodoris krebsii (Mörch, 1863)
(Figs. 1G-H, 7, 8A)

Doris (Rhacodons) krebsii Mörch 1863: 34.
Doridopsis subpellucida Abraham 1877: 265–266, pl. XXX, fig. 36.
Doriopsis atropos Bergh 1879: 49–64.

Type material: *Doris krebsii*. Syntypes: ZMUC 94, ZMUC 101, ZMUC 400, ZMUC 401, St

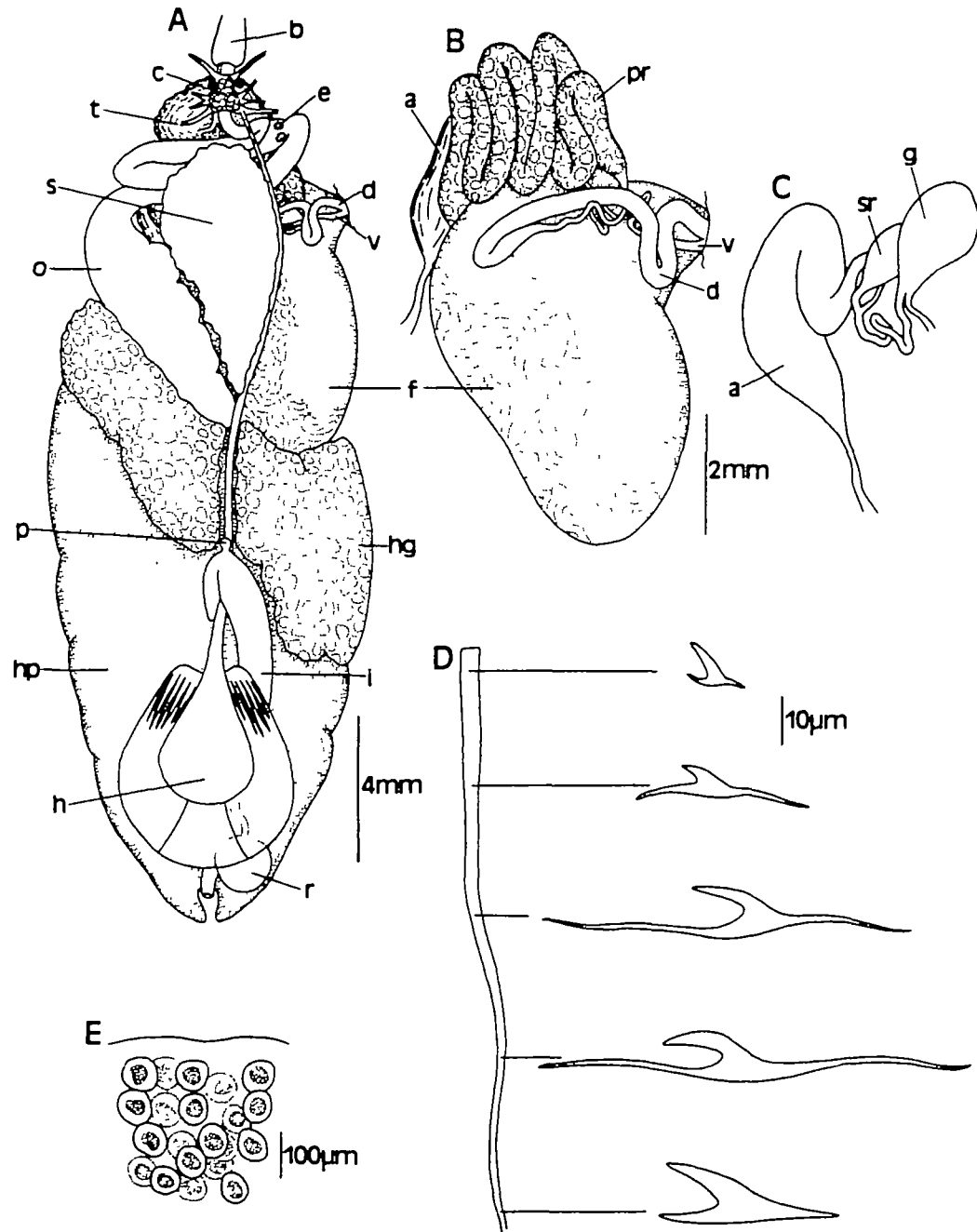


Figure 7. *Dendrodoris krebsu* (LZUO 120.15). **A.** Dorsal view of the internal organs. **B.** Reproductive system. **C.** Genital organs previously hidden under the prostate. **D.** Shape and disposition of the hooks along the male eversible cirrus. **E.** Detail of the egg mass. Abbreviations. a, ampulla; b, pharyngeal bulb, c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; g, gametolytic gland, h, heart, hg, hermaphrodite gland; hp, digestive gland, i, intestine; o, oesophagus; p, pyloric gland; pr, prostate; r, renal sac; s, blood gland, sr, seminal receptacle, t, ptyaline gland, v, vagina.

Thomas and Vieques, 10 specimens 13–23 mm preserved length (one of them partially dissected by the authors, another dissected here by dorsal incision, the male eversible cirrus was mounted in glycerin).

Doridopsis subpellucida. Holotype: BMNH 1839.12.27.32, St. Vincent, 1 specimen 19 mm preserved length, very contracted (partially dissected by dorsal incision, the male eversible cirrus is mounted for SEM).

Doriopsis atropos. Syntypes: ZMUC 1979, Rio de Janeiro, Brazil, 4 specimens 26, 44, 45 and 61 mm preserved length (one of them, 66 mm, dissected by the authors by lateral incision, another, 45 mm, dissected here by dorsal incision, with the male eversible cirrus mounted in glycerin).

External morphology (Fig. 1G-H): The background colour of the body can be white, yellow, brown or black. Usually in white or yellow specimens there are dark spots on the dorsum. No relation between size and pigmentation has been observed in adult specimens.

Gills have the same colour as the body with the exterior border pigmented in white. The rhinophores are usually very small in relation to the body size. They are black with the apex white. The juvenile specimens are uniformly red.

No spicules were observed in our material. The mantle margin is striated and as wide as the foot.

Anatomy (Fig. 7A-D): The oesophagus has roughly four folds. Just beside the third fold there are two oesophageal glands. The intestine has a small pyloric gland. The heart connects by the aorta with the blood gland, which covers a large portion of the reproductive system.

The reproductive system has a prostate several times longer than its width. The deferent duct has a narrow and folded proximal region. The ampulla is large and it has only one fold. The deferent duct is almost three times longer than the vagina. There is a mucus-forming section differentiated in the female gland. The gametolytic gland is twice as large as the seminal receptacle and they are joined by a short duct. The male eversible cirrus has numerous small hooks with an elongated bases, their variable shape is shown in Figure 7D.

Spawn (Fig. 7E): The egg is spirally coiled, 5 mm in height and 0.4 mm width. The eggs,

yellow in colour, are arranged in parallel lines of about 20, and protected into a spherical capsule. Eggs measured 62–72 μm (mean: 66 μm). Capsules measured 83–93 μm (mean 85 μm).

Distribution (Fig. 8A): After its original description from St Thomas and St. Croix (Mörch, 1863), *Dendrodoris krebsii* has been reported from Brazil (Marcus, 1957), Curaçao (Marcus & Marcus, 1963; 1970), Venezuela (Marcus & Marcus, 1967a), the Caribbean coast of Colombia (Marcus, 1976; Bandel, 1976), Panama (Meyer, 1977), Barbados (Marcus & Hughes, 1974; Edmunds & Just, 1985), St Kitts (Marcus & Marcus, 1963; 1970), Guadeloupe (Thompson, 1980), Jamaica (Thompson, 1980), Bahamas (Marcus & Marcus, 1967a), Florida (Marcus & Marcus, 1967a) and Georgia, U.S.A. (Marcus & Marcus, 1967c).

Remarks: *Dendrodoris krebsii* was described by Mörch (1863) based on several preserved specimens from the Danish Antilles. In the short Latin text there is no anatomical description, and it is very difficult to recognise this species based on it. Some years later, Abraham (1877) described *Doridopsis subpellucida* from the Lesser Antilles, also from preserved specimens. Only external features were given, and there was no distinctive characters in the description. Finally, Bergh (1879) described *Doriopsis atropos* from the South of Brazil, which was fully redescribed by Marcus (1957) as *Dendrodoris atropos*, giving anatomical details.

In the following years, records of *Dendrodoris* from the Caribbean Sea were attributed to *Dendrodoris krebsii* (Marcus & Marcus, 1963; 1967a; 1967c; 1970; Marcus, 1976; Meyer, 1977; Bandel, 1976; Marcus & Hughes, 1974; Thompson, 1980 and Edmunds & Just, 1985). The name *Dendrodoris atropos* was used for specimens from the Tropical Pacific coast of America (Thompson, 1980) and *Dendrodoris subpellucida* was not used. Only Thompson (1980) suggested that this latter species was probably a synonym of *D. krebsii*.

Our study of the type material of these three nominal species, confirms that their anatomical features (reproductive system, male cirrus hooks) are identical, and that they should be considered synonyms.

