

## TAXONOMY AND OCCURRENCE OF *DENDRODORIS NIGRA* AND *DENDRODORIS FUMATA* (NUDIBRANCHIA: DENDRODORIDIDAE) IN THE INDO-WEST PACIFIC REGION

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### ABSTRACT

The nudibranch *Dendrodoris nigra* (Stimpson, 1855) has hitherto been considered as a single, highly polychromic species. Our investigations of external morphology, anatomy and colour variation have revealed more than one species exists. This conclusion gives credibility to the previous discovery of differing developmental patterns within *D. nigra*. Besides *D. nigra*, we recognise *Dendrodoris fumata* (Rüppell & Leuckart, 1830) which has three distinguishable colour forms. The occurrence of *D. nigra* is confirmed to be extensive, however, the species was not found to be circum-Australian as previously reported. The presence of *D. fumata* in Australia is confirmed and the species is also reported from Hong Kong and Fiji for the first time. The clear separation of these two species and recognition of the different colour forms will permit a more accurate picture of their distribution.

### INTRODUCTION

The nudibranch *Dendrodoris nigra* (Stimpson, 1855) reputedly has a wide Indo-Pacific distribution (Allan, 1947; Kay & Young, 1969; Edmunds, 1971; Thompson, 1975; Willan & Coleman, 1984), common occurrence (Edmunds, 1971; Thompson, 1975; Gosliner, 1987; Wells & Bryce, 1993) and very considerable colour polymorphism (Eliot, 1905; Kay, 1979). However, a summary of previous morphological references (Brodie, 1991) concerning *Dendrodoris nigra* and externally-similar, sympatric species highlighted extensive taxonomic confusion.

Although Gohar & Soliman (1967) recorded the lack of a vestibular gland in the reproductive system of *Dendrodoris fumata* (Rüppell & Leuckart, 1830), they believed *Dendrodoris nigra* (Stimpson) to be a junior synonym of this species. In 1971, Edmunds published diagrams of the anatomy of *Dendrodoris nigra* (showing a

vestibular gland in the reproductive system) but stated that he had not dissected enough material to decide whether *D. nigra* always had a vestibular gland present and therefore was unable to decide if the two species, i.e., *D. nigra* and *D. fumata*, were conspecific or not. Although numerous authors have commented on the considerable colour variation attributed to *D. nigra*, the limits of this variation have never been systematically documented or morphologically compared. Similarly, although several authors have mentioned that juvenile *D. nigra* are orange or red (e.g. Kay & Young, 1967; Thompson, 1975; Gosliner, 1987) this has never been supported by morphological examination.

This study aims at taxonomic clarification of *Dendrodoris nigra* and *Dendrodoris fumata* in the Indo-west Pacific. A synonymy for each species is given and the use of a combination of characters for the determination of species is strongly encouraged. On the basis of our descriptions, we have developed a key for the identification of these two species in the Indo-west Pacific.

Although the tropical Atlantic nominal species *Dendrodoris krebsii* (Mörch, 1863) and *D. atropos* (Bergh, 1879) obviously form part of the *D. nigra* complex, they have been omitted from this analysis because of the lack of comparative material.

### METHODS

Live specimens of dendrodorids were narcotised with menthol flakes, then preserved in approximately 9% formalin in seawater. One hundred and eighty-two specimens (81 *Dendrodoris nigra* and 101 *Dendrodoris fumata*) were dissected under a binocular dissecting microscope and anatomical drawings were made with the aid of a camera lucida. Penial armature

was observed in some specimens. The method of preparation for penial study required living specimens to be relaxed by refrigeration at 4°C, followed by freezing. This elicited penial eversion and ensured that there was no deterioration of the penial armature by formalin. Specimens were thawed immediately prior to examination and the penis excised. It was then examined microscopically.

Body measurements for live animals refer to crawling dimensions of extended animals and correspond to the standard lengths Am, Mx and Bx as defined for nudibranchs by Risso-Dominguez (1963).

Fresh egg masses, primarily those laid in the laboratory, but occasionally those collected from the field, were also examined. After removal from the substratum, a section was cut from the centre of each ribbon and the diameters of 10 eggs and 10 capsules were recorded using an optical micrometer.

Material examined from the collection of the senior author (Brodie Collection) is prefixed BC; from the collection of Dr R.C. Willan denoted RCW; from the private collection of Mr Scott Johnson, denoted SJ; from the Museum and Art Gallery of the Northern Territory, Darwin prefixed NTM; from the Australian Museum, Sydney AMS; from the Museum of Victoria MV; from the South Australian Museum, Adelaide SAM; and from the Western Australian Museum, Perth WAM.

Voucher specimens of each species have been lodged with the Museum of Tropical Queensland, Townsville, which is the North Queensland Branch of the Queensland Museum (QM).

The following abbreviations are used to denote the institutions contacted regarding type material: BMNH—The Natural History Museum, London; CAS—Chicago Academy of Sciences; ANS—Academy of Natural Sciences, Philadelphia; USNM—National Museum of Natural History, Smithsonian Institution, Washington D.C.; HUM—Humboldt University Museum, Berlin.

## SYSTEMATIC DESCRIPTIONS

### *Dendrodoris nigra* (Stimpson, 1855) (Figures 1 A & B; 2 A–H)

Voucher specimens (None intended as a neotype): QM MO18866, QM MO18870, QM MO18871, QM MO18872.

#### Synonymy

*Doris nigra* Stimpson, 1855: 380.

*Doris atroviridis* Kelaart, 1858: 104–105.

*Hexabranchnus nebulosus* Pease, 1860: 33.

*Doridopsis nigra* (Stimpson).—Alder & Hancock, 1864: 128, pl. 31, figs. 13–16; Abraham, 1877: 242; Eliot, 1905: 275–277.

*Actinodoris australis* Angas, 1864: 49, pl. 4, fig. 8.

*Doris debilis* Pease, 1871: 11–12, pl. 5, fig. 2.

*Doris rubrilineata* Pease, 1871: 12–13, pl. 3, fig. 2.

*Doris sordida* Pease, 1871: 14, pl. 4, fig. 2.

*Doriopsis nebulosa* (Pease).—Bergh, 1875: 95, pl. 7, fig. 5; pl. 11, fig. 24.

*Doris mariei* Crosse, 1875: 307–308, pl. 12, fig. 1.

*Goniodoris montrouzieri* Crosse, 1875: 311–313, pl. 12, fig. 4.

*Doridopsis nebulosa* (Pease).—Abraham, 1877: 242, species number 14.

*Doridopsis australiensis* Abraham, 1877: 263, pl. 30, figs. 25, 26.

*Doriopsis nigra* (Stimpson) var. *coerulea* Bergh, 1880: 181–184.

*Doriopsis nigra* (Stimpson) var. *nigerrima* Bergh, 1888: 756.

*Doriopsis nigra* (Stimpson) var. *brunnea* Bergh, 1890: 966.

*Doriopsis nigra* (Stimpson).—Bergh, 1905: 169, pl. 2, fig. 13; Vayssière, 1912: 80–81, pl. 1, fig. 3.

*Doriopsis nigra* (Stimpson) var. *luteo-punctata* Bergh, 1905: 170, pl. 2, fig. 14.

*Doridopsis* (sic) *nigra* (Stimpson) Eliot, 1913: 33–34, pl. 2, fig. 13 (error pro *Doridopsis nigra*).

*Dendrodoris nigra* (Stimpson).—O'Donoghue, 1924: 561–562; O'Donoghue, 1929: 827; Allan, 1947: 458–459; Baba, 1949: 154–155, pl. 26, figs. 98, 99; Risbec, 1953: 20, fig. 2; Kenny, 1960: 225; Burn, 1962: 166–167; Burn, 1965: 87; Er. Marcus & Burch, 1965: 250; Burn, 1966a: 275; Kay & Young, 1969: 218–219, figs. 68, 71; Miller, 1969: 542; Kenny, 1970: 90; Er. & Ev. Marcus, 1970: 170; Ev. & Er. Marcus, 1970: 206, fig. 74; Edmunds, 1971: 383–385, fig. 21; Thompson, 1975: 504, figs. 5 f, g; Willan & Morton, 1984: 96; Wells & Bryce, 1993: 142 species number 183 only.

*Doridopsis montrouzieri* (Crosse).—Risbec, 1928: 63–64, pl. 4, fig. 2, text fig. 5.

*Doridopsis mollis* Risbec, 1928: 65–66, pl. 2, fig. 4, text fig. 6.

*Dendrodoris melaena* Allan, 1932: 98–99, pl. 5, fig. 11.

*Cryptodoris* sp. Ostergaard, 1950: 109, fig. 36.

*Dendrodoris montrouzieri* (Crosse).—Risbec, 1953: 20; Risbec, 1956: 27.

*Doridopsis macfarlandi* Ostergaard, 1955: 128, fig. 13.

*Dendrodoris erubescens* (Bergh).—Er. Marcus & Burch, 1965: 250–251 (misidentification—not *Doriopsis erubescens* Bergh, 1905).

