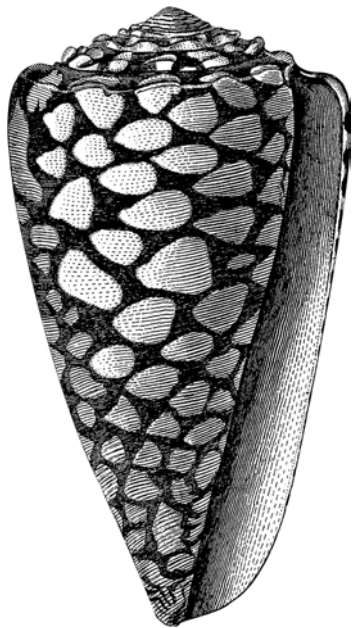


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## How many species of *Hexabranchnus* (Opisthobranchia : Dorididae) are there?

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### Abstract

Anatomical examination of several specimens of *Hexabranchnus*, collected from the extreme boundaries of its geographic range and other localities, revealed that there are two distinct species within this genus. One of these species is widely distributed throughout the tropical Indo-Pacific. The oldest available name for the Indo-Pacific species is *Hexabranchnus lacer* (Cuvier, 1804). The study of the original type material of *H. lacer* confirmed that it is a senior synonym of other names introduced subsequently, including *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830), which is the name most commonly used for this species. However, according to the provisions of the International Code of Zoological Nomenclature (Article 23.9.1), the name *H. sanguineus* has precedence over *H. lacer*, which has never been used as valid, except for the original description. *Hexabranchnus praetextus* Ehrenberg, 1828 is also a senior synonym of *H. sanguineus* that has not been used as valid since its original description and it is also invalidated under the provisions of Article 23.9.1.

The other species, *Hexabranchnus morsomus* Ev. Marcus & Er. Marcus, 1962, appears to be endemic to the Caribbean Sea. *Hexabranchnus sanguineus* and *H. morsomus* are clearly distinguishable by the morphology of the reproductive system and the radula. Hypotheses on the speciation process that took place in *Hexabranchnus*, the possible origin of the two species and the geographic range of the genus are discussed.

### Introduction

A number of species belonging to genus *Hexabranchnus* have been described from the tropical Indo-Pacific (Table 1). Most of these nominal species had been distinguished, when originally introduced, by differences in the colour pattern. Eliot (1910) suggested that it was highly probable that all the common species of *Hexabranchnus* were varieties of the same species, with the possible exception of *Hexabranchnus adamsii* Gray, 1850. He commented that the valid name for the most common Indo-Pacific species was probably *Hexabranchnus marginatus* (Quoy & Gaimard, 1832). Since then, a few more species of *Hexabranchnus* have been introduced. Ostergaard (1955) described *Hexabranchnus aureomarginatus* and *H. tinkeri* from Hawaii. Marcus and Marcus (1962) agreed in considering all the Indo-Pacific species as synonyms but, at the same time, described the new species, namely *H. morsomus*, from the Caribbean Sea. These authors justified the introduction of a new species of this genus based on morphological differences and the geographic isolation of the Caribbean.

Steps towards the synonymisation of all species of *Hexabranchnus* were taken up again by Gohar and Soliman (1963), who illustrated the colour variation within *Hexabranchnus sanguineus* in a small geographic area in the Red Sea. More recently, Thompson (1972) argued that the colour pattern of the species of *Hexabranchnus* is extremely variable and regarded all the Indo-Pacific species as synonyms (including *H. aureomarginatus* and *H. tinkeri*), but he did not provide anatomical evidence to sustain this conclusion. Regarding *H. morsomus*, Thompson (1972) stated that there are no compelling reasons to separate it from the Indo-Pacific species besides the geographic range and small radular differences, and regarded both species as synonyms. In addition, Thompson (1972)

**Table 1. Available species names introduced for Indo-Pacific species of *Hexabranchnus*, including authorship, publication date and type locality**Names marked with an asterisk have been synonymized with *H. sanguineus* by Thompson (1972)

Species name	Type locality
<i>Doris lacera</i> Cuvier, 1804	Timor
* <i>Hexabranchnus praetextus</i> Ehrenberg, 1828	El Tûr, Egypt (Red Sea)
<i>Doris sanguinea</i> Rüppell & Leuckart, 1830	El Tûr, Egypt (Red Sea)
* <i>Doris flammulata</i> Quoy & Gaimard, 1832	Tonga
* <i>Doris marginata</i> Quoy & Gaimard, 1832	Amboina
<i>Heptabranchnus burnetti</i> A. Adams, 1848	Borneo
<i>Hexabranchnus adamsii</i> J. E. Gray, 1850	Borneo
<i>Hexabranchnus sandwichensis</i> J. E. Gray, 1850	Hawaii
* <i>Doris cardinalis</i> Gould, 1852	Honolulu, Hawaii
<i>Doris sumptuosa</i> Gould, 1852	Tonga
<i>Doris superba</i> Gould, 1852	Tutuilla, Samoa
<i>Doris cardinalis</i> Gould, 1852	Honolulu, Hawaii
* <i>Doris sandwichensis</i> Souleyet, 1852	Hawaii
<i>Doris gloriosa</i> Kelaart, 1858	Tricomalie, Sri Lanka
* <i>Hexabranchnus pulchellus</i> Pease, 1860	Hawaii
* <i>Hexabranchnus suzensis</i> Abraham, 1876	Red Sea
* <i>Hexabranchnus pellucidulus</i> Abraham, 1876	Unknown
<i>Aethedoris indica</i> Abraham, 1877	Madras, India
* <i>Hexabranchnus aneiteumensis</i> Abraham, 1877	Aneiteum, New Hebrides
* <i>Hexabranchnus mauritiensis</i> Abraham, 1877	Mauritius
* <i>Hexabranchnus orbicularis</i> Abraham, 1877	Mauritius
* <i>Hexabranchnus anaiteus</i> Bergh, 1878	New Hebrides
<i>Hexabranchnus faustus</i> Bergh, 1878	Aibukit, Palau
<i>Hexabranchnus notatus</i> Bergh, 1878	Tonga
<i>Hexabranchnus petersi</i> Bergh, 1878	Mozambique
* <i>Albania formosa</i> Collingwood, 1881	Ke Lung, Taiwan
* <i>Doris imperialis</i> Kent, 1897	Abrolhos Islands
* <i>Hexabranchnus digitatus</i> Eliot, 1903	Maldive Islands
* <i>Hexabranchnus plicatus</i> Hägg, 1903	El Tûr, Egypt (Red Sea)
<i>Hexabranchnus marginatus</i> var. <i>moebii</i> Eliot, 1905	Zanzibar
<i>Hexabranchnus punctatus</i> Bergh, 1905	West of Sulawesi, Indonesia
* <i>Hexabranchnus aureomarginatus</i> Ostergaard, 1955	Waikiki, Hawaii
* <i>Hexabranchnus tinkeri</i> Ostergaard, 1955	Waikiki, Hawaii