Several authors (Collier & Farmer, 1964; Marcus & Marcus, 1967b; Bertsch, 1973, 1979) have reported specimens of the genus *Dendro-*

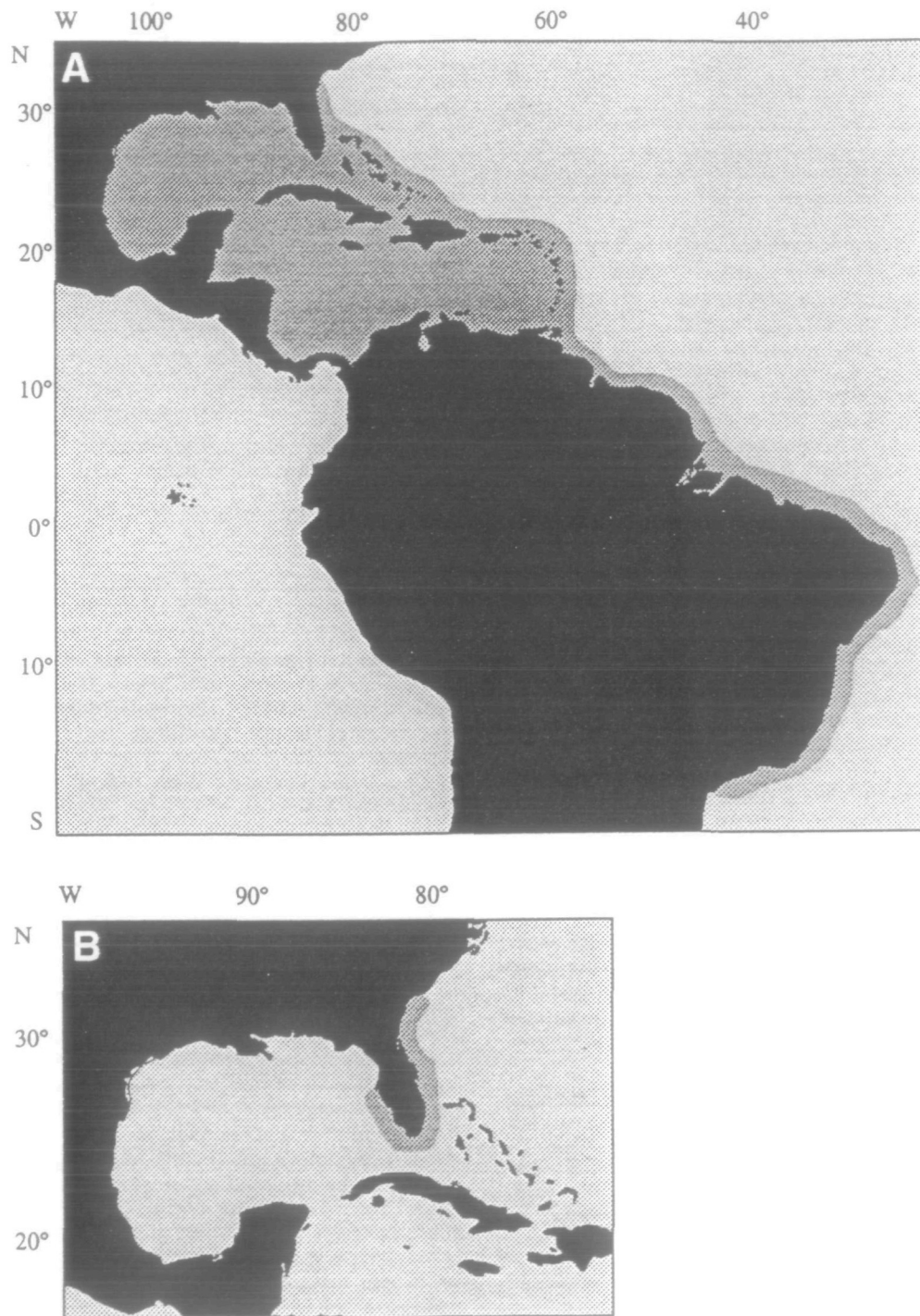


Figure 8. Maps of the known distribution of the Western Atlantic described species of the genus *Dendrodoris* A. *Dendrodoris krebsii*. B. *Dendrodoris warta*.

doris from the American Pacific coast under the name *Dendrodoris krebsii*, considering that this species occurs in both Atlantic and Pacific Oceans. However, specimens collected from the American Pacific coast were black coloured with a red line around the mantle margin. These characteristics never occur in *D. krebsii*, nor other Atlantic species. On the other hand, Thompson (1980) considered that specimens from the Atlantic, named *D. krebsii*, are different from specimens from the Pacific, named *Dendrodoris atropos*, forgetting that *D. atropos* was originally described from South Brazil.

We studied several specimens from the Galapagos Islands and the Pacific coast of Mexico, to compare with the Atlantic species. These animals are externally identical to those previously recorded from this area (Collier & Farmer, 1964; Marcus & Marcus, 1967b; Bertsch, 1973, 1979). We think that Pacific material resembles the original description of *Dendrodoris nigra* (Stimpson, 1855), a species described from Japan (Stimpson, 1855) as black coloured with red edge of the mantle. It is not clear whether the Pacific specimens belong to the former species, but obviously they are not *D. krebsii* nor any other Atlantic species. The external appearance, the reproductive system features and the male cirrus hooks are very different between specimens from both coasts of America. For this reason we do not agree with the hypothesis that animals have dispersed through the Panama Canal.

Anatomical differences separate *Dendrodoris krebsii* from other Atlantic species. Only the reproductive system of *Dendrodoris grandiflora* resembles that of *D. krebsii*, and it seems that both species are close. However, the morphology of the male eversible cirrus hooks of *D. krebsii* are very different from those of *D. grandiflora*, and it clearly separates both species.

Material examined CUBA—Havana (23°08'N, 82°24'O), 17 Jul. 1988, 4 specimens 12–25 mm preserved length, coll. Espinosa (LZUO 120.15); 29 Apr. 1989, 1 specimen 2 mm preserved length (LZUO 117.37); 17 Jun. 1990, 1 specimen 17 mm preserved length (BMNH 1993157); 27 May 1993, 1 specimen 5 mm preserved length (LZUO 117.10); 20 Jun. 1993, 1 specimen 17 mm preserved length (LZUO 117.59). Cabo Frances, Pinos Island (21°36'N, 83°10'W), 22 Apr 1989, 1 specimen 17 mm preserved length (LZUO 109.57); 22 Apr 1984, 1 specimen 18 mm preserved length (LZUO 117.38). Diego Pérez Key (22°02'N, 81°33'W), 8 Jul. 1988, 1 specimen 16 mm preserved length (LZUO 117.36).

Cienfuegos (21°08'N, 80°28'W), 20 Jun. 1993, 1 specimen 52 mm preserved length (BMNH 1993155). LESSER ANTILLES—St Thomas (18°20'N, 64°55'W) and Vieques (18°08'N, 65°24'W), 10 specimens 13–23 mm preserved length (ZMUC 94, ZMUC 101, ZMUC 400, ZMUC 401), SYNTYPES of *Doris krebsii*. St Vincent (13°13'N, 60°12'W), 1 specimen 19 mm preserved length (BMNH 1839.12.27.32), HOLOTYPE of *Dondopsis subpellucida*. BRAZIL—Rio de Janeiro (22°55'S, 43°15'W), 4 specimens 36, 44, 45 and 61 mm preserved length (ZMUC 1979), SYNTYPES of *Doriopsis atropos*. Niteroi (22°55'S, 43°10'W), 1981, 1 specimen 38 mm preserved length, coll. Epifanio (LZUO 120.21); 1 specimen 20 mm preserved length, coll. Epifanio (BMNH 1993156). Itacurussá (22°56'S, 43°55'W), 1962, 1 specimen 18 mm preserved length, coll. Epifanio (LZUO 117.19).

Dendrodoris senegalensis Bouchet, 1975

(Figs. 2C–D, 4C & 9)

Dendrodoris senegalensis Bouchet 1975: 124–127, figs. 3–4, pl. I.

Type material: According to the original description (Bouchet, 1975) the type material of *Dendrodoris senegalensis* includes one lectotype (selected by Bouchet, 1975): MNHN, Senegal, 18 mm preserved length; and two paralectotypes: MNHN, Senegal, 10 and 17 mm preserved length (one of them, 17 mm, dissected by the author). Also, it includes three paralectotypes deposited in the Museum der Humboldt-Universität of Berlin, Germany, and another deposited in the Département de Biologie Marine de l'Institut Fondamental d'Afrique Noire of Dakar, Senegal. However, these specimens must be considered as holotype and paratypes.

External morphology (Fig. 2C–D): The background colour of the body is very variable, it can be white, yellow, orange, brown, grey or black. Most of specimens studied have dark grey or black spots on the dorsum. No relationship between size and pigmentation has been observed in adult specimens.

The rhinophores and the gills are similar in colour to the body, with the apex (in the rhinophores) and the exterior border (in the gills) white. Juvenile specimens are uniformly red.

No spicules were observed. The mantle margin is wide and strongly striated. It is about as wide as 1/2 the foot.