#### Comments on Synonymy

*Doris atroviridis*, which Kelaart (1858) described from Sri Lanka, is without doubt the same as Stimpson's *Dendrodoris nigra* having a crimson 'line' and white spots to the mantle.

*Hexabranchnus nebulosus* Pease, described from Hawaii, was shifted into *Doridopsis* by Abraham (1877). In doing so, he listed as a synonym *Doriopsis nebulosa* according to Bergh. These three combinations, *Hexabranchnus nebulosus*, *Doridopsis nebulosa* and *Doriopsis nebulosa* were synonymised with *Dendrodoris nigra* by Kay & Young (1969). Abraham (1877) also synonymised *Doris atrata* Kelaart, *Doris atroviridis* Kelaart and *Doriopsis nigra* Bergh with *Doridopsis nigra* (Stimpson). We agree with the latter

two synonymies, but have made *Doris atrata* a synonym of *Dendrodoris fumata* for reasons discussed later under that species.

We have included *Doris debilis* Pease, *Doris rubri-lineata* Pease and *Doris sordida* Pease as new synonyms on the basis of Pease's (1871) descriptions, his accompanying plates and our current knowledge of colour variation in *Dendrodoris nigra*. Although a very large gill is reported for *Doris debilis*, and this is atypical of *Dendrodoris nigra*, such enlargement and flattening can result from heat stress and water with low oxygen tension. The colour description and plate figure of *Doris debilis* provided by Pease, depicts animals with clustered white dots on the mantle. This leaves no doubt that *Doris debilis* is a synonym of *Dendrodoris nigra*.

We have included *Doris mariei* Crosse, which was described from New Caledonia, as a new synonym on the basis of Crosse's (1875) colour plate.

*Goniodoris montrouzieri* Crosse was shifted into *Doridopsis* by Risbec (1928), and in 1953 Risbec moved it again, this time into *Dendrodoris*. In doing so, he listed it as a separate species to *Dendrodoris nigra* (Stimpson), however, strangely on the same page he also listed *G. montrouzieri* (Crosse) in the synonymy of *D. nigra* (Stimpson). Finally in 1956, Risbec listed *Dendrodoris montrouzieri* and *Dendrodoris nigra* as separate species. However, we have no doubt that *G. montrouzieri* is a colour variant of *Dendrodoris nigra*.

We have included *Doridopsis australiensis*, originally described by Abraham from New South Wales, Australia, in our synonymy on the basis of its dark body colour, white tipped rhinophores and Abraham's comment that there was a close resemblance to *Actinodoris australis* Angas, also described from New South Wales. *A. australis* was synonymised with *Dendrodoris nigra* (Stimpson) by Risbec (1953) and Burn (1965), while both *Doridopsis australiensis* and *Actinodoris australis* were synonymised with *Dendrodoris nigra* by Thompson (1975).

We totally support the opinion of Barnard (1927) that the four colour varieties of *Doridopsis nigra* named by Bergh (1880, 1888, 1890, 1905) are synonyms of *Dendrodoris nigra* (Stimpson).

*Doridopsis mollis*, originally described by Risbec from New Caledonia, was later synonymised with *Dendrodoris nigra* by himself (Risbec 1953). We accept this synonymy. *Dendrodoris melaena*, which was originally described from Sydney, Australia, was later synonymised with *Dendrodoris nigra* by Allan (1947). We have examined the holotype of *D. melaena* and agree with her synonymy. *Doridopsis macfarlandi* (Ostergaard, 1955), the replacement name for *Cryptodoris* sp. (Ostergaard, 1950), is another synonym from Hawaii. We accept Kay & Young's (1969) synonymy of this species with *Dendrodoris nigra*. We consider the small orange *Dendrodoris erubescens* of Er. Marcus & Burch (1965) to be misidentified i.e., not *Doridopsis erubescens* Bergh, 1905, but a juvenile *Dendrodoris nigra*.

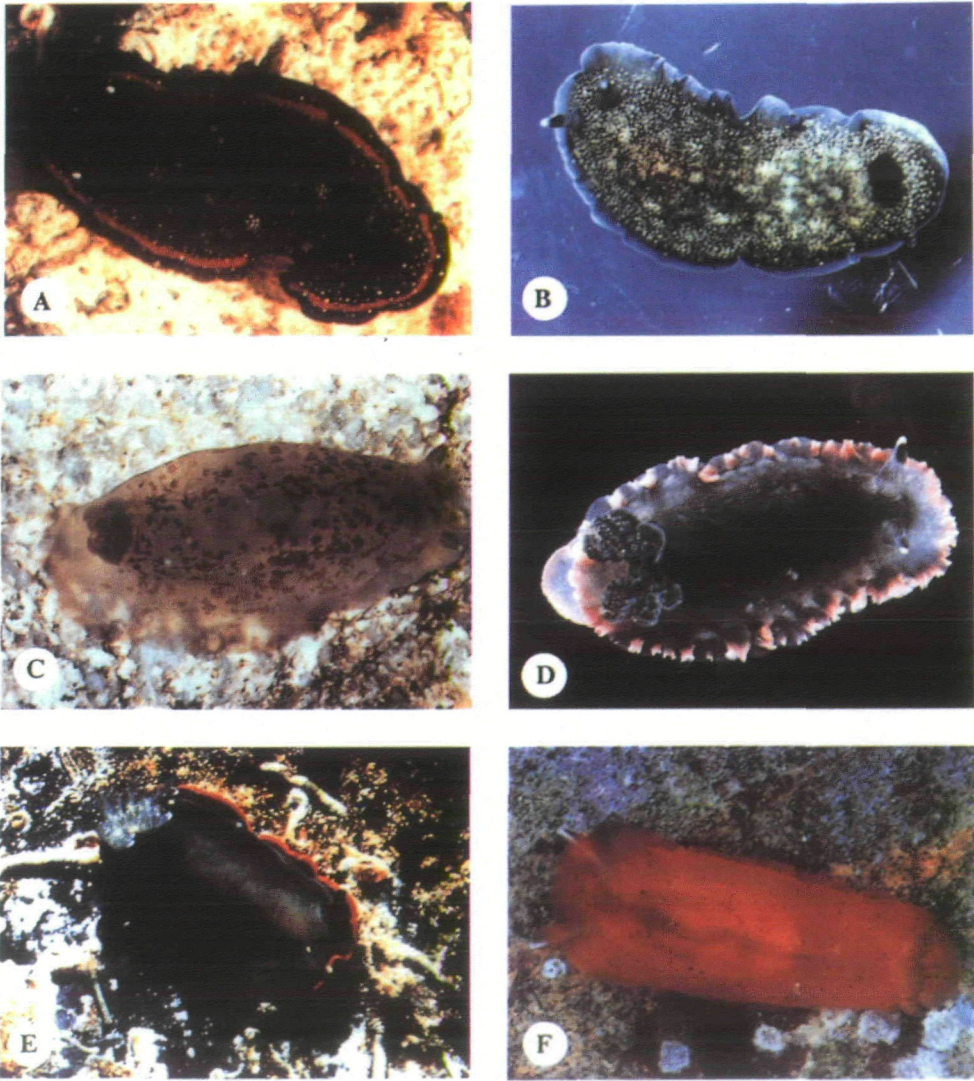
The name *Dendrodoris nigra* has been misapplied to specimens of *D. fumata* (black form) on several

occasions (Orr, 1981; Willan & Coleman, 1984; Burn, 1989; Wells & Bryce, 1993, photograph 182 only). Since *D. nigra* is known to be variable, and the characteristics of *D. fumata* have not previously been elucidated, this confusion is not unexpected.

Popular books that contain coloured photographs of *Dendrodoris nigra* are those by Bertsch & Johnson (1981), Gosliner (1987) and Wells & Bryce (1993, photograph 183 only). However not one of these photographs depicts the very common colour variety (Figure 1A), that with a submarginal red mantle ring.