considered that *H. sanguineus* was the oldest available name for this species. Currently, this name is used widely as the valid name for the tropical Indo-Pacific species of the genus. Whether *H. morsomus* is the same species is an open question.

In the present study, I attempt to determine how many valid species of *Hexabranchnus* there are, based on the study of specimens collected from the extreme boundaries of the geographic range of the genus. The material examined is deposited at the following institutions: Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, USA (CASIZ), Instituto Nacional de Biodiversidad, Costa Rica (INBio), Natural History Museum of Los Angeles County, USA (LACM), Muséum National d'Histoire Naturelle, Paris, France (MNHN), Marine Invertebrate Museum, University of Miami, USA (UMML) and Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (MNH).

## Systematics

Family **HEXABRANCHIDAE** Bergh, 1891

Genus *Hexabranchnus* Ehrenberg, 1831

*Hexabranchnus* Ehrenberg, 1828–31 [1831]: [30]. Type species (by subsequent designation of J. E. Gray, 1847): *Hexabranchnus praetextus* Ehrenberg, 1828.

### Diagnosis

Dorsum smooth, lacking tubercles. Head with two large, flattened and lobate oral tentacles. Anterior border of the foot simple. Gill contractile, not retractile. Radula composed of simple, hamate teeth. Labial cuticle completely covered with rodlets. Buccal mass with numerous and strong muscles attached. Penis and vagina devoid of hooks. Vestibular or accessory glands absent.

### Remarks

The genus *Hexabranchnus* has been traditionally placed within the cryptobranch dorids, despite the fact that it lacks the major synapomorphy of this clade, which is the ability to retract the gill into the gill pocket.

Fischer (1880–1887) introduced the taxon Cryptobranchia and included *Hexabranchnus* as one of its three members. Subsequently, Bergh (1891) placed *Hexabranchnus* in its own family, also within the cryptobranch dorids. These opinions were later sustained in the classifications by Odhner in Franc (1968), Thompson (1976) and Rudman (1998). More recently, Wägele and Willan (2000) showed that *Hexabranchnus* is the sister taxon to cryptobranch dorids, but at the same time, they excluded this genus from the Cryptobranchia on the basis of the absence of a retractable gill.

Further phylogenetic studies are necessary to resolve the systematic position of *Hexabranchnus*, which appears to be a derived phanerobranch rather than a cryptobranch dorid (Wägele and Willan 2000).

***Hexabranchnus sanguineus*** (Rüppell & Leuckart, 1830)

(Figs 1A,C, 2–4)

*Doris lacera* Cuvier, 1804: 452, 453–465, 473, pl. 73, figs 1–3 (*nomen oblitum*).

*Doris sanguinea* Rüppell & Leuckart, 1828–30: 28–29, pl. 8, fig. 1 (*nomen protectum*).

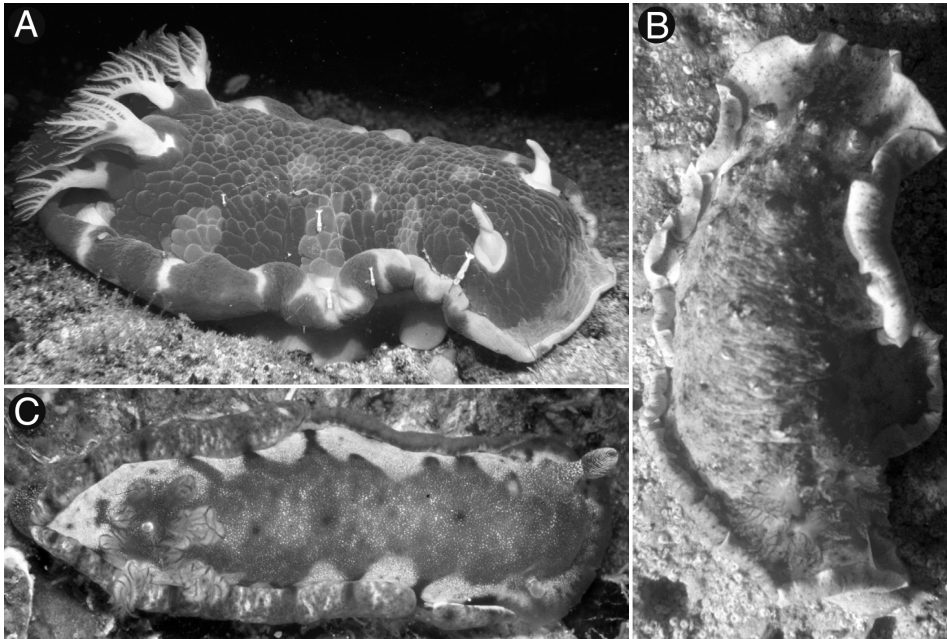
(For a complete list of synonyms, see Table 1).

### Material examined

*Syntypes.* *Doris lacera* Cuvier. Indian Ocean (= Mer des Indes): date and exact locality unknown, two specimens 30 and 76 mm preserved length, dissected (MNHN).