Anatomy (Fig. 9A–D): The oesophagus has three folds. Just beside the second fold there

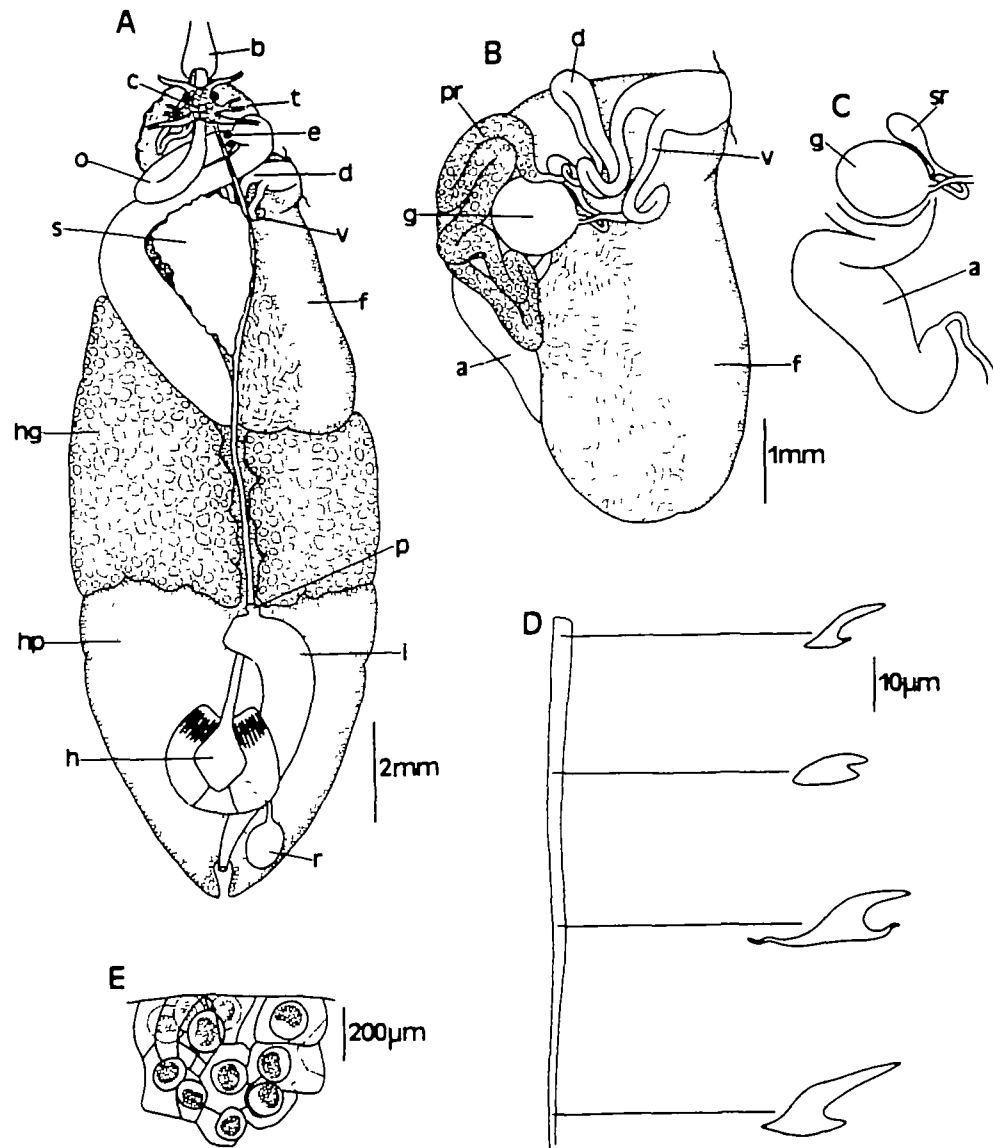


Figure 9. *Dendrodoris senegalensis* (LZUO 11715) **A.** Dorsal view of the internal organs **B.** Reproductive system. **C.** Genital organs previously hidden under the prostate **D.** Shape and disposition of the hooks along the male eversible cirrus. **E.** Detail of the egg mass. Abbreviations. a, ampulla; b, pharyngeal bulb; c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; g, gametolytic gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine, o, oesophagus; p, pyloric gland; pr, prostate; r, renal sac; s, blood gland; sr, seminal receptacle; t, ptyaline gland; v, vagina.

are two oesophageal glands. The intestine has a small pyloric gland. The heart connects by the aorta with the blood gland, which covers a large portion of the reproductive system.

The reproductive system has a prostate several times longer than wide. The deferent

duct does not have a differentiated proximal region. The ampulla is small and has two folds. The deferent duct is as wide as the vagina, and presents one characteristic fold on its middle section pointed towards the head of the animal. The vagina decreases in width as it

approaches the gametolytic gland. The gametolytic gland is several times larger than the seminal receptacle and both connect by a very short duct, wider than the distal portion of the vagina. The male eversible cirrus has numerous small hooks, their variable shape is shown in figure 9D.

Spawn (Fig. 9E): The egg mass is spirally coiled, 4 mm in height and 1 mm in width. The eggs are yellow in colour and arranged in irregular lines of about 17 individuals, and protected by spherical capsules. These capsules are also enclosed by other larger polyhedron-shaped capsules. The spherical capsules measured 104–125 µm (mean: 110 µm).

Distribution (Fig. 4C): This species is only known from the Cape Verde Islands and Senegal.

Remarks: *Dendrodoris senegalensis* was first reported by Sourie (1958) from Dakar, Senegal, as *Dendrodoris* sp. and by Eliot (1906) from the Cape Verde Islands as *Dendrodoris grandiflora*. Later, Bouchet (1975) described *D. senegalensis* based on material from Senegal.

Externally, *Dendrodoris senegalensis* is very close to *Dendrodoris grandiflora*. Nevertheless, the characteristic male cirrus hooks of *D. senegalensis*, with a very narrow base, and the always present fold in the deferent duct of *D. senegalensis* which is pointed towards the head, distinguish clearly both species.

Dendrodoris krebsii resembles *Dendrodoris senegalensis* in certain anatomical details such as the width and length of the prostate. However, the shape of the egg mass and the male cirrus hooks clearly separate them.

Material examined: SENEGAL—Dakar (14°40'N, 17°25'W), 1949, 1 specimen 32 mm preserved length, coll. Monod and Manny (MNHN); 13 Mar. 1957, 1 specimen 19 mm preserved length, coll. Marche-Marchad (MNHN); 4 Aug. 1959, 2 specimens 35 and 44 mm preserved length, coll. Marche-Marchad (MNHN), 14 Sept. 1973, 2 specimens 3–5 mm preserved length, coll. Bouchet (MNHN). CAPE VERDE ISLANDS—Calhau, São Vicente Island (16°50'N, 24°51'W), 15 Aug. 1985, 1 specimen 4 mm preserved length (LZUO 117.63) Salamanza Bay, São Vicente Island (16°50'N, 24°57'W), 19 Aug. 1985, 4 specimens 15–27 mm preserved length (LZUO 120.07); 20 Aug. 1985, 9 specimens 6–12 mm preserved length (LZUO 117.18); 18 Jun. 1955, 2 specimens 11–12 mm preserved length, coll. Cademot (MNHN). Rabo de Junco, Sal Island (16°35'N, 22°58'W), 18 May 1987, 1 specimen 23 mm

preserved length, coll. Rolán (BMNH 1993154). Palhoma Cape, Sal Island (16°49'N, 22°58'W), 3 May 1987, 3 specimens 6–16 mm preserved length, coll. Rolán (LZUO 117.15). Serra Negra, Sal Island (16°37'N, 22°54'W), 19 May 1987, 2 specimens 9–12 mm preserved length, coll. Rolán (LZUO 117.11). Mordeira, Sal Island (16°39'N, 22°56'W), 10 Aug. 1985, 3 specimens 7–18 mm preserved length (LZUO 109.63); 7 Aug. 1985, 1 specimen 15 mm preserved length (LZUO 109.65); 8 Aug. 1985, 5 specimens 9–18 mm preserved length (LZUO 117.19). Fontona, Sal Island (16°44'N, 22°59'W), 13 Aug. 1985, 2 specimens 11–12 mm preserved length (LZUO 109.64). Tarrafal, São Tiago Island (15°16'N, 23°46'W), 22 Aug. 1985, 1 specimen 16 mm preserved length (LZUO 117.13). Furna Bay, Brava Island (14°46'N, 24°42'W), 9 May 1987, 1 specimen 9 mm preserved length, coll. Rolán (LZUO 117.14). Sal Rei, Boavista Island (16°09'N, 22°57'W), 23 Aug. 1985, 1 specimen 20 mm preserved length (LZUO 117.16); 1980, 1 specimen 12 mm preserved length, coll. Rolán (LZUO 117.32). Pau Seco, Maio Island (15°17'N, 23°13'W), 1984, 1 specimen 21 mm preserved length, coll. Rolán (LZUO 117.33), 1980, 1 specimen 18 mm preserved length, coll. Rolán (LZUO 117.35).

Dendrodoris warta Marcus & Gallagher, 1976
(Figs. 2A, 8B & 10)

Dendrodoris warta Marcus & Gallagher 1976:
353–355, figs. 1–5.