#### Material examined

**Christmas Island, Indian Ocean.** (1) Steep Point, two specimens (7, 7 mm long, preserved), 13 February 1987, WAM 566-86. **Hong Kong.** (1) South Ninepin; one specimen (30 mm long, live), 3 May 1987, AMS C153334. **Australia, Queensland.** (1) Cackle Bay, Magnetic Island, Townsville: one specimen (64 mm long, live), 12 January 1990, BC G2; one specimen (65 mm long, live), 13 October, 1989, BC F81; one specimen (52 mm long, live), 20 June 1989, BC F39; one specimen (2.5 mm long, live at collection, 29 mm long, live before preservation), 22 June 1990, BC 182. (2) Picnic Bay, Magnetic Island, Townsville; one specimen (20 mm long, live), 8 April 1989, BC DN8. (3) Michaelmas Cay, off Cairns; two specimens (7, 11 mm long, preserved), 4 November 1972, AMS C89790. (4) Coconut Beach, Lizard Island; one specimen (23 mm long, preserved), 2 June 1979, AMS C115959. (5) Myora Spit, North Stradbroke Island, Moreton Bay; one specimen (41 mm long, preserved), May 1985, RCW. **Australia, New South Wales.** (1) Hastings Point: one specimen (40 mm long, live), May 1987, RCW; one specimen (42 mm long, live), 24 April 1981, RCW. (2) Arrawarra Headland, Coffs Harbour: one specimen (23 mm long, preserved), 28 February 1987, AMS C152709; three specimens (11, 17, 30 mm long, preserved), 16 March 1988, AMS C155793; one specimen (37 mm long, live), 18 November 1990, BC via C. Buchanan. (3) Long Reef, Collaroy: Holotype of *Dendrodoris melaena* Allan, 1932, one specimen (26 mm long, preserved), October 1930, AMS C57541; seven specimens (9, 15, 25, 29, 34, 41, 46 mm long, preserved), 5 April 1979, AMS C114835. (4) Elizabeth Reef, Coral Sea 29° 55.8' S 159° 0.13' E; one specimen (25 mm long, live), 14 December 1987, AMS C155076. (5) Bonnie Hills, 20 km south Port Macquarie; one specimen (26 mm long, live), 20 May 1989, RCW. **Australia, Western Australia.** (1) Vlamingh Head, Rottneest Island; ten specimens (14, 15, 15, 17, 17, 18, 18, 21, 22, 25 mm long, preserved), 7 March 1984, WAM 581-84 (in part). (2) Eagle Bay, Rottneest Island; 12 specimens (22, 22, 25, 30, 30, 31, 32, 36, 36, 43, 43, 50 mm long, preserved), 7 March 1984 WAM 583-84. **Australia, Northern Territory.** (1) Coral Bay, Port Essington; one specimen (15 mm long, preserved), 15 September 1985, NTM P1152. **Papua New Guinea.** (1) 'The Chimney', Madang Lagoon; one specimen (10 mm long, preserved), 17 January 1988, RCW. (2) Rasch Passage, Madang Lagoon; one specimen (16 mm long, live), 12 January 1988, RCW.



**Figure 1.** Photographs of live animals showing external features. **A.** *Dendrodoris nigra*, 38 mm, Suva, Fiji. **B.** *Dendrodoris nigra*, 45 mm, Suva, Fiji. **C.** *Dendrodoris fumata* (grey form), 52 mm, Magnetic Island, Australia. **D.** *Dendrodoris fumata* (grey form), 30 mm, Sydney, Australia. **E.** *Dendrodoris fumata* (black form), (size unknown) Albany, Western Australia. **F.** *Dendrodoris fumata* (orange/red form), 25 mm, Keppel Island, Australia.

**Marshall Islands.** (1) Kwajalein: two specimens (9, 12 mm long, preserved), 2 February 1990, SJ. (2) Roi-Namur; two specimens (4, 17 mm long, preserved), 25 May 1990, SJ. (3) Vjelang Atoll: two specimens (21, 24 mm long, preserved), 29 July 1982, SJ. **Fiji, Viti Levu Island.** (1) Nasese-Vieuto, Suva: two specimens (30, 35 mm long, live), 20 September 1984, BC A15 & BC A16; one specimen (27 mm long, live), 18 October 1986, BC B85; one specimen (33 mm long, live), 1 March 1987, BC G20; 17 specimens (4.5, 7, 9, 11, 12, 12, 15, 16, 17, 19, 19, 21, 25, 26, 29, 33, 35 mm long,

live), 30 January 1988, BC Z1–Z17. (2) Makaluva Island, Suva: one specimen (22 mm long, live), 9 September 1984, BC A13.

*Description*

In life, the body is relatively low and elongate, with smooth, often undulating margins. The mantle may be broad or narrow depending on the animal's state of activity. A number of soft,

low pustules are present on the central dorsum, and these are more pronounced in larger individuals. Overall, animals are generally black or dark grey, often with white spots on the mantle (Figure 1B). There can also be a submarginal red ring to the mantle margin (Figure 1A). An extensive analysis of adult colour variation and the ontogenetic colour changes that *D. nigra* undergoes is described in detail by Brodie (unpublished data).

The foot, which often extends a few millimetres behind the mantle, is strongly transversely grooved to the anterior (Figure 2A). The head is extremely small and bears a pore-like mouth. The oral tentacles are thin, rounded ridges, fused anteriorly with the undersurface of the mantle, and fused posteriorly with the foot. The rhinophoral pockets have simple, thin, slightly elevated rims. The rhinophoral stalk is slightly tapering while the clavus is rounded, both stalk and clavus being similar in height (Figure 2B). The clavus bears approximately 17, sloping lamellae in adult animals. In adults, the clavus tilts backwards and is thus set at an angle to the stalk. A narrow but distinct ridge runs down the midline of the sloping, upward face. There is only a slight indentation where the lamellae join the posterior midline of the claval face. The branchial pocket is simple. The gills are finely branched (Figure 2C) and number 6–10. When extended, in live material, they form an incomplete circle around the tubular, darkly pigmented anal papilla. Posteriorly, there is a gap in the branchial cirlet. Individual gills are often cupped inward, as is the entire gill plume. The entire plume is directed posteriorly when the animal is moving.

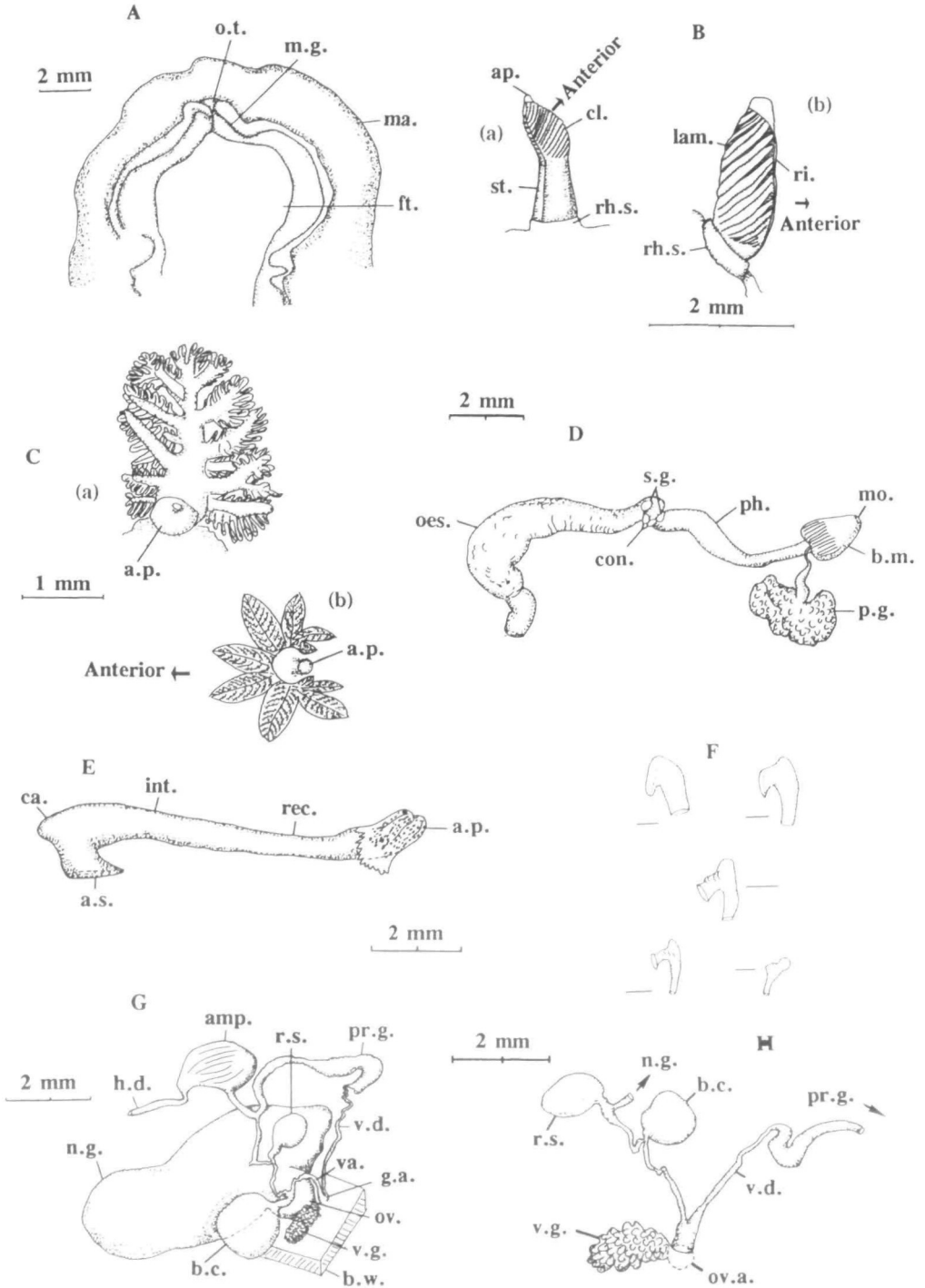
The tissue envelope which surrounds the viscera is translucent white, and often sprinkled with fine, dark flecks. A duct from the relatively large, paired, white ptyaline gland enters the oral tube close to the mouth (Figure 2D). The smooth, elongate pharynx doubles back on itself where the cerebral ganglia occur. At this point, the relatively small, sessile salivary glands are present, one on each side. The orange oesophagus expands and its walls appear granulose. A considerable amount of black pigment is often present on the oesophageal surface. The stomach itself is deeply embedded in the posteriorly bilobed digestive gland, and separation of the two organs during dissection is difficult. The intestine emerges from the mid-dorsal surface of the cream to brown digestive gland. Immediately upon emerging, the intestine turns to the right and a caecum is present (Figure 2E). This caecum varies from small and barely

noticeable to large and bulbous (Figure 2F) from specimen to specimen. Sometimes it has a patch of black pigment on its surface. A series of small, lobe-like ridges is sometimes seen to the left of the caecum on the intestine's dorsal surface. The intestine then turns to the right again, widens a little, and passes rearwards on top of the posterior digestive gland until it reaches the relatively short, broad, pigmented anal papilla. Pigment associated with the anal papilla may be lost in preserved material.