*Syntypes.* *Hexabranchnus praetextus* Ehrenberg. Egypt: El Tûr (= Tor), date unknown, one specimen 125 mm preserved length (MNHB 566); El Tûr (= Tor), date unknown, one specimen 110 mm preserved length, partially dissected (MNHB 567).

*Other material examined.* **Hawaii:** Pono Kai Condominium, Kappa, Kunai Island, 27 Feb. 1986, one specimen 48 mm preserved length, dissected, collected by M. T. Ghiselin (CASIZ 074266). **South Africa:** exact locality unknown, Natal, Nov. 1992, dissected, collected by A. Camnell (CASIZ 087386). **Mozambique Channel:** reef near Hotel Coelacanth, north end of Moroni, Grand Comore Island, 6 Mar. 1975, one specimen 104 mm preserved length, dissected, collected by S. Earle and A. Giddings (CASIZ 068296). **Madagascar:** Tire Reef, 2 km north of Mora Mora Village, 9 Apr. 1989, two specimens 94–100 mm preserved length, dissected, collected by T. M. Gosliner (CASIZ 071897). **Philippines:** Fishery Station Ground, Zamboanga City, Oct. 1947, one specimen 110 mm preserved length, collected by J. S. Domantay (LACM 140743).



**Fig. 1.** Living animals. *A*, *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830) from Indonesia, photograph by M. J. Adams. *B*, *Hexabranchnus morsomus* Marcus & Marcus, 1962 from Panama, photograph by H. Bertsch. *C*, *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830) from the Philippines, photograph by A. Valdés.

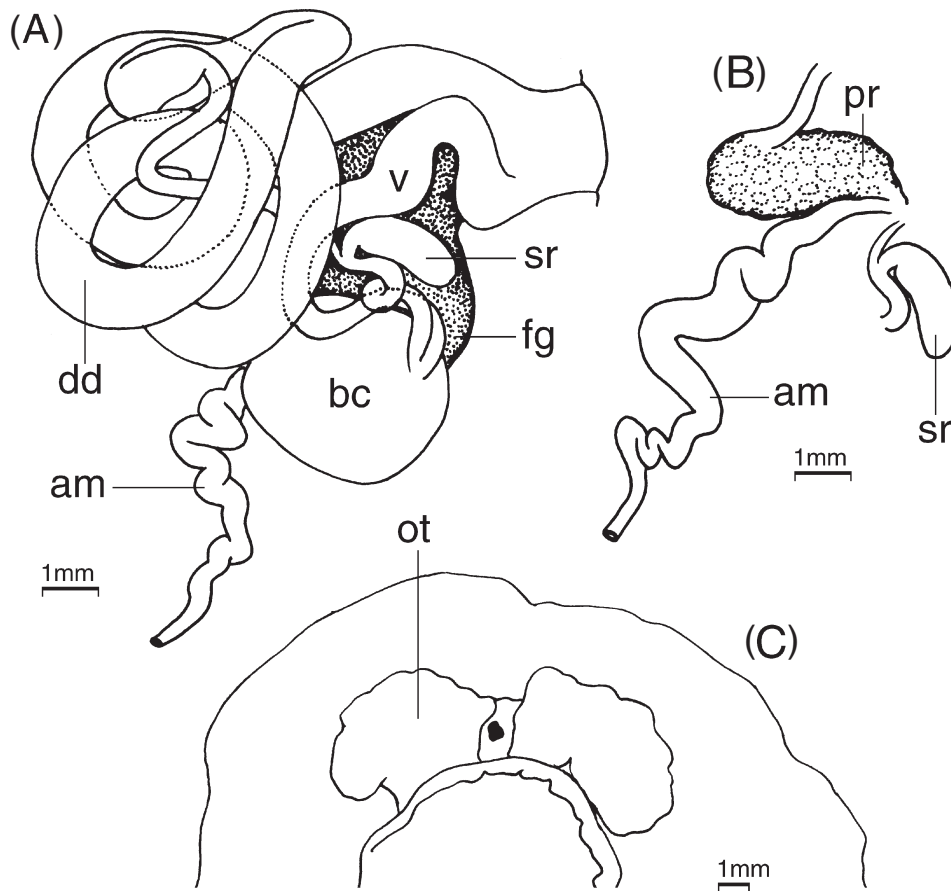
#### *External morphology*

The general colour of the living animals is highly variable, from pale orange to bright red (Fig. 1*A*). In some specimens, there are a number of small white or yellowish dots on some areas or on the entire dorsum (Fig. 1*C*). Other specimens have large bright red or pinkish spots, or a pale concentric band. Sometimes, the mantle margin is surrounded by a white or yellow line. In other specimens, there is a white area on the inner side of the mantle margin that is visible when the animal is swimming. The rhinophores are red to yellowish, with white spots in some specimens. The gill has normally the same colour as the dorsum, with the rachises of the branchial leaves white or yellowish. The dorsum is smooth. There are seven to nine tripinnate, non-retractile branchial leaves. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 45 lamellae in a 100-mm preserved length specimen.

Ventrally, there are two large, flattened and lobate oral tentacles (Fig. 2*B*). The anterior border of the foot is simple, lacking a notch and a groove.