Type material: *Dendrodoris warta*. Holotype. USNM 763414, Boca Ciega, Florida, U.S.A. (27°47'N, 82°47'W), July–Sep. 1972, 1 specimen. Paratypes: FSBC I 10744, Boca Ciega, Florida, U.S.A. (27°47'N, 82°47'W), July–Sep. 1972, 1 specimen 44 mm preserved length (dissected by the authors); FSCB I 11101, Boca Ciega, Florida, U.S.A. (27°47'N, 82°47'W), July 1972, 1 specimen 26 mm preserved length; USNM 710770, Boca Ciega, Florida, U.S.A. (27°47'N, 82°47'W), 1 specimen 36 mm preserved length, contracted (dissected by the authors).

External morphology (Fig. 2A): The background colour of the body is dark brown. The dorsum is covered with large, pinky-beige tubercles or warts which are irregular in shape and variable in size. Tubercles are never present on the border of the mantle.

The rhinophores are brown, with the lamellae and the apex white. The gills are dark brown with the external edge pigmented in white.

No spicules are present on the dorsum. The mantle margin is narrow, about 1/5 the width of foot, and striated.

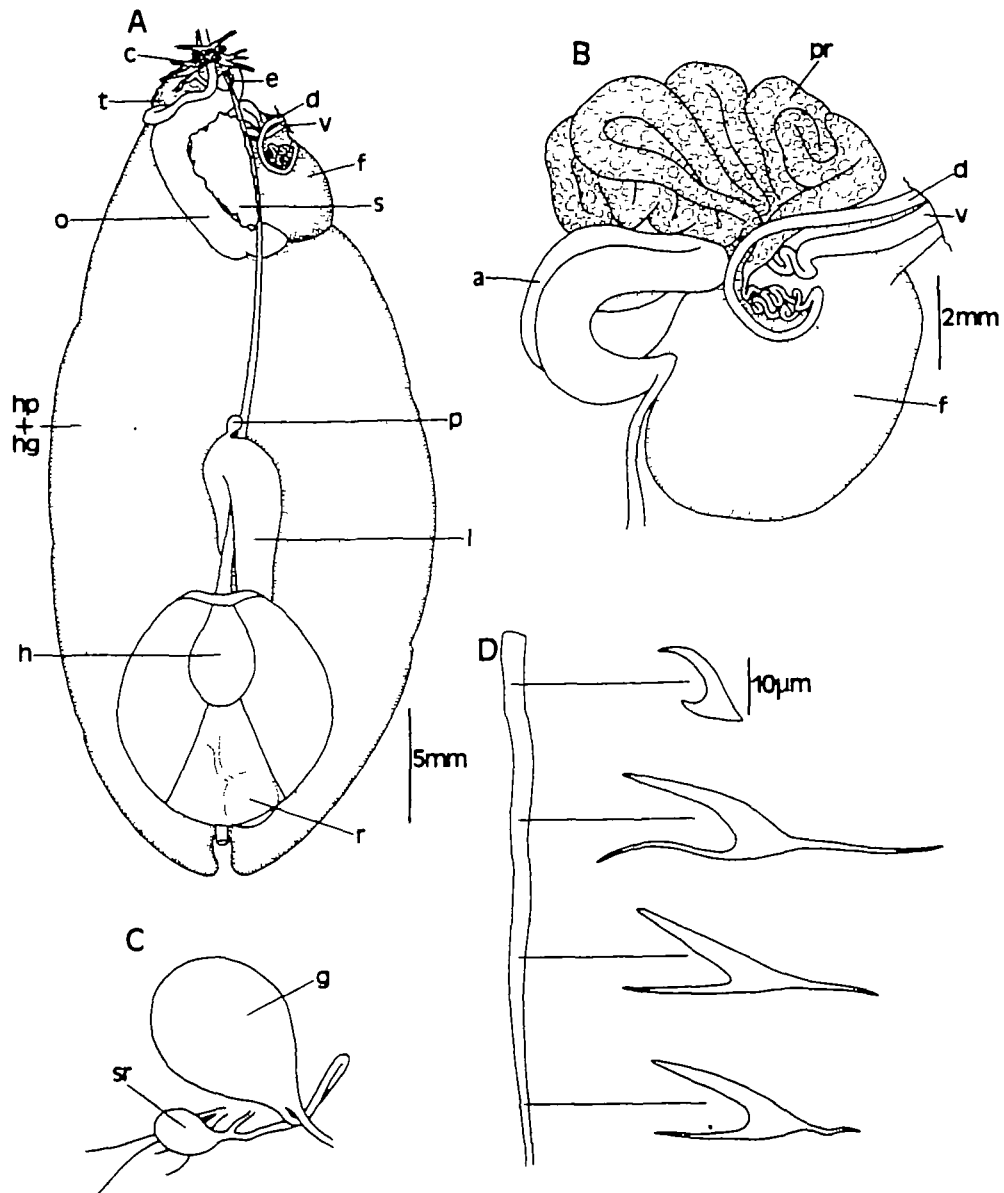


Figure 10. *Dendrodoris warta* (FSBC I 54894) **A.** Dorsal view of the internal organs. **B.** Reproductive system. **C.** Genital organs previously hidden under the prostate. **D.** Shape and disposition of the hooks along the male eversible cirrus. Abbreviations: a, ampulla; b, pharyngeal bulb; c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; g, gametolytic gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; o, oesophagus; p, pyloric gland; pr, prostate; r, renal sac; s, blood gland; sr, seminal receptacle; t, ptyaline gland; v, vagina.

Anatomy (Fig. 10): The oesophagus has four folds, just beside the third fold there are two oesophageal glands. The intestine has a conspicuous pyloric gland. The heart connects by

the aorta with the blood gland which covers a large portion of the reproductive system.

The reproductive system has a prostate many times longer than its width. The deferent

duct has a narrow, very long and folded proximal region. The vagina is wider than the deferent duct. The ampulla has three folds. There is no mucus portion differentiated in the female gland. The gametolytic gland is ten times larger than the seminal receptacle. Both connect by a quite long duct. The male eversible cirrus has numerous hooks with elongate bases, their variable shape is shown in Figure 10D. The hermaphrodite gland is not clearly separated from the digestive gland.

Spawn: According to Marcus & Gallagher (1976), the egg mass is spirally coiled, 35 mm in diameter and 10 mm in height. The eggs are orange in colour and protected by a spherical capsule. The spherical capsules measured approximately 170 µm, and the eggs 120 µm.

Distribution (Fig. 8B): This species has only been reported from the U.S.A., Florida (Marcus & Gallagher, 1976) and South Carolina (Eyster, 1980)

Remarks: *Dendrodoris warta* is clearly different from the other Atlantic species of *Dendrodoris* by the presence of warts on the dorsum. Other *Dendrodoris* species that have tubercles on the body are *Dendrodoris gemmacea* (Alder & Hancock, 1864) and *Dendrodoris tuberculosa* (Quoy & Gaimard, 1832), both from the Indo-Pacific. However, the position of the tubercles is very different among these three species. *D. gemmacea* has two rows of tubercles along the body (Alder & Hancock, 1864), *D. tuberculosa* is covered by large tubercles topped by smaller ones (Quoy & Gaimard, 1832), whereas in *D. warta* all tubercles are of equal size and spread across the dorsum.

Other tuberculated Indo-Pacific species of *Dendrodoris* have a similar external morphology to *Dendrodoris gemmacea* and *Dendrodoris tuberculosa*, and probably are synonyms. *Dendrodoris clavulata* (Alder & Hancock, 1864) and *Dendrodoris mammosa* (Abraham, 1877) are very close to *D. gemmacea*. Also, *Dendrodoris carbunculosa* (Kelaart, 1858), *Dendrodoris rugosa* (Pease, 1860), *Dendro-*

doris pustulosa (Alder & Hancock, 1864) and *Dendrodoris morulifer* Allan, 1932 resemble *D. tuberculosa*.

Material examined: U.S.A.—Boca Ciega, Florida (27°47'N, 82°47'W), July-Sep. 1972, 1 specimen 36 mm preserved length (USNM 710770), PARATYPE of *Dendrodoris warta*; 1 specimen 26 mm preserved length (FSBC I 11101), PARATYPE of *Dendrodoris warta*; 1 specimen 44 mm preserved length (FSBC I 10744), PARATYPE of *Dendrodoris warta*. Cape Canaveral, East coast of Florida (30°29'N, 80°11'W), 28 Aug. 1974, 1 specimen 71 mm preserved length, R/V Hernan Cortez (FSBC I 54894). Sixty five miles West of Egmont, West coast of Florida (27°37'N, 83°58'W), 20 Nov 1966, 1 specimen 63 mm preserved length, R/V Hernan Cortez (FSBC I 54893), 1 Sep 1967, 1 specimen 55 mm preserved length, R/V Hernan Cortez (FSBC I 54892).