A small, translucent hermaphroditic duct leaves the ovotestis to the right of the oesophagus mid-way down the anterior face of the digestive gland. This duct connects to the ampulla (Figure 2G) which is pyriform, relatively large, and yellow, with some superficial brown pigment. The hermaphrodite duct leaves the ampulla on the right side towards its distal end and divides into two ducts, one leading to the prostate, the other to the nidamental gland. The glandular prostate, which is generally uniform in appearance, connects to the long, smooth vas deferens, which ends in the penis. The penis is armed with approximately 18 transverse rows of small hooks each approximately 7  $\mu\text{m}$  in height. The vaginal duct leaves the nidamental gland adjacent to the ampullary duct. Almost immediately along its length is a short duct leading to the club-shaped receptaculum seminis (Figure 2H). The vagina then enters the spherical bursa copulatrix. *In situ*, the vagina is thin and sinuous compared with the vas deferens which is thicker-walled and straighter. The receptaculum seminis is small and white, while the bursa is larger and rounded, with a white or dark core within the thin, translucent wall. Significantly, a large, prominent vestibular gland is always present on the outside of the oviduct just before it joins the body wall. This finely lobulate gland is generally white in colour, but it can sometimes be translucent.

#### Remarks

Some may dispute our selection of the name *Dendrodoris nigra* (Stimpson) to designate this species. For example, how do we know that the species, which consistently possesses a vestibular gland as part of its reproductive system, is really Stimpson's *D. nigra*? Owing to the probable absence of any type material (ANS; CAS; USNM, pers. comm.), our decision is based solely on the content of Stimpson's (1855) original description. He referred to this species as 'Small, subelliptic, somewhat



elongated . . . branchial cluster small . . . and nearly erect'. He summarised the colour precisely: 'Colour variable, usually black, always very dark; mantle often dotted with white and margined with red; tentacula always tipped with white.' During our investigations no species other than the one we have named *D. nigra*, was ever found to have white specks on its mantle. The shape of the body and gill are also characteristic of our *D. nigra*, and all of these characters in combination allow separation of this species from *D. fumata*.

The distributional range of *Dendrodoris nigra* is confirmed to be extensive as previously reported, i.e., most tropical and warm temperate seas except Pacific and Atlantic coasts of tropical America. However, within Australia, *D. nigra* has a southern limit of Botany Bay on the east coast and Rottnest Island, near Perth on the west coast. Although *D. nigra* was previously reported as a eurythermal species that extended all round the Australian coastline (Kenny, 1960; Burn 1962), including Tasmania (Willan & Coleman, 1984; Wells & Bryce, 1993), our study indicates that *D. nigra* is probably a subtropical and tropical species, as there are no confirmed records from Australia's southern coastline. It is obvious that, both within Australia and overseas, *D. fumata* has often been mistaken for *D. nigra*, thus clouding the real occurrence of each species.

*Dendrodoris fumata* (Rüppell & Leuckart,  
1830)  
(Figures 1 C – F; 3 A – G)

On the basis of our own study we have found *Dendrodoris fumata* to have three anatomically indistinguishable colour forms. These three forms are particularly important for the following reasons. The grey form (Figure 1C & D) links our species firmly to the original description of *D. fumata* by Rüppell & Leuckart (1830) and the important work of Gohar & Soliman

(1967). The black form (Figure 1E) has to date been widely recognised as '*Dendrodoris nigra*'. This is shown by its erroneous photographic use in Morton & Miller (1968), Orr (1981), Willan & Coleman (1984), Burn (1989) and Wells & Bryce (1993). While the orange/red form (Figure 1F) has been widely recognised under the species name *rubra* by Kelaart (1858), Alder & Hancock (1864), Collingwood (1881), Eliot (1905), Bergh (1875), White (1951), Miller (1969), Ev. & Er. Marcus (1970) and Edmunds, (1971). The following account will therefore be separated into the grey, black and orange/red forms where appropriate.

Voucher specimens (None intended as neotypes): (grey form), QM MO18869; (black form), QM MO 18868; (orange/red form), QM MO18867.

*Synonymy*

**grey form**

*Doris fumata* Rüppell & Leuckart, 1830: 29, pl. 8, fig. 2.

*Doris atrata* Kelaart, 1858: 103–104.

*Dendrodoris* (= *Doridopsis*) *fumata* (Rüppell & Leuckart).—Gohar & Soliman, 1967: 31–54.

**black form**

*Doridopsis arborescens* Collingwood, 1881: 134–135, pl. 10, figs. 15–17.

*Dendrodoris nigra* (Stimpson).—Burn, 1957: 22; Burn, 1966b: 349; Orr, 1981: 37; Willan & Coleman, 1984: 41 species number 128; Burn, 1989: 769, pl. 53.4; Wells & Bryce, 1993: 141, species number 182 only (misidentification—not *Doris nigra* Stimpson, 1855).

**orange/red form**

*Doris rubra* Kelaart, 1858: 101–102 (Stimpson, 1855) not *Doris rubra* Risso, 1818 nor *Doris rubra* d'Orbigny, 1837).

*Doridopsis rubra* (Kelaart).—Alder & Hancock, 1864: 126, pl. 31, figs. 1, 2; Collingwood, 1881: 135–136, pl. 10, fig. 18; Eliot, 1905: 279 (not *Doris rubra* Risso, 1818 nor *Doris rubra* d'Orbigny, 1837).

**Figure 2.** Drawings of preserved *Dendrodoris nigra*. **A.** Ventral view of the anterior portion of the foot. **B.** (a) Lateral view of the rhinophore redrawn from Ostergaard (1955). (b) Lateral view of the retracted rhinophore showing the clavus, sloping lamellae and anterior midline ridge. **C.** Gills showing (a) the branching and (b) schematic diagram of branchial arrangement. **D.** Profile view of the anterior half of the alimentary canal. **E.** Posterior alimentary canal. **F.** Variation in development of the caecum. Bars = 1 mm. **G.** Composite view of the reproductive system. **H.** Terminal section of the reproductive system, with the oviduct removed, showing position of the vestibular gland. Abbreviations: amp., ampulla; ap., apex; a.p., anal papillae; a.s., aperture to stomach; b.c., bursa copulatrix; b.m., buccal mass; b.w., body wall; ca., caecum; cl., clavus; con., central nerve ring; ft., foot; g.a., genital atrium; h.d., hermaphroditic duct; int., intestine; lam., lamellae; ma., mantle; mo., mouth; m.g., mucus groove; n.g., nidamental glands; oes., oesophagus; o.t., oral tentacles; ov., oviduct; ov.a., oviducal aperture; p.g., ptyaline gland; ph., pharynx; pr.g., prostate gland; rec., rectum; rh.s., rhinophoral sheath.; ri., ridge; r.s., receptaculum seminis; s.g., salivary glands; st., stalk; va., vagina; v.d., vas deferens; v.g., vestibular gland.

- Doriopsis rubra* (Kelaart).—Bergh, 1875: 217.  
*Doriopsis erubescens* Bergh, 1905: 173-174, pl. 3, fig. 15.  
*Doriopsis rosea* Vayssière, 1912: 82-83, pl. 1, fig. 2, pl. 10, fig. 153.  
*Doridopsis communis* Risbec, 1928: 67-69, pl. 1, fig. 6, text fig. 7.  
*Doridopsis communis* var. *rosea* Risbec, 1928: 68-69, pl. 1, fig. 5.  
*Doridopsis communis* var. *nigra* Risbec, 1928: 69, pl. 5, fig. 7.  
*Dendrodoris rubra* (Kelaart).—White, 1951: 250, fig. 20; Miller, 1969: 542; Ev. & Er. Marcus, 1970: 206-207, figs. 71-73; Edmunds, 1971: 386, fig. 22.  
*Dendrodoris erubescens* (Bergh).—Risbec, 1956: 26-27.  
*Dendrodoris fumata* (Rüppell & Leuckart).—Wells & Bryce, 1993: 138, species number 178.  
*Dendrodoris nigra* (Stimpson).—Valdés, Ortea, Ávila & Ballesteros, 1996: 12, fig. 2B (misidentification—not *Doris nigra* Stimpson, 1855).