#### *Anatomy*

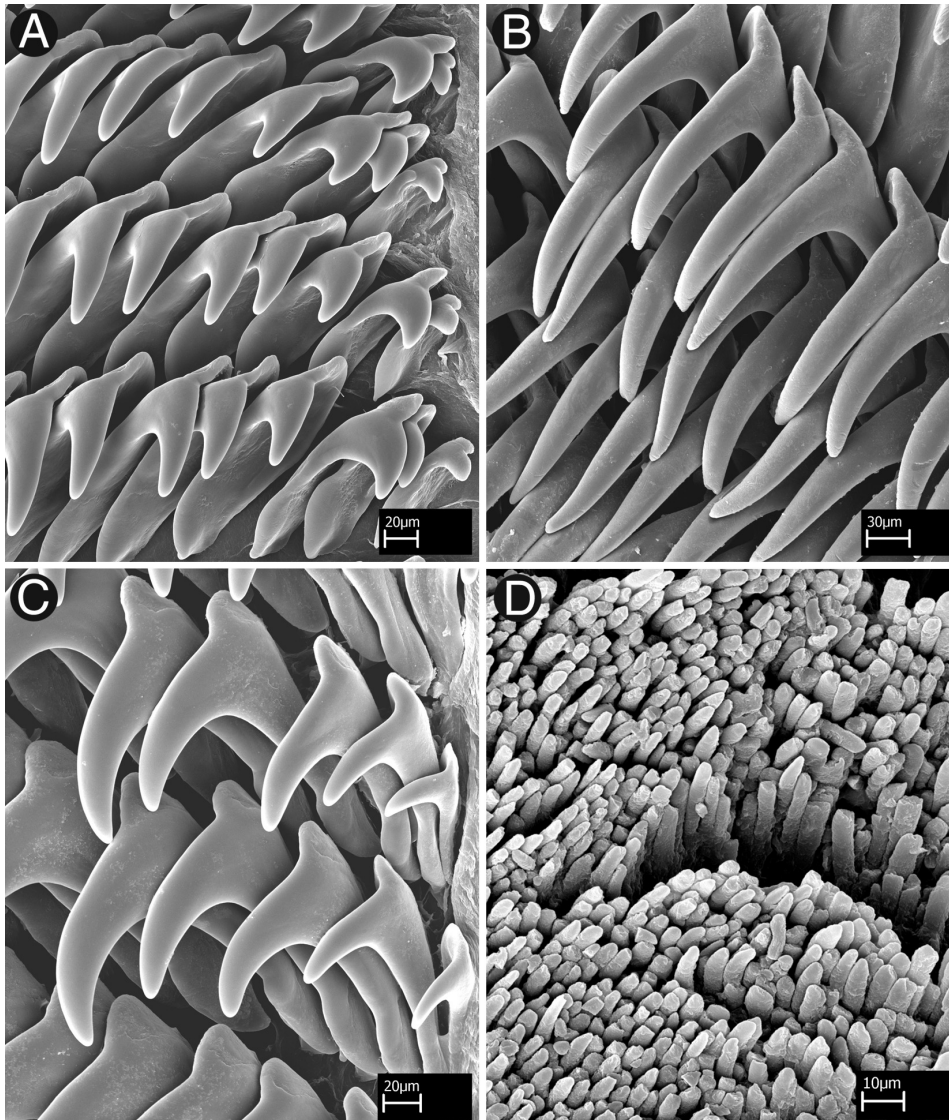
The radular formula is  $33 \times 49.0.49$  in a 32-mm preserved length specimen (CASIZ 087386),  $35 \times 48.0.48$  in a 48-mm preserved length specimen (CASIZ 074266) and  $36 \times 77.0.77$  in a 100-mm preserved length specimen (CASIZ 071897). There are no rachidian teeth in any of the specimens examined. The innermost lateral teeth are hamate, with a long apical prolongation and a short, curved cusp (Figs 3*A*, 4*A*). In some rows, there is an additional cusp on the outer side of the innermost tooth. The mid-lateral teeth are also



**Fig. 2.** *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830), anatomy (CASIZ 074266). *A*, Reproductive system. *B*, Detail of several reproductive organs. *C*, Ventral view of the mouth area. am, Ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr, prostate; sr, seminal receptacle; v, vagina.

hamate, but larger and having a longer cusp than the inner laterals (Figs 3*B*, 4*B*). The outermost teeth become smaller again and are similar in shape to the mid-laterals, also having an apical prolongation (Figs 3*C*, 4*C*). The jaws are composed of a number of small and simple rodlets, approximately 30  $\mu\text{m}$  long (Figs 3*D*, 4*D*).

The reproductive system is triaulic (Fig. 2*A*). The ampulla is very long and convoluted. It branches into the prostatic portion of the deferent duct and the short oviduct that connects to the female glands. The deferent duct is very long and convoluted. The prostatic portion occupies the most proximal end of the deferent duct and is short and glandular; it connects to a short, thin duct that expands into the long, wide, muscular and convoluted ejaculatory portion of the deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is devoid of hooks. The vagina is also wide, long and convoluted. At its proximal end, the vagina connects to the rounded bursa copulatrix. From the bursa copulatrix leads another duct that connects to the beam-shaped seminal receptacle and the female glands.