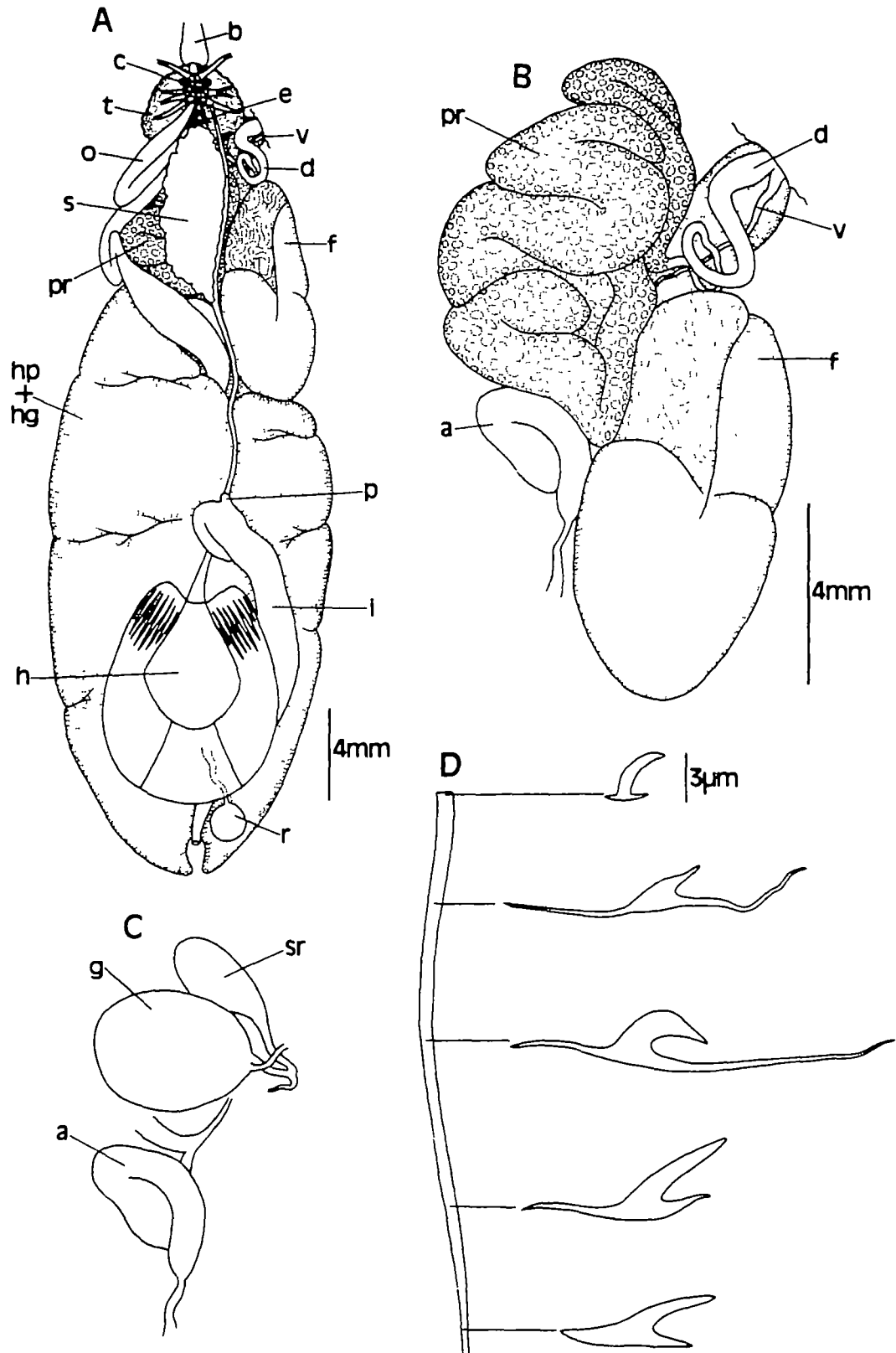
Dendrodoris angolensis Valdés & Ortea, new species
(Figs. 2F, 11 & 12C)

Type material: *Dendrodoris angolensis*. Holotype: MNHN, Luanda, Angola (8°46'S, 3°13'E), 1981, 1 specimen 38 mm preserved length, coll. Gofas; paratypes: MNHN, Luanda, Angola (8°46'S, 13°13'E), 1981, 2 specimens 29 and 38 mm preserved length, coll. Gofas; MNCN 15.05/17229, São Tiago, Angola (8°35'N, 7°21'E), 8 July 1990, 1 specimen 22 mm preserved length, coll. Rolán.

External morphology (Fig. 2F): The dorsal coloration is yellow, orange or pale brown, with darker spots of orange, red or black. These spots generally occur in the centre of the dorsum, and have a diffuse edge. The mantle margin is usually edged by a thin red line. The rhinophores have the same colour as the dorsum, with the lamellae and the apex red. The gills usually have the same colour as the body, with the margins edged in red. The mantle edge is slightly striated and as wide as 1/3 of the foot width.

Anatomy (Fig. 11): The oesophagus is long, with four folds. Just before the second fold

Figure 11. *Dendrodoris angolensis* (LZUO 117.25). A. Dorsal view of the internal organs. B. Reproductive system. C. Genital organs previously hidden under the prostate. D. Shape and disposition of the hooks along the male eversible cirrus. Abbreviations: a, ampulla; b, pharyngeal bulb; c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; g, gametolytic gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; o, oesophagus; p, pyloric gland; pr, prostate; r, renal sac; s, blood gland; sr, seminal receptacle; t, ptyaline gland; v, vagina.



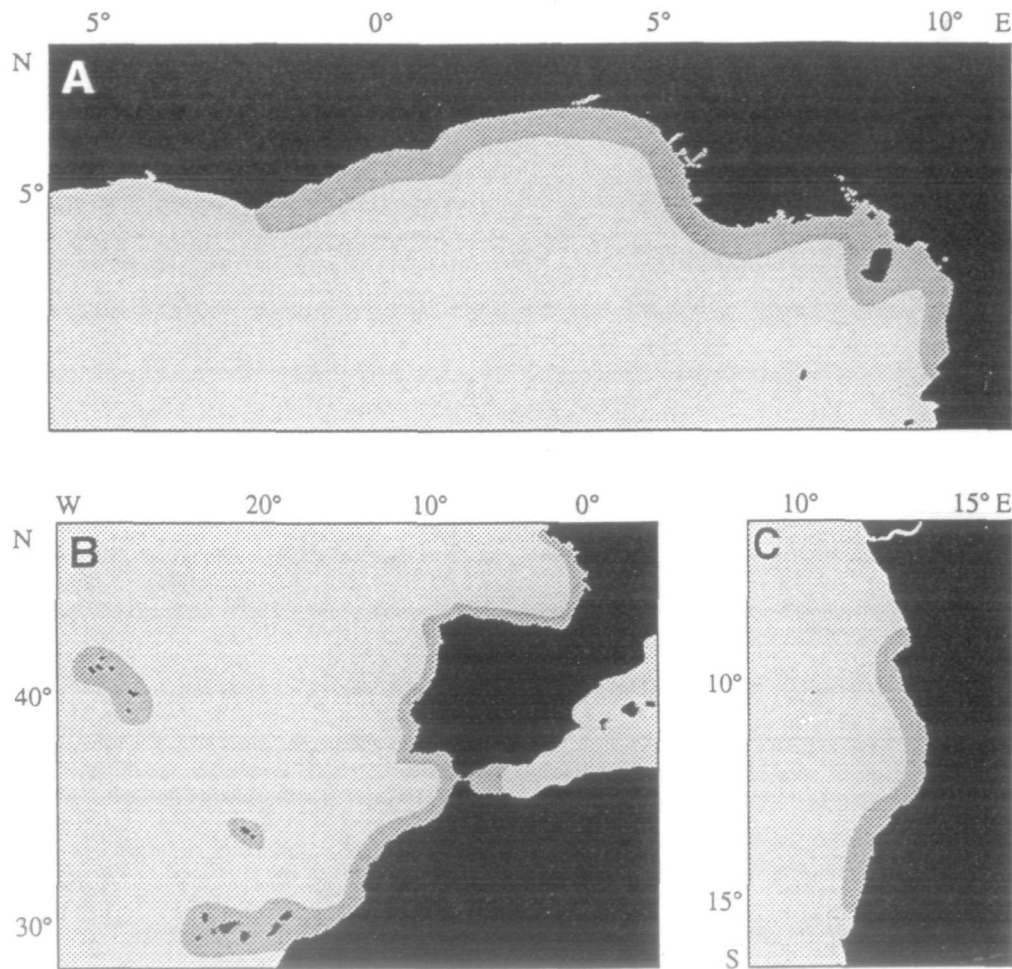


Figure 12. Maps of the known distribution of the Atlantic new species of the genus *Dendrodoris*. A. *Dendrodoris guineana*. B. *Dendrodoris heryira*. C. *Dendrodoris angolensis*.

there are two oesophageal glands. The intestine has a small pyloric gland. The heart connects by the aorta with the blood gland, which covers a large portion of the reproductive system.

The reproductive system is characterised by a long, tubular and granular prostate. The ampulla is small, with two folds. The gametolytic gland is spherical, and connects with the seminal receptacle by a folded duct which is wider than the distal portion of the vagina. The deferent duct is short and similar in size to the vagina. There is a distinct mucus portion in the female gland. The male eversible cirrus has numerous small hooks with elongate bases, their variable shape is shown in Figure 11D.

Spawn: The orange eggs are oval shaped and surrounded by a spherical capsule. Eggs measured 52–83 μm in length (mean: 64 μm); capsules measured 114–125 μm (mean: 122 μm).