#### Comments on Synonymy

##### grey form

Our use of the name *Dendrodoris fumata* is based on the close match of our material with the original description by Rüppell & Leuckart (1830). The colour plate, that accompanied their account of Red Sea molluscs, shows a broad, smoke grey animal with paler, wavy, mantle margins. In the absence of the type material of *Doris fumata* Rüppell & Leuckart (HUM, pers. comm.), it is our intention to designate a neotype once a suitable grey Red Sea specimen is available. Our decision to use this name is reinforced by the fact that Gohar and Soliman came to the same conclusion in 1967. We have included *Doris atrata* Kelaart from Sri Lanka as a new synonym on the basis of colour and Kelaart's decision to separate it from *Doris atroviridis* (= *Dendrodoris nigra*) on the basis of seasonality and the characters of young specimens.

The best illustration and previous description of adults of this grey form of *Dendrodoris fumata* is that by Gohar & Soliman (1967).

##### black form

Our synonymy of *Doridopsis arborescens* with *Dendrodoris fumata* (black form) stems from Collingwood's (1881) original description of *D. arborescens* in which he states that his new species although very similar to *D. nigra* 'appears quite distinct'. Collingwood also says that considering the 'tendency to variation' of *D. nigra* that the observation of a series might cause a different opinion to be formed about the separation of *D. arborescens*. In this respect, our morphological study confirms the validity of Collingwood's original decision to separate the two species. A lack of type material (BMNH, pers. comm.) prohibits morphological confirmation. However, unlike many other nineteenth century descriptions of nudibranchs, which were sketchy to the point of being useless, Collingwood's was sufficiently precise to

enable recognition of this variation with confidence. The distinctiveness of *D. fumata* (black form) is reflected by Collingwood's choice of phrases like 'light chestnut' as regards the mantle margin, 'large ... very conspicuous' as regards the gills, and 'light greyish' as regards the apices of the gills. Obviously, he was so impressed by the magnitude of the branchial plume, he named his species for it. *Doridopsis* (= *Dendrodoris*) *arborescens* (Collingwood) was erroneously synonymised with *Doris nigra* (Stimpson) by Er. Marcus & Burch (1965) and Edmunds (1971).

All of the specimens designated as *Dendrodoris nigra* in the synonymy above are misidentifications i.e., they are not *Doris nigra* Stimpson, 1855. All are new synonyms and possess the set of external features displayed by *Dendrodoris fumata* (black form) i.e., very large dark gills with pale apices, very dark mantle with a thin red margin and a lack of white specks on the dorsum. The preserved specimens described by Burn (1966b) as *Dendrodoris nigra* (SAM D14878) have been examined and we have no hesitation in synonymising these animals with the black form of *Dendrodoris fumata*.

The two best photographs of the black form of *Dendrodoris fumata* are in popular books (Willan & Coleman, 1984; Wells & Bryce, 1993) under the name *Dendrodoris nigra*, and both depict specimens from Western Australia.

##### orange/red form

We have not included *Dendrodoris cuprea* Ehrenberg, 1831 in our synonymy because we do not consider the available data strong enough to do so.

We have discounted *Doris fumosa* Quoy & Gaimard, 1832 as another name for this species on the basis of Pruvot-Fol's (1934) revision of the opisthobranchs of Quoy and Gaimard. Pruvot-Fol determined that it was not possible to be certain that *Doris fumosa* (Quoy & Gaimard) and Kelaart's *Doris rubra* were the same.

The name *Dendrodoris rubra* (Kelaart, 1858) has general acceptance (e.g., Miller, 1969; Edmunds, 1971) for specimens represented by this colour variation. The name *Doris rubra* was twice used to designate dorid nudibranchs prior to its use by Kelaart, firstly by Risso (1818) and secondly by d'Orbigny (1837). Both Risso's and d'Orbigny's names apply to *Rostanga rubra* (Pruvot-Fol, 1954: 277). The account of *D. rubra* by Kelaart (1858) matches our material of *Dendrodoris fumata* (orange/red form) except for the words 'Mantle ... maculated with irregularly shaped dark brick red or purple spots'. Edmunds (1971) reports similar markings in some but not all of his specimens. Since our material is internally indistinguishable from that of Edmunds we have no hesitation in synonymising *Dendrodoris rubra* (Kelaart) with the orange/red form of *Dendrodoris fumata*.

Bergh (1875) acknowledged that his *Doriopsis rubra* was the same as *Doris rubra* of Kelaart (1858) and *Doridopsis rubra* Alder and Hancock (1864). Much later (Bergh, 1905), he described *Doriopsis erubescens* on the basis of one specimen from



'Saleyer' (= Selayar) Island, southern Sulawesi, Indonesia, stating that the species might be identical to one already created. We can see no reason why this species should be considered different to Kelaart's *Doris rubra*. Perhaps Bergh considered *D. rubra* and *D. erubescens* to be different species only because they were geographically separated? Bergh's (1905) description (translucent light violet-reddish with star-like gills) and colour drawing of a living *D. erubescens* match our present description well.

Although *Doriopsis rosea* Vayssière (1912) was described from preserved material, it matches our description of *Dendrodoris fumata* (orange/red form) and is therefore included as a further new synonym.

Eliot (1913) separated as new var. *nigromaculata* from *Doridopsis rubra* because of its larger size and colour. This variation was illustrated by Baba (1949). Our investigations do not permit a direct comparison of this variation, but morphological data from Japan (K. Baba, pers. comm.) indicate this name may not be applicable to *D. fumata*.

In 1928 Risbec described *Doridopsis communis* as well as two varieties, *rosea* and *nigra*, based on live material from New Caledonia. Later, Risbec (1953) synonymised *Doridopsis communis* with *Dendrodoris erubescens* Bergh. In Risbec (1928) all three animals are described and shown in colour plates and we can find no reason why all three names should not be newly synonymised under the orange red form of *Dendrodoris fumata*.

Good colour photographs of the orange/red form of *Dendrodoris fumata* can be found in Wells & Bryce (1993: 139) and Valdés *et al.* (1996), the latter incorrectly under the name *Dendrodoris nigra*.

#### Material examined

##### grey form

**Hong Kong.** (1) Breakers Reef; one specimen (45 mm long, preserved), 19 April 1983, AMS C139120. **Australia, Northern Territory.** (1) East Point, Darwin Harbour, Darwin: one specimen (97 mm long, live), 23 June 1987, AMS C153598; one specimen (33 mm long, live), 29 June 1987, AMS C153616. **Australia, Queensland.** (1) Cockle Bay, Magnetic Island, Townsville; one specimen (45 mm long, live), 21 May 1990, BC G14; two specimens (68, 57 mm long, live), 7 August 1988, BC DN4 (small) & G19; one specimen (61 mm long, live), 11 November 1989 BC F86; one specimen (15 mm long, live at capture, 30 mm long, live before preservation), 19 June 1990, BC 176; one specimen (11 mm long live at capture, 30 mm long, live at preservation), 22 June 1990, BC 184. (2) Picnic Bay, Magnetic Island, Townsville; one specimen (75 mm long, live), 30 July 1988, BC DN4 (large) (3) Hervey Bay; one specimen (85 mm long, live), May 1981, RCW. (4) Sandgate, Bramble Bay, Moreton Bay; two specimens (23, 37 mm long, live), 7 September 1981, RCW. (5) Myora Spit, North Stradbroke Island, Moreton Bay: two specimens (53, 54 mm long, live), 21 September 1980, RCW; one specimen (60 mm long, live), 1 October 1980, RCW. (6) Marine Station, Dunwich, North Stradbroke Island, Moreton

Bay; two specimens (24, 24 mm long, preserved), 25 September 1988, RCW. **Australia, New South Wales.** (1) Fly Point, Port Stephens; one specimen (62 mm long, live), 23 November 1989, RCW. (2) Callala Point, Jervis Bay; 4 specimens (20, 27, 30, 32 mm long, live), 20 November 1984, AMS C144047. (3) White Horse Point, Balmain, Sydney; twelve specimens (6, 6, 8, 8, 8, 9, 11, 12, 15, 17, 20, 22 mm long, preserved), 4 April 1981, AMS C127569. (4) Lilli Pilli, Port Hacking; one specimen (31 mm long, live), 9 September 1984, RCW. **Fiji.** (91) Nasese-Vieuto, Suva, Viti Levu; one specimen (27 mm long, live), 23 March 1985, BC A42.