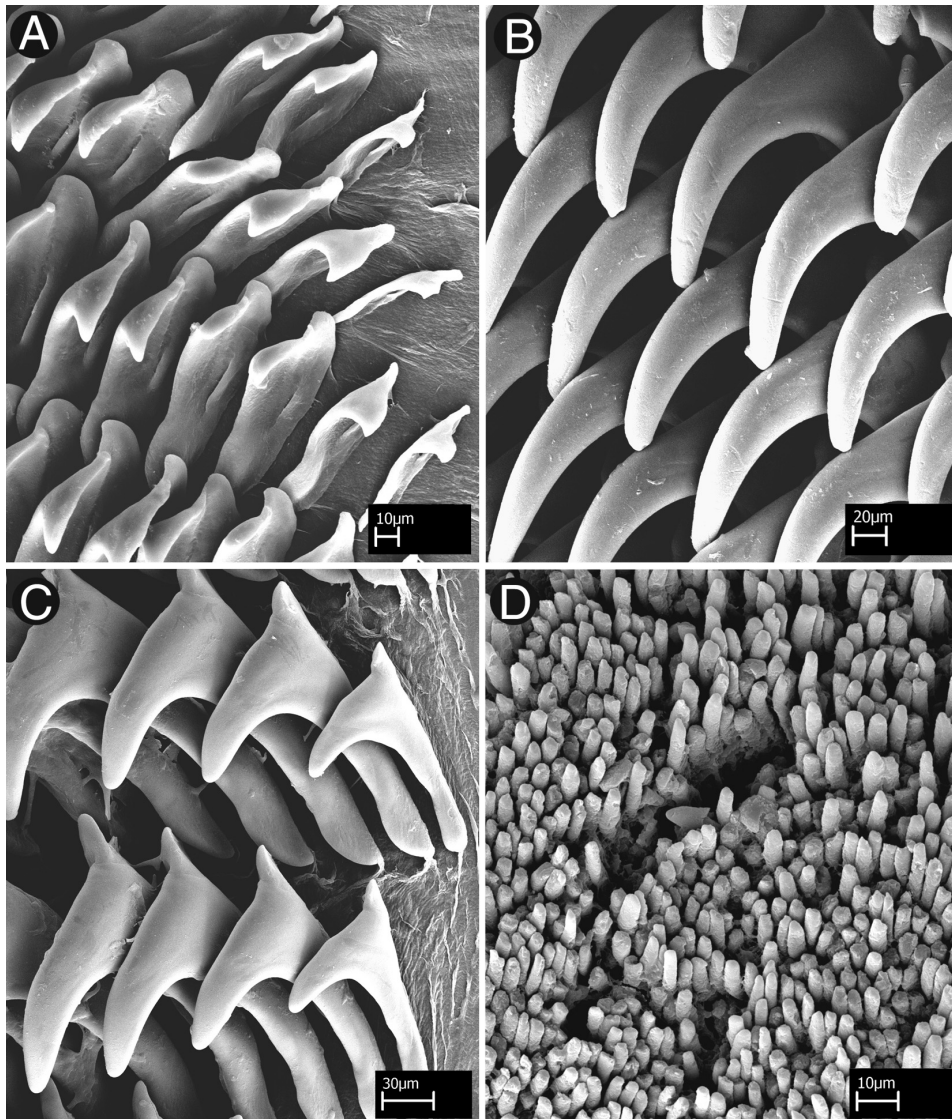
**Fig. 3.** *Hexabranhus sanguineus* (Rüppell & Leuckart, 1830); scanning electron micrographs of a specimen from South Africa (CASIZ 087386). *A*, Inner lateral teeth. *B*, Lateral teeth from the central portion of the half-row. *C*, Outermost lateral teeth. *D*, Jaw elements.

#### *Geographic range*

There are numerous references to this species throughout the tropical Indo-Pacific, from East Africa and the Red Sea to Hawaii (Thompson 1972).

#### *Remarks*

Comparison between tropical Indo-Pacific specimens of *Hexabranhus*, collected from the two opposite boundaries of its geographic range (East Africa and Hawaii) and other localities, confirms that there are no consistent morphological or anatomical differences



**Fig. 4.** *Hexabranhus sanguineus* (Rüppell & Leuckart, 1830); scanning electron micrographs of a specimen from Hawaii (CASIZ 074266). *A*, Inner lateral teeth. *B*, Lateral teeth from the central portion of the half-row. *C*, Outermost lateral teeth. *D*, Jaw elements.

and, therefore, that only one species of *Hexabranhus* occurs in this region. Similar conclusions had already been attained by Eliot (1910) and Thompson (1972), but never sustained by anatomical studies.

Following Thompson (1972), all modern authors have been using the name *H. sanguineus* for the tropical Indo-Pacific species of this genus. However, examination of the syntypes of *Doris lacera* Cuvier, 1804 confirms that they belong to the same species and that *Hexabranhus lacera* constitutes a senior synonym of *H. sanguineus*. *Doris lacera* has been ignored by all authors dealing with the *Hexabranhus* problem. According to the



International Code of Zoological Nomenclature (ICZN 1999), if a senior synonym has not been used as a valid name after 1899 and its junior synonym has been used for the same species in at least 25 papers, published by at least 10 authors in the immediately preceding 50 years and encompassing a span not less than 10 years, the usage of the junior synonym must be maintained (Article 23.9.1). The name *H. lacer* has only been used as valid in its original description in 1804, whereas the name *H. sanguineus* is in constant usage in modern literature. More than 30 papers, books and field guides using the name *H. sanguineus* as valid have been published during the past 20 years by more than 15 authors. Therefore, the name *H. sanguineus* is here conserved (*nomen protectum*) and *H. lacer* is regarded as invalid (*nomen oblitum*).

According to Winckworth (1941), the original description of *H. sanguineus* and some other species of nudibranchs (see Rüppell and Leuckart 1828–1830; pp. 23–47) was most likely published in 1830. Another synonym of *H. sanguineus*, namely *Hexabranchnus praetextus*, was first and validly introduced in a plate published in 1828, but the written description of the species appeared in 1831 (Winckworth 1941). Again, the name *H. praetextus* has only been used as valid in its original description in 1828–1831. Therefore, the name *H. sanguineus* is here conserved (*nomen protectum*) and *H. praetextus* is regarded as invalid (*nomen oblitum*).

Recently, Johnson (2001) posted photographs of *Hexabranchnus* specimens from Hawaii, which show remarkable colour differences with other specimens of *H. sanguineus* from Hawaii and other Indo-Pacific localities. Johnson (2001) suggested the possibility that the distinct specimens could belong to the species *Hexabranchnus aureomarginatus* Ostergaard, 1955, but anatomical information is required to confirm this. In the meantime, *H. aureomarginatus* is maintained as a synonym of *H. sanguineus*.

### ***Hexabranchnus morsomus* Ev. Marcus & Er. Marcus, 1962**

(Figs 1B, 5–6)

*Hexabranchnus morsomus* Marcus & Marcus, 1962: 468–471, figs 16–17.