Distribution (Fig. 12C): This species is only known from Angola.

Etymology: The name of this species is derived from Angola.

Remarks: *Dendrodoris angolensis* is distinguished by its diffused black spots and a red mantle margin. *Dendrodoris lumbata* and *Dendrodoris senegalensis* can both have similar coloration to *D. angolensis*, but they lack a red mantle margin and do not have diffuse dark

spots. Internally *D. angolensis* resembles *Dendrodoris guineana*, but differs considerably in the shape of the male cirrus hooks and prostate. The shape of the male cirrus hooks of *Dendrodoris angolensis* are similar to *D. senegalensis*, but these two species differ in the morphology of the reproductive system.

Dendrodoris angolensis is easily separated from *Dendrodoris callosa* (Bergh, 1907) and *Dendrodoris caesia* (Bergh, 1907), two *Dendrodoris* described by Bergh (1907) from False Bay (South Africa). *D. callosa* has hard spicules on the body while *D. caesia* is bluish in colour with dark spots. Two other species from South Africa are *Dendrodoris capensis* (Bergh, 1907) and *Dendrodoris nigra*, both recorded from Natal Province in the Indian Ocean (Bergh, 1907) and externally very different from *D. angolensis*. Also, Gosliner (1987) described two unnamed species from the Indian ocean coast of South Africa. The former, *Dendrodoris* sp. 1, is greenish with black and opaque white mottled in the gills, and the another one, *Dendrodoris* sp. 2, has pink tubercles on the dorsum. Both animals appear to be juvenile specimens of other Indo-Pacific species of *Dendrodoris*.

Material examined. ANGOLA—Luanda (8°49'S, 13°13'E), 1981, 1 specimen 38 mm preserved length, coll. Gofas (MNHN), HOLOTYPE of *Dendrodoris angolensis*; 2 specimens 29–38 mm preserved length, coll. Gofas (MNHN), PARATYPES of *D. angolensis*; 1982, 1 specimen 12 mm preserved length, coll. Gofas (MNHN), 17 Feb. 1990, 1 specimen 17 mm preserved length, coll. Rolán (LZUO 117.28); 20 Aug 1989, 1 specimen 25 mm preserved length (LZUO 117.25). Luanda (8°46'S, 13°13'E), 1981, 2 specimens 35–45 mm preserved length, coll. Gofas (LZUO 120.20); 18 July 1989, 1 specimen 18 mm preserved length, coll. Rolán (LZUO 117.27). Bissonga (13°46'S, 12°30'E), 25 July 1990, 1 specimen 16 mm preserved length (LZUO 117.26). Santa María Bay (13°29'S, 12°29'E), Dec. 1981, 4 specimens 15–36 mm preserved length, coll. Gofas (MNHN); 4 Aug. 1982, 2 specimens 27–31 mm preserved length, coll. Gofas (MNHN). Amelia Beach (15°01'S, 12°08'E), 1981, 1 specimen 14 mm preserved length, coll. Gofas (MNHN). São Tiago Beach (8°35'N, 7°21'E), 8 July 1990, 1 specimen 22 mm preserved length, coll. Rolán (MNCN 15.05/17229) PARATYPE of *D. angolensis*; 1981, 1 specimen 7 mm preserved length, coll. Gofas (MNHN); 1982, 2 specimens 14–22 mm preserved length, coll. Gofas (MNHN); 30 Feb. 1990, 1 specimen 21 mm preserved length, coll. Rolán (LZUO 117.29); 8 July 1990, 2 specimens 10–24 mm preserved length, coll. Rolán (LZUO 117.24). Musulo Bay (9°02'N, 15°02'E), 1981, 1 specimen 22 mm preserved length, coll. Gofas (MNHN)

Dendrodoris guineana Valdés & Ortea, new species
(Figs. 2E, 12A & 13)

Type material: *Dendrodoris guineana*. Holotype: MNCN 15.05/15829, Bata, Equatorial Guinea (1°50'N, 9°43'E), May 1983, 1 specimen 16 mm preserved length, coll. Templado; paratypes: MNCN 15.05/15829, Bata, Guinea Equatorial, May 1983. 1 specimen 12 mm preserved length, leg. Templado; MNCN 15.05/15830, Takoradi, Ghana (4°53'N, 1°46'W), 5 Mar. 1993, 1 specimen 24 mm preserved length, leg. Templado.

External morphology (Fig. 2E): Only 3 specimens of this species have been examined. In the specimen from Ghana the background coloration of the dorsum is pale grey with darker grey spots present over the entire body. The basic colour of the specimens from Guinea Equatorial is red, without spots. The rhinophores are similar in colour to the dorsum. The gills are the same colour as the dorsum. The mantle edge is slightly striated and narrow, being 1/10 of the foot width.

Anatomy (Fig. 13): The oesophagus has two folds, beside the second one there are two small oesophageal glands. The intestine has a large pyloric gland. The heart connects by the aorta with a small blood gland, which covers only a portion of the oesophagus.

The reproductive system has a short and tubular prostate, a few times longer than its width. The ampulla is small, with three folds. The deferent duct is wider than the vagina. The spherical gametolytic gland connects with the seminal receptacle by a duct twice as large as the distal portion of the vagina. There is no distinct mucus portion in the female gland. The male eversible cirrus has numerous small hooks with an elongate bases, their variable shape is shown in Figure 13D.

Distribution (Fig. 12A): This species is presently known only from the Gulf of Guinea, from Ghana to Equatorial Guinea.

Etymology: The name of this species is derived from the Gulf of Guinea.

Remarks: *Dendrodoris guineana* is distinctive and can be recognised by its internal features. The shape of the male cirrus hooks of *Dendrodoris senegalensis* resembles those of

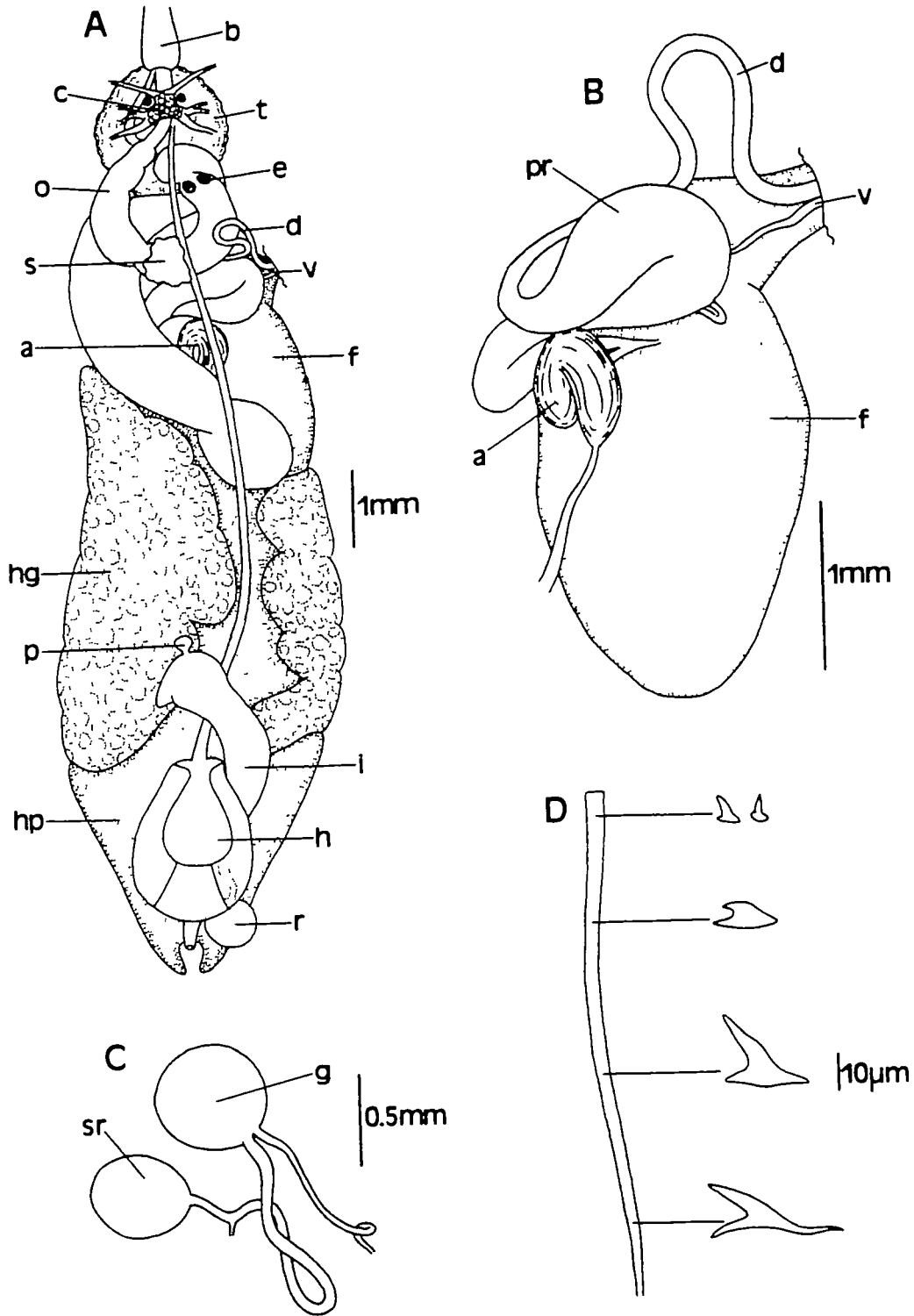


Figure 13. *Dendrodoris guineana* (MNCN 15 05/15829) **A.** Dorsal view of the internal organs. **B.** Reproductive system. **C.** Genital organs previously hidden under the prostate. **D.** Shape and disposition of the hooks along the male eversible cirrus. Abbreviations. a, ampulla; b, pharyngeal bulb; c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; g, gametolytic gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; o, oesophagus; p, pyloric gland; pr, prostate; r, renal sac; s, blood gland, sr, seminal receptacle; t, ptyaline gland; v, vagina

D. guineana. However, the former species differs in other anatomical features such as the shape of the prostate and the ampulla. The characteristic short and wide prostate of *D. guineana* is similar in appearance to that of *Dendrodoris limbata*, but both species are easily distinguished from each other by differences in the male cirrus hooks and external colour.