##### black form

**Hong Kong.** (1) Breakers Reef; four specimens (30, 33, 35, 38 mm long, preserved), 19 April 1983, AMS C139015. **Australia, Queensland.** (1) Cockle Bay, Magnetic Island, Townsville: one specimen (25 mm long, live), 20 July 1989, BC F40; one specimen (54 mm long, live), 19 July 1989, BC F62; one specimen (34 mm long, live), 19 July 1989, BC F66. (2) Pallarenda, Townsville: one specimen (52 mm long, live), 6 December 1989, BC F50. **Australia, New South Wales.** (1) Arrawarra Headland, Coffs Harbour, one specimen (24 mm long, live), 18 November 1990, BC. (2) Northbridge Baths, Middle Harbour, Sydney: one specimen (35 mm long, preserved), 3 October 1976, AMS C108937. **Australia, Victoria.** (1) Portarlington: two specimens (17, 20 mm long, preserved), 29 January 1955, MV F20994. (2) Altona: one specimen (45 mm long, preserved), February 1933, MV F23498. (3) French island: one specimen (length not recorded), 22 January 1972, MV F58714. (4) Walkerville: one specimen (18 mm long, preserved), date unknown, MV F24891. **Australia, South Australia.** (1) American River, Kangaroo Island; 11 specimens (26, 28, 28, 32, 32, 34, 34, 35, 35, 37 mm long, preserved), approximately 1965, SAM D14878. (2) Coffin Bay, Eyre Peninsula; 3 specimens (45, 57, 58 mm long, live), February 1985, AMS C145117. (3) Kirton Point Wharf, Port Lincoln, Eyre Peninsula; 3 specimens (40, 57, 78 mm long, live), February 1985, AMS C145126. (4) Coobowie, Gulf St. Vincent; 6 specimens (8, 9, 10, 14, 14, 17 mm long, preserved), 1957, MV F20766. (5) Aldinga, Gulf St. Vincent; 5 specimens (9, 9.5, 10, 13, 15 mm long, preserved), 13 December 1970, MV F58708. **Australia, Western Australia.** (1) Emu Point, Oyster Harbour, Albany: one specimen (18 mm long, preserved), 15 February 1983, WAM 819-83; two specimens (7, 52 mm long, preserved), 7 February 1983, WAM 754-83, WAM 760-83. (2) Vlamingh Head, Rottnest Island: one specimen (19 mm long, preserved), 7 March, 1984, WAM 581-84 (in part).

##### orange/red form

**Tanzania.** (1) Mbudya Island, 14 km north Dar es Salaam; one specimen (18 mm long, live), 4 October 1977, AMS C163624. **Australia, Queensland.** (1) Great Keppel Island; one specimen (25 mm live), 14 May 1988, BC E2. (2) Cockle Bay, Magnetic Island, Townsville; one specimen (32 mm long, live), 17 August 1989, BC F61; one specimen (10 mm long, live

when collected, 38 mm, live at preservation), 17 July 1989, BC G3; one specimen (4 mm long, live when found, 16 mm long live when preserved), 21 May 1990, BC 142. (3) Swain Reefs—21° 22'S, 151° 41'E; one specimen (23 mm long, live), 10 January 1985, AMS C145049. (4) Peel Island, Moreton Bay; one specimen (25 mm long, preserved), 24 September 1984, RCW. (5) Myora Spit, North Stradbroke Island, Moreton Bay; one specimen (20 mm long, preserved), 21 August 1982, RCW. **Australia, New South Wales.** (1) White Horse Point, Balmain, Sydney; two specimens (13, 22 mm long, live), 8 June 1980, AMS C122212. **Australia, Western Australia.** (1) Slate Island, Kimberley; one specimen (13 mm long preserved), 9 July 1988, WAM 201-88. **Norfolk Island.** (1) Slaughter Bay; two specimens (14, 19 mm long, preserved), 13-14 December 1988, AMS C157762. (2) Offshore from 'Crystal Pool', southern coast; one specimen (13 mm long, live), 16 March 1992, RCW.

## DESCRIPTION

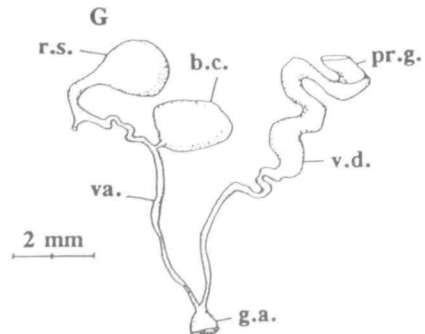
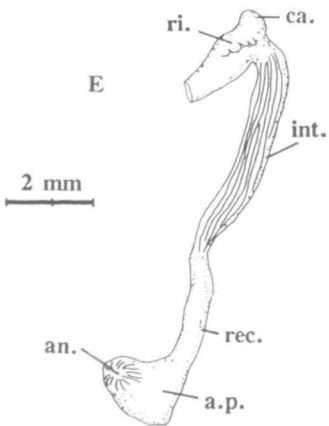
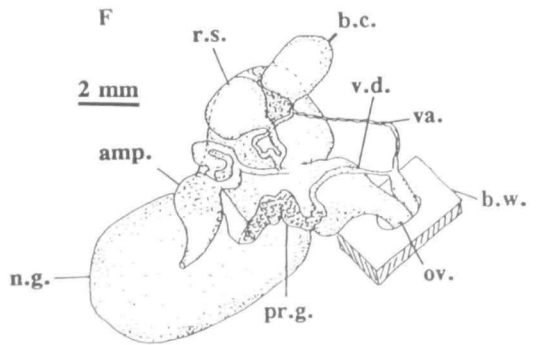
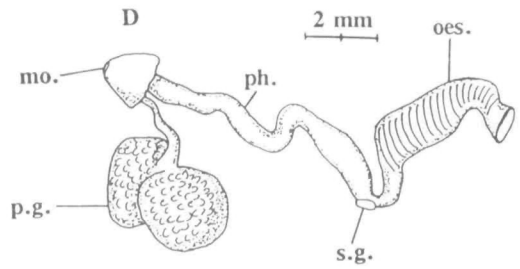
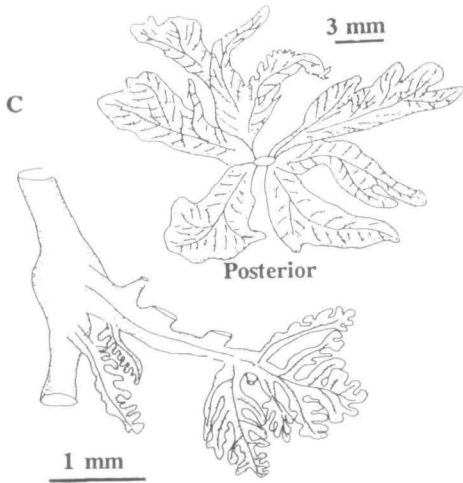
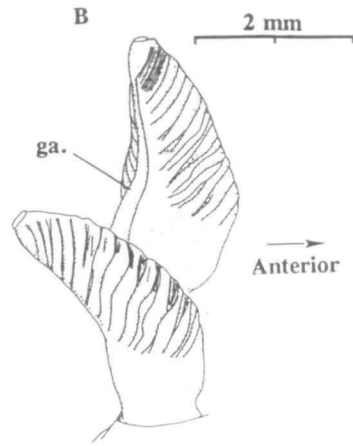
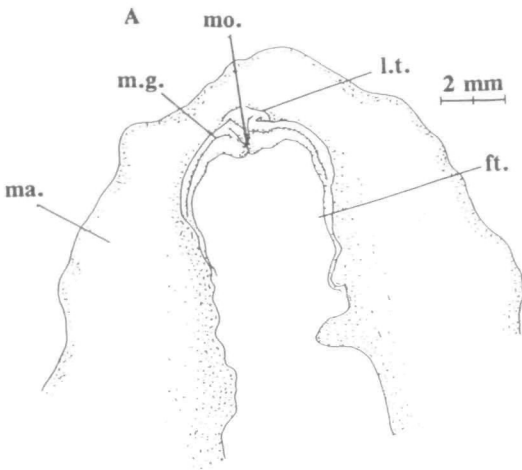
In life, the mantle surface is smooth and its margin thin. The number of vertical folds around the mantle margin is variable, possibly increasing ontogenetically. The anterior margin of the foot (Figure 3A), head, mouth and oral tentacles are as described for *D. nigra*. The rhinophores (Figure 3B) show some variation in shape between colour forms. In live healthy individuals the gills are held open over the dorsum (Figure 3C), although the individual plumes are sometimes cupped inward. Each plume is very finely subdivided (Figure 3C), particularly in larger individuals. The anal papilla interrupts the gill circling posteriorly. There is some variation in the size of individual gills i.e., the two anterior, or the two posterior plumes often appear smaller than the rest. We attribute this variation to an increase in the number of branchiae with size and/or distortion caused by preservation.

The visceral envelope is translucent. A lateral view of the anterior section of the digestive system is shown in Figure 3D. A tapering duct from the lobulate, ptyaline glands enters the oral tube just after the mouth. The smooth, elongate muscular pharynx broadens and, then

passes into the oesophagus. At this point are situated a pair of small, sessile, salivary glands. The oesophagus then enters the stomach, which is deeply embedded in the posteriorly bilobed digestive gland. The posterior section of the digestive system is shown in Figure 3E. After emerging in an upward direction from the stomach, the full translucent intestine becomes visible near the centre of the digestive gland and then turns sharply to the right. At this point a small caecum is present and a series of soft lobe-like ridges can sometimes be seen on the dorsal surface of the intestine, immediately anterior to the caecum. The intestine then runs posteriorly over the viscera, and narrows towards the rectum before terminating within the sometimes pigmented anal papilla.