#### *Material examined*

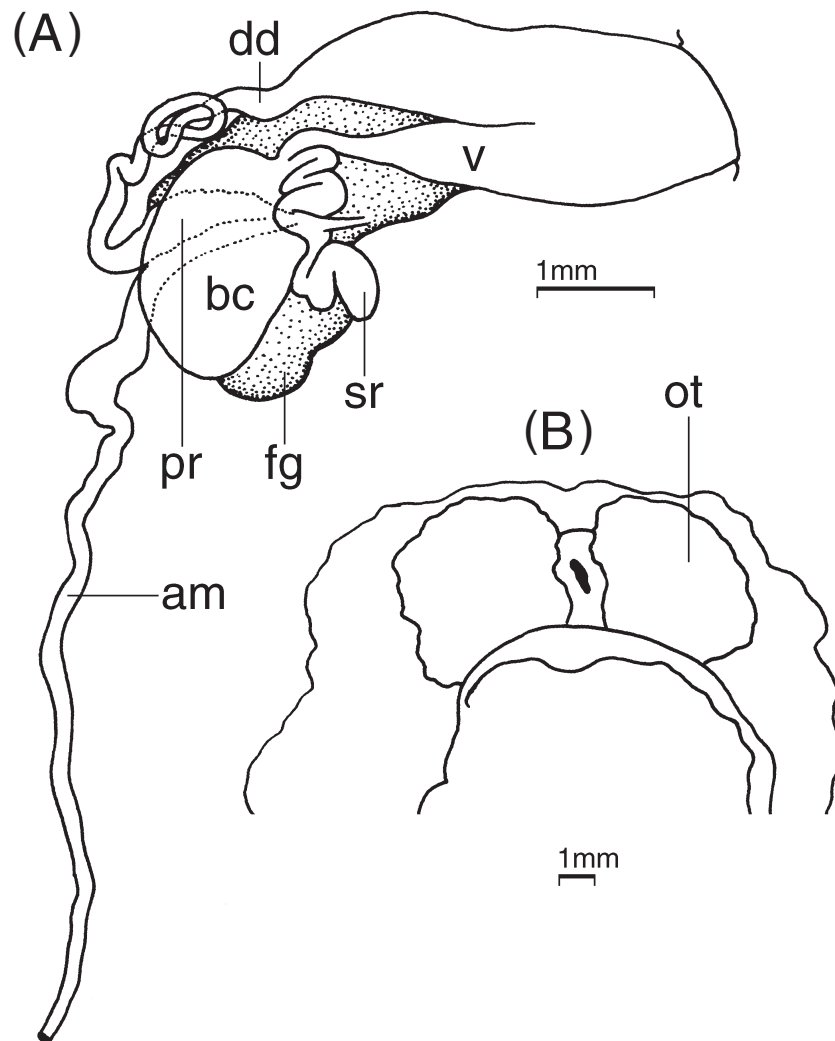
*Holotype.* British Virgin Islands, Virgin Gorda, Harbour of Spanish Town, 4 Dec. 1959, 26 mm preserved length, dissected, collected by A. Chess (UMML 302696).

*Other material examined.* **Costa Rica:** Punta Mona (on the west side of the islet), Limón, 19 Oct. 1998, 0 m depth, one specimen 52 mm preserved length, dissected, collected by S. Ávila (INBio 1495908).

#### *External morphology*

The general colour of the living animals is orange to reddish, with an irregular pattern of pale orange or yellow pigment. Some specimens have a white powdery colour (Fig. 1B). The mantle margin has a large whitish band situated on the inner end that is only visible when the animal is swimming. The rhinophores are uniformly reddish. The gill is reddish with the apices white. The dorsum is smooth. There are six to seven tripinnate, non-retractile branchial leaves. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 30 lamellae in a 52-mm preserved length specimen.

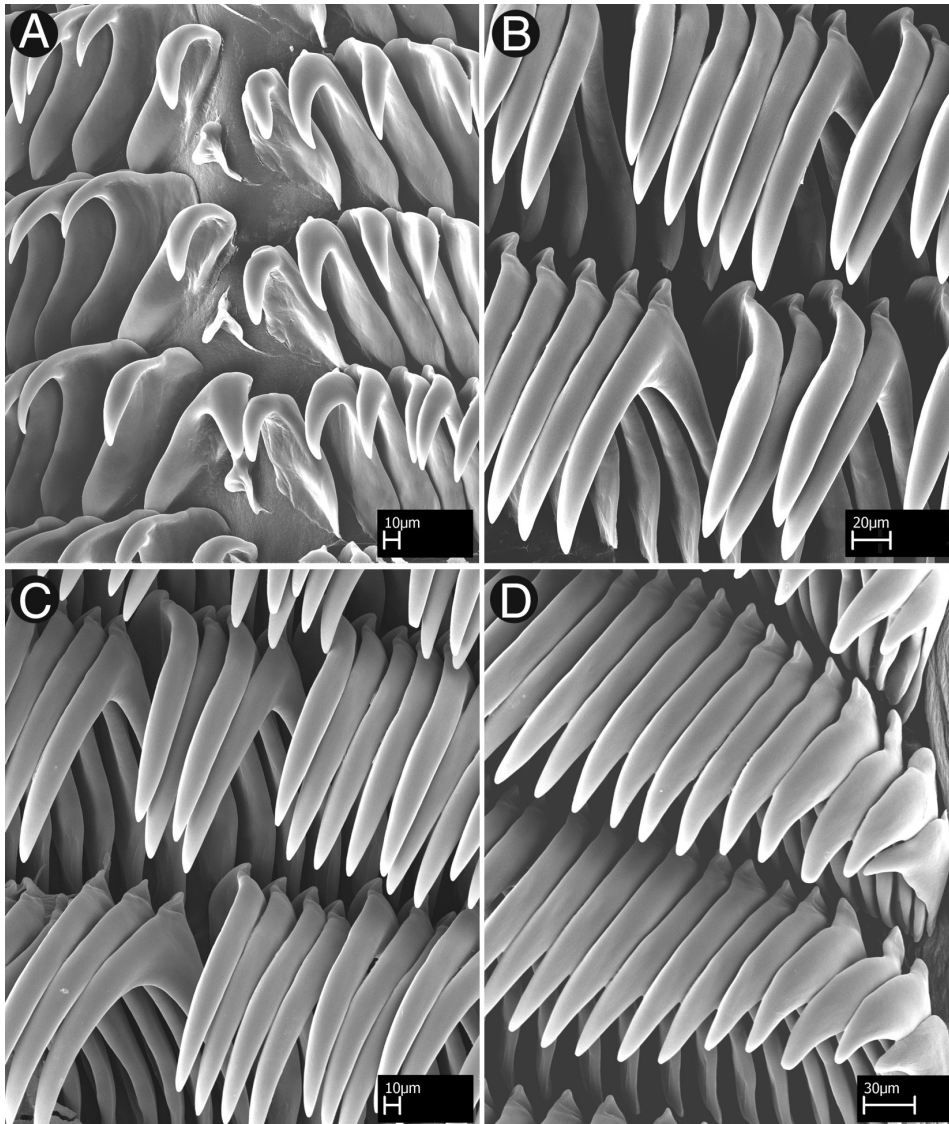
Ventrally, there are two large, flattened and lobate oral tentacles (Fig. 5B). The anterior border of the foot is simple, lacking a notch and a groove.