D. guineana is here described from three small but mature specimens. Further studies are necessary to complete the knowledge of the colour variability and biology of this species

***Dendrodoris herytra* Valdés & Ortea, new species**
(Figs. 2G-H, 12B & 14)

Dendrodoris sp. García-Gómez 1984: 211–212.

Type material: *Dendrodoris herytra*. Holotype: MNHN, Madeira Island, Portugal (29°54'N, 17°00'W), 1 May 1993, 1 specimen 16 mm preserved length, coll. Wirtz; paratypes: MNCN 15.05/15831, Oviñana, Spain (43°35'N, 6°14'W), Jan. 1975, 1 specimen; MCNT Mo/00178, Gando Bay, Gran Canaria Island, Spain (27°56'N, 15°21'W), 7 May 1980, 1 specimen, coll. Pérez-Sánchez.

External morphology (Fig. 2G-H): The most usual background colour of this species is uniformly pale red. Some specimens have a yellowish background colour with red (or exceptionally pale green) spots. One specimen from the Canary Islands is grey with black spots. The rhinophores and the gills are the same colour as the body, with the apex (in the rhinophores) and the exterior border (in the gills) pigmented in white. Juvenile specimens are uniformly pale red. The dorsal surface is smooth, however soft wrinkles may occur in some specimens. The edge of the mantle is very delicate, slightly striated and very variable in size, from 1/10 to 1/2 of the foot width. The gills are conspicuously short, and never reach the edge of the mantle.

Anatomy (Fig. 14): The oesophagus has 5 folds, and two oesophageal glands just before the second fold. The intestine has a large and spherical pyloric gland on its proximal portion. The heart connects by the aorta with the blood gland which only covers a small portion of the prostate.

The reproductive system has a very long, tubular and granular prostate. The ampulla is kidney-shaped, without folds. The oval gametolytic gland connects with the seminal receptacle by a duct twice as large as the distal portion of the vagina. The male eversible cirrus has numerous small hooks with an elongate bases, their variable shape is shown in Figure 14D.

Distribution (Fig. 12B): This species is only known from the North Eastern Atlantic. The most northerly record is from the north of Spain, and the southerly from the Canary Islands.

Etymology: The name of this species is derived from the latinization of the feminine singular nominative of the ancient Greek adjective ἐρυθρός, α, ον, which means red, the colour more common in the adults of *Dendrodoris herytra*.

Remarks: The most typical colour of adult *Dendrodoris herytra* is uniform red. However, considerable individual variation in dorsal pattern occurs in this species. One form is grey with black spots, and was described by Odhner (1932) from the Azores as *Dendrodoris grandiflora*.

Dendrodoris herytra can be easily separated from *Dendrodoris guineana*, the other usually red *Dendrodoris* species. The bases of the male cirrus hooks in *D. herytra* are much larger than in *D. guineana*. Also the prostate of *D. herytra* is longer than in *D. guineana*.

Externally, the gills of *Dendrodoris herytra* are very characteristic, being conspicuously short, and predominantly pink. Juveniles of *Dendrodoris grandiflora*, *Dendrodoris senegalensis* and *Dendrodoris subpellucida*, are red like adult *D. herytra*, but they change in appearance as they grow. *D. herytra* is distin-

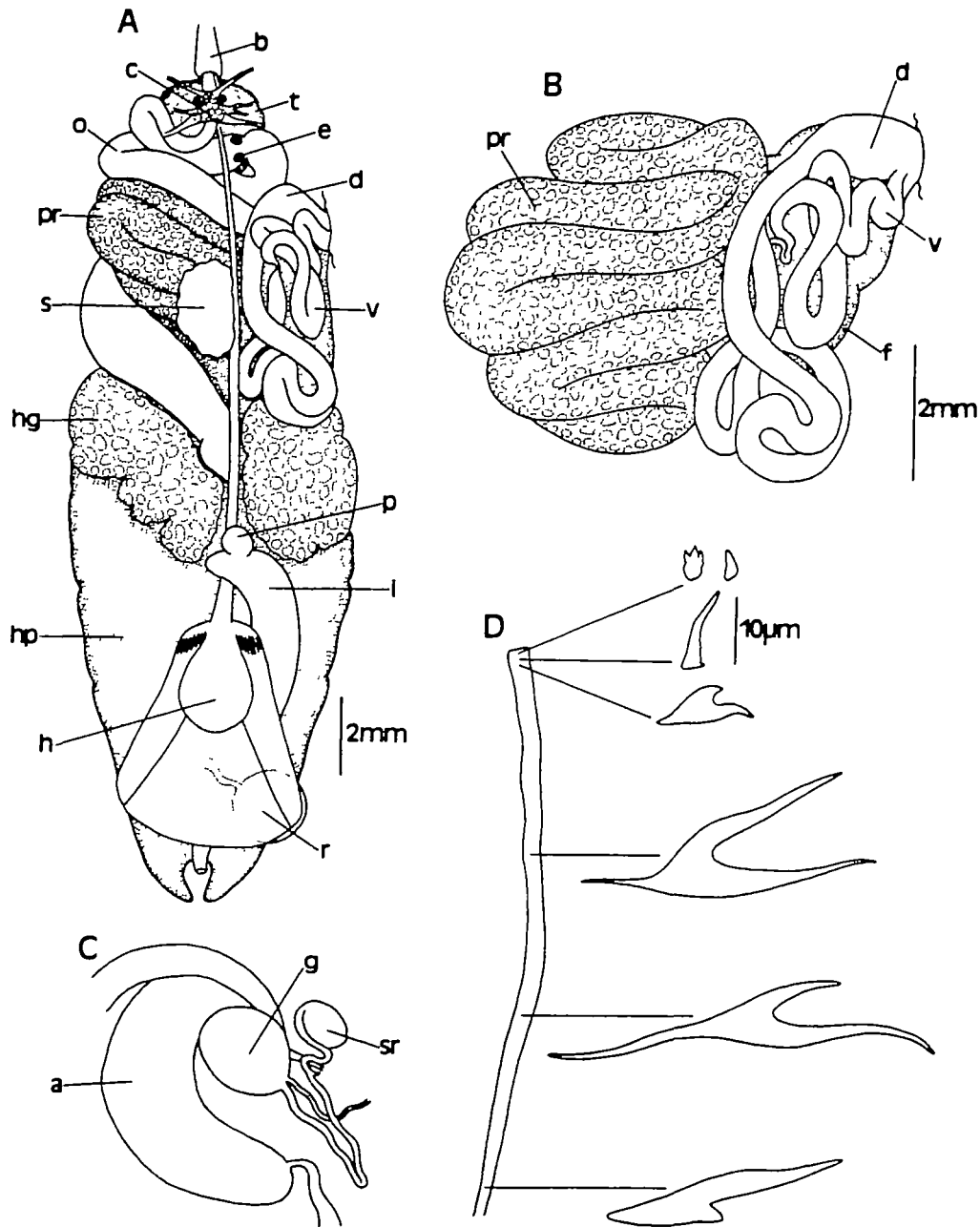


Figure 14. *Dendrodoris herytra* (LZUO 117.04). A. Dorsal view of the internal organs. B. Reproductive system. C. Genital organs previously hidden under the prostate. D. Shape and disposition of the hooks along the male eversible cirrus. Abbreviations. a, ampulla; b, pharyngeal bulb; c, central nervous system; d, deferent duct; e, oesophageal glands; f, female gland; g, gametolytic gland; h, heart; hg, hermaphrodite gland; hp, digestive gland; i, intestine; o, oesophagus; p, pyloric gland; pr, prostate; r, renal sac; s, blood gland; sr, seminal receptacle; t, ptyaline gland; v, vagina.

guished from other *Dendrodoris* species by its long deferent duct and the shape of its male cirrus hooks.