A composite view of the reproductive system is shown in Figure 3F. The relatively slender, translucent hermaphroditic duct emerges from the centre of the anterior face of the ovotestis/digestive gland mass immediately beside the oesophagus. It then passes to the ampulla, which is generally pyriform but can become elongate (presumably when distended with autospERM) until it curves back on itself in a laterally pressed spiral. The ampulla's upper surface often bears some dark brown pigment. The ducts connecting the ampulla, nidamental glands and prostate gland are compressed against the surface of the nidamental gland for some distance and are thus difficult to trace. The ampullary duct divides into two branches. The proximal vas deferens widens to enter the glandular prostate and the other duct leads to the nidamental glands. The prostate gland, which folds upon itself, is quite long and is often separable into two distinct sections. The proximal section is solid, while the distal section is more translucent. The prostate gradually narrows to form a smooth vas deferens, which terminates in the penis. The vas deferens and vagina enter a common genital atrium (Figure 3G) before opening to the exterior. The vaginal duct leading from the nidamental gland is narrow and almost immediately along its length is a short duct leading to the club-like receptaculum seminis (Figure 3G). The next section of

**Figure 3.** Drawings of preserved *Dendrodoris fumata*. **A.** Ventral view of the anterior body. **B.** Lateral view of the rhinophores. **C.** Schematic diagram showing gill arrangement and fine branching of the individual plumes. **D.** Lateral view of the anterior digestive system. **E.** Dorsal view of the posterior digestive system. **F.** Composite view of the reproductive system. **G.** Distal portion of the reproductive system. Abbreviations: amp., ampulla; an., anus; a.p., anal papilla; b.c., bursa copulatrix; b.w., body wall; ca., caecum; ft., foot; ga., groove; g.a., genital atrium; gp., groove; int., intestine; ma., mantle; m.g., mucus groove; mo., mouth; n.g., nidamental gland; oes., oesophagus; l.t., oral tentacle; ov., oviduct; p.g., ptyaline gland; ph., pharynx; pr.g., prostate gland; ri., ridges; r.s., receptaculum seminis; s.g., salivary gland; va., vagina; v.d., vas deferens.



the vagina is longer and quite twisted before it enters the often larger, spherical, bursal copulatrix. The vaginal duct is initially very contorted after emerging from the bursa copulatrix, but straightens prior to its emergence at the genital aperture. Like the vas deferens, it is translucent. No vestibular gland is present on the broad oviduct, which enters the body wall adjacent to the common genital aperture.

#### Colour forms

##### grey

In live material the distinctive characters of this variety are the large size (Table 1) and broad, translucent grey mantle (Figure 1C) with wavy margins. The body colour can also include variable levels of yellow, brown or pink (Figure 1D). A distinct band of irregular indentations around the mantle edge, which is particularly noticeable from the ventral side, can be reinforced by a different colour (e.g. pale grey, dark grey or pink). Several irregular, grey patches can be present on the central dorsum (Figure 1C). The rhinophores (Figure 1C) are conical, often without any distinct angle at the intersection of the stalk and the tapering clavus. In a live adult, the rhinophoral stalk often exceeds the clavus in both height and width. There is a strong groove down the midline of the posterior club face (Figure 3B) and a weak ridge along the anterior midline. Fourteen to 18 sloping lamellae are present on the clavus of an adult animal. The penis is armed with approximately 18 rows of evenly spaced, microscopic (8  $\mu\text{m}$  high) hooks (Table 2). Alternate rows are staggered in their alignment, while the hooks curve away from the penial tip. The length of the armed area is approximately 250  $\mu\text{m}$  and seems to begin a short distance from the tip of the penis.

##### black

In life, this variety is black with a thin red border at the extreme margin of the mantle (Figure 1E). Its distinctive characters are: its very large, dark, spreading gills with pale apices; large, broad, very dark mantle with a thin red marginal border; and lack of white specks on the dorsum. The rhinophores are as described for *D. nigra* except that the rhinophoral clavus bears approximately 20 sloping lamellae in adult animals. No penial armature was found by us (Table 2), but this could well be the result of not being able to examine an everted penis.

##### orange/red

Overall, the animal is orange to red, sometimes with irregular black, brown, grey or purple patches or small dark purple spots to the mid-dorsum (Figure 1F). The rhinophores are as described for *D. nigra*, although the claval anterior midline ridge can sometimes be indistinct. The lamellae of the clavus slope posteriorly and range in number from 10–18 depending on an animal's length. A 70  $\mu\text{m}$  long section at the tip of the penis is armed with numerous, thorn-like spines, approximately 12  $\mu\text{m}$  in height (Table 2) and 18  $\mu\text{m}$  apart. Proximally, the spines are far less dense, approximately 35  $\mu\text{m}$  apart.

#### Remarks

In comparison to *Dendrodoris nigra*, the distinctive characters of *D. fumata* are: its lack of vestibular gland within the reproductive system; relatively large, broad mantle often with wavy margins; and its outward spreading gills in unstressed individuals.

Despite their colour differences, the anatomical similarity of the three colour forms of *D. fumata* oblige us to combine them into one species. It is possible that further studies of

**Table 1.** Relative body measurements for *Dendrodoris nigra* and three colour forms of *Dendrodoris fumata* studied at Cockle Bay, Magnetic Island, Australia over a 2 year period.

| Species  | Length (mm) [mean] | Mantle width (mm) [mean] | Foot width (mm) [mean] |
|--|--------------------|--------------------------|------------------------|
| <i>Dendrodoris nigra</i><br>n = 121                  | 3–75<br>[26]       | 1–32<br>[10]             | 1–22<br>[7]            |
| <i>Dendrodoris fumata</i> (black form)<br>n = 6      | 5–62<br>[36]       | 2–42<br>[21]             | 2–45<br>[13]           |
| <i>Dendrodoris fumata</i> (orange/red form)<br>n = 9 | 3–34<br>[18]       | 1–14<br>[7]              | 1–10<br>[6]            |
| <i>Dendrodoris fumata</i> (grey form)<br>n = 47      | 10–95<br>[44]      | 4–40<br>[22]             | 3–24<br>[11]           |

**Table 2.** Reports of penial armature in *Dendrodoris nigra* and the three colour forms of *Dendrodoris fumata*.

| Species                                     | Description   | Reference   |
|---|---|---|
| <i>Dendrodoris nigra</i>                    | Numerous hooks, 7 $\mu\text{m}$ long, line lumen of ejaculatory duct.   | Kay & Young (1969)  |
|   | About 150 hooked spines on slender penis, about 5 $\mu\text{m}$ .   | Edmunds (1971)  |
|   | 18 rows of 7 $\mu\text{m}$ spines.  | This study  |
| <i>Dendrodoris fumata</i> (black form)      | No armature found (likely an artifact).   | This study  |
| <i>Dendrodoris fumata</i> (orange/red form) | Lower portion of the vas deferens and glans are heavily armed with minute spines. These have a fairly broad base from which rises a hook or spine of rather irregular and varying shape.                          | Eliot (1913) as <i>D. rubra</i> var. <i>nigromaculata</i> |
|   | 15 $\mu\text{m}$ penial spines on penis.  | Ev. & Er. Marcus (1970) as <i>D. rubra</i>                |
|   | Slender penis (500 $\mu\text{m}$ long and 60 $\mu\text{m}$ in diameter) with 6 $\mu\text{m}$ thornlike spines erroneously reported to be in duct rather than on penis. Numerous 12 $\mu\text{m}$ spines on penis. | Edmunds (1971) as <i>D. rubra</i>                         |
|   |   | This study  |
| <i>Dendrodoris fumata</i> (grey form)       | Cylindrical brownish glans armed with 15 longitudinal rows of fine hooks.   | Gohar & Soliman (1967)                                    |
|   | 18 rows of 8 $\mu\text{m}$ spines on penis.   | This study  |

ecology and DNA may reveal evidence that would allow each colour form to be recognised as a separate species.

Although earlier reports indicated that the grey form of *Dendrodoris fumata* (Figure 1C) was restricted to the Red Sea, our records from Hong Kong, Fiji and Australia reveal this variation to be Indo-Pacific in occurrence. Within Australia it would appear that this form has a southern limit of Jervis Bay in southern New South Wales. Since the characteristics of *D. fumata* were not previously well known, the realities of its occurrence are as yet unreported. Both within Australia and overseas, the grey form of *D. fumata* has often been mistaken for the more common *D. nigra*.

The black form of *Dendrodoris fumata* (Figure 1E) has previously been ignored under the misapprehension that it was merely a colour form of *Dendrodoris nigra*. The separation of *D. nigra* and this form of *D. fumata* is complicated by way of the similarity in mantle colour and markings. However, the black form of *D. fumata* never has specks (of any colour) on its mantle, while its red mantle ring is well defined, relatively narrow, always present and always marginal. The distinctive characters of *D. fumata* (black form) are therefore: its very large, dark gills with pale apices; large, very dark mantle with a thin red marginal border; and lack of white specks on the black dorsum.