**Fig. 5.** *Hexabranhus morsomus* Marcus & Marcus, 1962; anatomy (INBio 1495908). *A*, Reproductive system. *B*, Ventral view of the mouth area. am, Ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr, prostate; sr, seminal receptacle; v, vagina.

#### Anatomy

The radular formula is  $41 \times 116.1.116$  in a 52-mm preserved length specimen (INBio 1495908) and  $40 \times 90.1.90$  in a 26-mm preserved length specimen (UMML 302696). There is a small, triangular rachidian tooth in each row. The rachidian teeth have a single, central cusp and a convex base (Fig. 6*A*). The innermost lateral teeth are hamate, with a small apical prolongation and a short, curved cusp (Fig. 6*A*). The mid-lateral teeth are also hamate, but larger and have a longer and more straight cusp than the inner laterals (Fig. 6*B,C*). The outermost teeth become smaller again and are similar in shape to the mid-laterals, having longer apical prolongations and shorter cups (Fig. 6*D*). The labial cuticle is smooth, devoid of jaws.



**Fig. 6.** *Hexabranhus morsomus* Marcus & Marcus, 1962; scanning electron micrographs (INBio 1495908). *A*, Rachidian and inner lateral teeth. *B*, Inner lateral teeth from the central portion of the half-row. *C*, Outer lateral teeth from central portion of half-row. *D*, Outermost lateral teeth.

The reproductive system is triaulic (Fig. 5A). The ampulla is very long and convoluted. It branches into the prostatic portion of the deferent duct and a short oviduct that connects to the female glands. The deferent duct is long and convoluted and narrows abruptly at the end of the ejaculatory portion. The prostatic portion occupies the most proximal end of the deferent duct and is short and glandular; it connects to a long, thin and convoluted duct that expands into the wide and muscular ejaculatory portion of the deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is devoid of hooks. The vagina is wide and short. At its proximal end, the vagina connects to the rounded bursa copulatrix.

From the bursa copulatrix leads another duct that connects to the folded seminal receptacle and the female glands.

#### *Geographic range*

Only known from the Caribbean Sea, there are records from the British Virgin Islands (Marcus and Marcus 1962), Puerto Rico (Marcus and Marcus 1970), Panama (Meyer 1977) and Costa Rica (present paper).

#### *Remarks*

*Hexabranchnus morsomus* is clearly distinguishable from *H. sanguineus* in several regards. The radulae of the two specimens here studied of *H. morsomus* have rachidian teeth that are absent in all examined specimens of *H. sanguineus*. The inner, mid- and outer lateral teeth of *H. sanguineus* have a long apical prolongation that is absent or very small in *H. morsomus*. The outer teeth of *H. sanguineus* are hook shaped, whereas in *H. morsomus* they are more triangular. It is also remarkable that the labial cuticle of *H. morsomus* is smooth, whereas it is covered with numerous denticles in *H. sanguineus*.

In addition, the reproductive system of these two species is different. The deferent duct and vagina of *H. sanguineus* are very long and convoluted, whereas in *H. morsomus* they are much shorter. Also, the seminal receptacle of *H. sanguineus* is proportionally larger to the bursa copulatrix than that of *H. morsomus* and the duct connecting both organs is shorter in the former species. There is no question that these two species should be maintained separate.

Meyer (1977) considered that *H. morsomus* is most likely a synonym of *H. sanguineus*. She examined five specimens collected from Galeta Point, Panama, and found no rachidian teeth in the radula, except for a few rows in a 20-mm long specimen. Meyer (1977) concluded that this difference probably does not justify, by itself, the separation of two different species. All the specimens examined here of *H. morsomus* have rachidian teeth in all the rows of the radula and also show other consistent differences with specimens of *H. sanguineus* mentioned above. The lack of rachidian teeth in the Panama animals could be due to variability within *H. morsomus* or inaccurate observation (Meyer used a regular compound microscope and, sometimes, rachidian teeth are difficult to observe), but there are enough anatomical differences that justify the maintenance of *H. morsomus* as a valid taxon.

#### **Discussion**

The genus *Hexabranchnus* is distributed throughout the tropical Indo-Pacific, from Hawaii to East Africa, and in the Caribbean Sea, but it is absent from other tropical areas in the Eastern tropical Atlantic and the Eastern Pacific. Specimens of *Hexabranchnus* are normally found in shallow coral reef areas (Francis 1980), which are common in the Indo-Pacific and the Caribbean Sea.

There are no published phylogenies on this group that would allow developing a hypothesis about the relationships of *Hexabranchnus* and, therefore, about its origin. However, because there are no more species in this taxon or other dorid nudibranchs with similar anatomical or external features, it can be assumed that *H. sanguineus* and *H. morsomus* are sister taxa. In addition, there are several synapomorphies of *Hexabranchnus*, including the swimming and defensive behaviour (Marcus and Marcus 1962; Edmunds 1968; Bertsch and Johnson 1981), the large and lobate oral tentacles and the smooth dorsum devoid of spicules, that support the monophyly of this taxon.