The first record of this species was probably published by Vayssière (1913) from Biscay Bay, under the name *Dendrodoris limbata*. Records from the north of Spain under the names *Dendrodoris grandiflora* and *D. limbata* (see Ortea, 1977) must also be referred to *Dendrodoris herytra*. A specimen from Cies Islands (north of Spain) cited by Rolán, Otero & Rolán Álvarez (1989) under the name *D. grandiflora*, also appears to belong to *D. herytra*. Material from the Strait of Gibraltar has recently been allocated to the Pruvot-Fol's species *Dendrodoris languida* (García-Gómez, 1983). Despite this, García-Gómez (1984) discussed the identity of this specimen, proposing that definitive identification requires further anatomical studies. The external features of this animal are identical to our material of *D. herytra*.

Material examined: SPAIN—Muros de Nalón (43°33'N, 6°06'W), 25 Nov. 1988, 1 specimen 3 mm preserved length (LZUO 117.39); 16 Apr 1992, 1 specimen 6 mm preserved length (LZUO 112.80). Oviñana (43°35'N, 6°12'W), Jan. 1975, 1 specimen (MNCN 15.05/15831), PARATYPE of *Dendrodoris herytra*; 12 July 1975, 1 specimen 11 mm preserved length (LZUO 117.06); 12 July 1975, 1 specimen 20 mm preserved length (LZUO 117.04). Alborán Sea (35°56'N, 3°02'W), 11 July 1989, 1 specimen 32 mm preserved length (LZUO 106.07). ATLANTIC ISLANDS—Madeira Island, Portugal (29°54'N, 17°00'W), 1 May 1993, 1 specimen 16 mm preserved length, coll. Wirtz (MNHN), HOLOTYPE of *D. herytra*; 1 specimen 18 mm preserved length, coll. Wirtz (LZUO 120.18). Gando Bay (27°56'N, 15°21'W), Gran Canaria Island, Spain, 7 May 1980, 1 specimen, coll. Pérez-Sánchez (MCNT Mo/00178), PARATYPE of *D. herytra*.

DISCUSSION

Some authors (Baba, 1949; Steinberg, 1961; MacFarland, 1966), have suggested that *Doriopsilla* Bergh, 1880 should be considered a synonym of *Dendrodoris* Ehrenberg, 1831. Nevertheless, specimens of *Doriopsilla areolata* (type species of *Doriopsilla*) show many characters distinct from *Dendrodoris* species, such as the presence of minute rounded tubercles and hard spicules on the dorsum and the eccentric position of the anus (Ballesteros & Ortea, 1980). Usually, specimens with a soft body, without hard spicules and a delicate mantle margin belong to the genus *Dendro-*

doris. On the other hand, specimens with a rigid mantle, covered by hard spicules belong to the genus *Doriopsilla*.

Internally, the differences between the genera are more outstanding; the presence of a pair of ptyaline glands in *Dendrodoris* and the shape of the reproductive system, with a long tubular prostate and a distal connection between seminal receptacle and gametolytic gland, contrasts with the absence of ptyaline glands, a flat, non tubular prostate and a proximal connection between seminal receptacle and gametolytic glands in *Doriopsilla*. The position of the oral ganglia has also been used to distinguish these genera (Pruvot-Fol, 1930). It seems that in *Doriopsilla* the oral commissure, which connects the central nervous system with the oral ganglia, is very long, while in *Dendrodoris* it is very short. We have studied the nervous system of *Dendrodoris limbata* and *Doriopsilla areolata* verifying that this difference exists.

In this light, two nominal Mediterranean species included under the genus *Dendrodoris* should be transferred to the genus *Doriopsilla*. One of them, *Dendrodoris minima* Pruvot-Fol, 1951 was originally described as having large dorsal tubercles and the gills asymmetric to the right (Pruvot-Fol, 1951, p. 47). Also, *D. minima* seems to be a juvenile of *Dendrodoris racemosa* Pruvot-Fol, 1951, described in the same paper (Pruvot-Fol, 1951, p. 44) with identical features. The gills of this latter species, represented by Pruvot-Fol (1951, fig. 28D), are identical to those of the genus *Doriopsilla*. Both nominal species are probably synonymous with *Doriopsilla pelseneeri* described from the coast of Portugal.

The coloration of *Dendrodoris* species is very variable. Juveniles of most species are red, which changes to a variety of different colours as the animal grows. Specimens collected from the same locality can have different colours. We think that colour probably comes from the diet. Another hypothesis is that there could be a relation between colour and environment. Edmunds & Just (1985) have reported a change of colour in two juvenile specimens of *Dendrodoris krebsii* in a period of three days, when they were transferred from a stone covered with coralline algae to a black stone.

In recent papers concerning Atlantic species of *Dendrodoris*, the external morphology (coloration) and the shape of the digestive system was used to describe and redescribe species (Pruvot-Fol, 1951; 1953; Marcus, 1957:

Table 1. Comparative table of the Atlantic species of the genus *Dendrodoris*. Abbreviations: d, deferent duct; diam, diameter; g, gametolytic gland; sr, seminal receptacle; v, vagina.

Species	<i>D. limbata</i>	<i>D. grandiflora</i>	<i>D. krebsii</i>	<i>D. senegalensis</i>	<i>D. warta</i>	<i>D. angolensis</i>	<i>D. guineana</i>	<i>D. herytra</i>
Dorsal tubercles	-	-	-	-	+	-	-	-
Mantle margin width	± 1/2 of the foot width variable	as wide as the foot width variable	as wide as the foot width variable	± 1/2 of the foot width variable	± 1/5 of the foot width dark brown, beige warts similar to adults	± 1/3 of the foot width variable	± 1/10 of the foot width variable	1/10–1/2 of the foot width variable, usually red
Adult colour	yellow	red	red	red	similar to adults	?	probably red	red
Juvenile colour	yellow	red	red	red	adults	?	probably red	red
Mantle edge colour	yellow	-	-	-	brown, lamellae and apex white	red	-	-
Rhinophores colour	same as the dorsum, apex white medium	same as the dorsum, apex white long	black, apex white long	same as the dorsum, apex white long	brown, lamellae and apex white medium	as the dorsum, lamellae and apex red medium	same as the dorsum, apex white long	same as the dorsum, apex white short
Gills length								
Prostate length	short	long	medium	medium	long	long	short	long
Prostate width	wide	medium	narrow	narrow	medium	medium	medium	medium
g. diam.: sr. diam.	10:1	3:1	2:1	8:1	10:1	3:1	1.5:1	3:1
Ampulla folds	4	1	1	2	3	2	2	0
v. diam.: d diam.	1:2	4:1	3:1	1:1	1:2	5:1	2:1	2:1
Granular vagina	+	-	-	-	-	-	-	-
Middle male cirrus	very large, straight, base narrow,	small, curved, base large	small, a little curved, base large	small, curved, base narrow	large, straight, base large	very small, straight or curved, base large	small, straight, base narrow	large, straight, base large
hooks								
Eggs mean diam.	-	80 µm	66 µm	?	120 µm	64 µm	?	?
Capsule mean diam.	400 µm	160 µm	85 µm	110 µm	170 µm	122 µm	?	?

Marcus & Marcus, 1967a; 1967c; 1963; 1970 and Thompson, 1980), ignoring other anatomical characteristics. However, we have seen that external coloration is very variable in species of *Dendrodoris*. In the Atlantic Ocean, only *Dendrodoris limbata* is easily recognisable by the presence of a yellow mantle margin. Also, the red mantle margin is diagnostic for *Dendrodoris angolensis*, and *Dendrodoris herytra* can usually be recognised by the background colour.

Other external features, such as the rhinophores, the gills, the oral tentacles (reduced or absent in this genus), are very similar in all species. Only *D. angolensis* and *Dendrodoris krebsii* seem to have distinctive rhinophores, with the red lamellae and apex in the former and black with a white apex in the latter, quite different from the body colour. The texture of the mantle is very similar in all species, the exception is *D. warta* which is easily recognisable by its large dorsal tubercles. The digestive system has no good taxonomic features. All organs are very similar among different species.

On the other hand, there are several anatomical features that never vary in each species but are very variable between different species. These are the reproductive system, the male cirrus hooks and the egg mass. The size ratios between different genital organs (seminal receptacle diameter *versus* gametolytic gland diameter, deferent duct length *versus* vagina length, deferent duct width *versus* vagina width) are usually good characters for species recognition. The shape of the prostate is a diagnostic feature, as in *Dendrodoris limbata*, where it is very wide and short; in other species the prostate can be long, short, wide, narrow, but remains constant for each species. Also, the number of folds in the ampulla can help in the identification of species. The female gland is usually variable, its shape probably depending on the state of maturity. The presence of the hermaphrodite gland differentiated from the digestive gland can be useful in several species. Most importantly, the male cirrus hooks provide an exact diagnostic feature of each species. Optical microscopy show that each species has a different size, shape and disposition of the male cirrus hooks. Another useful character is the egg mass. The spawn of different species studied seems very characteristic, but further observations of a large number of egg masses are needed to confirm this.

In summary, several anatomical features

must be used to identify species with complete certainty, but we highly recommend observation of the male cirrus hooks under the microscope. On the other hand, external features and the digestive systems are unreliable, in most cases, for identification of Atlantic species.

As a result of our studies, only 9 of the 23 nominal species originally described from the Atlantic Ocean, Mediterranean and Caribbean Seas, are considered valid. The principal diagnostic features of these species are listed in Table 1.

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