This colour form of *Dendrodoris fumata* was originally described from the Haitian Straits off the coast of China under the name *Doridopsis arborescens*. We now report it from Hong Kong and Australia for the first time. Within Australia, this variety extends all round the coast except for the tropical section between North West Cape and Cape York thus giving it the widest occurrence of any of the three colour forms of *D. fumata* discussed in this present study. It is also possible that the black form of *D. fumata* is found in New Zealand (see Morton & Miller, 1968, Plate 21).

Since the characteristics of this form were not previously known, the extent of its Indo-Pacific occurrence is uncertain. The name *D. arborescens* has been suggested to include specimens from Japan, however, internal investigations (K. Baba, pers. comm.) have revealed some discrepancies which separate Japanese material from our *D. fumata*.

The distinctive characters of the orange/red form of *Dendrodoris fumata* (Figure 1F) are its orange to red colour and rhinophoral shape i.e., more like *D. nigra*. Our investigations confirm that *Dendrodoris fumata* (orange/red form) has an Indo-west Pacific occurrence. Within Australia, it has a southern limit of Sydney Harbour on the east coast, like a number of other Indo-Pacific species. The lack of records from Australia's southern coastline probably reflects a

**Table 3.** Comparative details of eggs and larvae for *Dendrodoris nigra* and the three colour forms of *D. fumata*, ( ) = no. egg masses observed, [ ] = no. individuals observed, \* generally yellow but occasionally cream or orange.

| Species            | <i>Dendrodoris nigra</i><br>[16] | <i>Dendrodoris fumata</i><br>(grey form)<br>[5] | <i>Dendrodoris fumata</i><br>(black form)<br>[1] | <i>Dendrodoris fumata</i><br>(orange/red form)<br>[2] |
|--------------------|----------------------------------|---|--|---|
| Mass diameter (mm) | 12.0–45.0<br>(18)                | 12.0–45.0<br>(5)                                | –  | 13<br>(1)   |
| No. whorls         | 1.2–3.8<br>(26)                  | 2.0–3.5<br>(8)                                  | 2.3–3.5<br>(2)                                   | 1.8<br>(1)  |
| Ribbon length (mm) | 34–262<br>(37)                   | 67–367<br>(10)                                  | 74–152<br>(4)                                    | 31–99<br>(2)  |
| Ribbon width (mm)  | 2.5–6.0<br>(36)                  | 4.0–6.0<br>(10)                                 | 3.0<br>(4)                                       | 3.0–4.0<br>(2)  |
| Zygotes/Mass       | 13,500–199,000<br>(34)           | 11,000–122,500<br>(9)                           | 8,500–25,500<br>(4)                              | 5,500–58,000<br>(2)                                   |
| Mass colour        | Yellow*                          | Cream   | Orange   | Yellow  |
| Capsule size (µm)  | 98.7–137.8<br>(36)               | 154.1–184.4<br>(9)                              | 166.2–224.0<br>(4)                               | 112.0–180.0<br>(2)                                    |
| Egg size (µm)      | 66.3–93.4<br>(35)                | 125.2–150.9<br>(6)                              | 133.6–159.0<br>(3)                               | 85.0–129.4<br>(2)                                     |

genuine absence. This form of *D. fumata* is the commonest species of dendrodorid at Norfolk Island (K. Whysall, pers. comm.).

Relative body measurements recorded for *Dendrodoris nigra* and the three colour forms of *Dendrodoris fumata* are compared in Table 1 and comparative details of their eggs and larvae are shown in Table 3.

Based on our examinations and taxonomic conclusions we have developed the following key to separate *Dendrodoris nigra* and *Dendrodoris fumata* in the Indo-west Pacific.

- 1 (a). Animal black or grey . . . . . 2
- 1 (b). Animal orange, pink or red . . . . . 4
- 2 (a). Mantle never spotted, always with thin marginal red border; gills with white apices . . . . . *D. fumata* (black form)
- 2 (b). Spots of colour may be present on the mantle, red border maybe present; gills without white apices . . . . . 3
- 3 (a). Animal grey; mantle never with white specks, margin occasionally pink, irregular grey patches sometimes present on mid-dorsum; gills flattened, entire plume spread outward when fully extended; pallial gonoduct without annexed vestibular gland . . . *Dendrodoris fumata* (grey form)
- 3 (b). Animal black or dark grey, often with white spots on mantle; gills erect, cupped inward, entire plume directed

- posteriorly when fully extended; vestibular gland annexed to pallial gonoduct . . . . . *Dendrodoris nigra* (adult)
- 4 (a). Mantle uniform in coloration, ornamented with irregular black or brown patches or small dark purple spots in some specimens; gills flattened, entire gill plume spread outward when fully extended . . . . . *Dendrodoris fumata* (orange/red form) (adult/juvenile)
- 4 (b). Animal less than 10 mm in length; mantle uniform in colouration and often ornamented with white specks; entire gill plume directed posteriorly when fully extended . . . . . *Dendrodoris nigra* (juvenile)

DISCUSSION

Overall, these investigations resolve the widespread confusion which has surrounded the taxonomy of these Indo-Pacific dendrodorids. Although the species discussed here are some of the most common, shallow water, Indo-Pacific nudibranchs known, this is the first comprehensive comparative survey of their morphological features and occurrence. Significant conclusions regarding the utility of characters in dendrodorid taxonomy are also highlighted.

*Dendrodoris nigra* is consistently distinguish-

able from *D. fumata* in possessing a vestibular gland in its reproductive system, however direct observation of this organ requires the death of each animal. Species separation using external characteristics is therefore highly desirable and largely achievable with the use of our key and colour photographs (Figures 1A–F). Confusion is most likely to occur between *D. nigra* and the black form of *D. fumata*. This latter species, although similar to *D. nigra* (i.e., being black with a red mantle border), never has any white specks on the dorsum, always has a thin red marginal border to the mantle and white apices to the gills and possesses a relatively larger gill plume that spreads over the body even in unstressed individuals.

The three colour forms of *D. fumata* are very similar to each other in both internal and external anatomy. However, they do show some differences in adult size (Table 1), egg mass colour and larval size (Table 3), and as already discussed, external coloration (Figures 1D–F). The difference in mantle colour is striking and this character alone is sufficient to separate them into forms. Detailed investigations of colour variation (Brodie, unpublished data) have revealed no evidence of continuous colour variation across these groups, however, transparencies of Australian Museum material from various localities in New South Wales, Australia (AMS C122212, C126974, C144047, C152707) suggest that a continuum may exist between the grey and orange/red forms.

Overall, the external features of importance for species separation are colour pattern (Figure 1), size (Table 1), gill structure and rhinophoral shape. Rhinophoral and gill structure are, on their own, unreliable taxonomic characters because of high intraspecific variation and the need for both species for comparison. Although our results indicate that characters pertaining to rhinophoral shape should always be considered in taxonomic divisions, as suggested by Burn (1962), it highlights that they must always be utilised in combination with other characters. Egg development (Rose, 1985) and diameter (Table 3) are also of taxonomic value.

Penial armature is apparently widespread (perhaps general) throughout the genus *Dendrodoris* (Burn, 1962) and we could detect only minor variation in this character between the specimens we examined. A comparison of our findings and those reported in the literature also shows little variation (Table 2). Discounting the measurements of Edmunds (1971) for *D. fumata* (orange/red form), which relate to an immature specimen, the only difference we

could find is the slightly larger size of the spines in *D. fumata* (orange/red form). Thus, if we consider that penial armature is very similar interspecifically, and that it can both change ontogenetically and deteriorate with preservation, it probably cannot be considered to be a useful taxonomic character.

Unlike the few works that give details of the internal morphology of members of the *D. nigra* complex [e.g. Gohar & Soliman (1967), Kay & Young (1969), Edmunds (1971)], we located a midgut caecum in both species examined. This caecum varies intraspecifically from distinct to barely detectable. The lobe-like ridges seen in the intestine near the caecum also vary intraspecifically. Therefore, neither the caecum nor the ridges have value for discriminating between these two species.

A clear separation of *Dendrodoris nigra* and *Dendrodoris fumata* has been achieved in this study. The three colour forms of *D. fumata* defined are particularly important for the following reasons. The grey form links our species firmly to the original description of *D. fumata* by Rüppell & Leuckart (1830) and the important detailed work of Gohar & Soliman (1967). The black form (Figure 1E) was erroneously recognised as *Dendrodoris nigra*. This is clearly shown by its photographic use in Morton & Miller (1968), Orr (1981), Willan & Coleman (1984), Burn (1989) and Wells & Bryce (1993). The orange/red form has previously been widely recognised under the species name *rubra* e.g. Kelaart (1858), Alder & Hancock (1864), Collingwood (1881), Eliot (1905), Bergh (1875), White (1951), Miller (1969), Ev. & Er. Marcus (1970) and Edmunds, (1971), Willan & Coleman (1984). More accurate identifications can now proceed and the true occurrence of each colour form and each species should then become documented.

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