Assuming that *Hexabranchnus* is monophyletic, there are two most likely hypotheses to explain the present distribution of its species. One would involve a split of the original geographic range of the ancestor of these two species and subsequent speciation. In this scenario, the most likely possibility is that the original range of the ancestor was divided during the closure of the Panama land bridge that ended 3.1 million years ago. The absence of *Hexabranchnus* species in the Eastern Pacific would be due to subsequent extinction. The vicariant event of the closure of the Panama land bridge has been widely described in the literature for numerous groups of marine animals (Collins 1996), including opisthobranchs (Valdés 2001), and it is considered as a classic example of marine vicariant generalised track (Humphries and Parenti 1986).

The second hypothesis requires that the origin of this genus is situated in either the tropical Indo-Pacific or the Caribbean and that one of these two original populations colonised the other region. This colonisation would have occurred before the closure of the east–west communication. In this scenario, species of *Hexabranchnus* probably never became established in the Eastern Pacific or Eastern Atlantic due to the absence of favourable conditions or went extinct subsequently. Accepting any of these hypotheses implies that the two species have been separated for a minimum of 3.1 million years, which would explain the notorious anatomical differences between them.

### Acknowledgments

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### References

- Bergh, R. (1891). Die cryptobranchiaten Dorididen. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* **6**, 103–144.
- Bertsch, H., and Johnson, S. (1981). ‘Hawaiian Nudibranchs.’ (Oriental Publishing Company: Honolulu, Hawaii.)
- Collins, T. (1996). Molecular comparisons of transisthmian species pairs: rates and patterns of evolution. In ‘Evolution and Environment in Tropical America’. (Eds J. B. C. Jackson, A. F. Budd and A. G. Coates.) pp. 303–334. (The University of Chicago Press: Chicago, Illinois.)
- Cuvier, G. L. (1804). Mémoire sur le genre *Doris*. *Annales du Muséum National d’Histoire Naturelle* **4**, 447–473, pls 73–74.
- Edmunds, M. (1968). On the swimming and defensive response of *Hexabranchnus marginatus* (Mollusca, Nudibranchia). *Journal of the Linnean Society, Zoology* **47**, 425–429.
- Ehrenberg, C. G. (1828–1831). *Symbolae physicae animalia evertebrata exclusis insectis. Series prima cum tabularum decade prima continent animalia Africana et Asiatica. Decas Prima.* In ‘Symbolae physicae, seu Icones adhuc ineditae corporum naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegyptum, Nubiam, Dengalam, Syriam, Arabiam et Habessiniam. Pars Zoologica, 4.’ (Eds F. G. Hemprich and C. G. Ehrenberg.) Pages unnumbered. (Officina Academica: Berlin.) Dates of publication: pls 1–2 [1828], text [1831].
- Eliot, C. N. (1910). Nudibranchs collected by Mr. Stanley Gardiner from the Indian Ocean in H. M. S. Sealark. *Transactions of the Linnean Society of London, Zoology* **13**, 411–438.
- Fischer, P. (1880–1887). ‘Manuel de Conchyliologie et de Paléontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles Siuvi d’un Appendice sur les Brachiopodes par D. P. Ehlert.’ (F. Savy: Paris.) Dates of publication: pp. 1–112 [1880], pp. 113–305 [1881], pp. 305–416 [1882], pp. 417–608 [1883], pp. 609–688 [1884], pp. 689–896 [1885], pp. 897–1008 [1886], pp. 1009–1369 [1887].

- Franc, A. (1968). Mollusques, gastéropodes et scaphopodes. In 'Traité de Zoologie. Anatomie, Systématique, Biologie', Vol. 5. (Ed. P. Grassé.) pp. 608–893. (Masson et Cie: Paris.)
- Francis, M. P. (1980). Habitat, food and reproductive activity of the nudibranch *Hexabranchnus sanguineus* on Tongatapu Island. *Veliger* **22**, 252–258.
- Gohar, H. A. F., and Soliman, G. N. (1963). The biology and development of *Hexabranchnus sanguineus* (Rüpp., and Leuck.) (Gastropoda, Nudibranchiata). *Publications of the Marine Biological Station, Al-Ghardaqa* **12**, 219–247.
- Gray, J. E. (1847). A list of the genera of recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London* **15**, 129–219.
- Humphries, C. J., and Parenti, L. R. (1986). 'Cladistic Biogeography.' (Clarendon Press: Oxford.)
- ICZN (1999). 'International Code Of Zoological Nomenclature.' (International Trust for Zoological Nomenclature: London.)
- Johnson, S. (2001). *Hexabranchnus 'aureomarginatus'* from Hawaii. On-line: <http://www.seaslugforum.net/hexasang2.htm> (Accessed: June 2001.)
- Marcus, Ev., and Marcus, Er. (1962). Opisthobranchs from Florida and the Virgin Islands. *Bulletin of Marine Science* **12**, 450–488.
- Marcus, Er., and Marcus, Ev. (1970). Opisthobranchs from Curaçao and faunistically related regions. *Studies on the Fauna of Curaçao and other Caribbean Islands* **33**, 1–129.
- Meyer, K. B. (1977). Dorid nudibranchs of the Caribbean coast of the Panama Canal Zone. *Bulletin of Marine Science* **27**, 299–307.
- Ostergaard, J. M. (1955). Some opisthobranchiate Mollusca from Hawaii. *Pacific Science* **9**, 110–136.
- Rudman, W. B. (1998). Class Opisthobranchia. In 'The Southern Synthesis. Fauna of Australia: Mollusca', Vol. 5. (Eds P. L. Beesley, G. I. B. Ross and A. Wells.) pp. 915–1035. (CSIRO Publishing: Melbourne.)
- Rüppell, E., and Leuckart, F. S. (1828–1830). Neue wirbellose Thiere des rothen Meers. In 'Atlas zu der Reise im Nördlichen Afrika. Erste Abtheilung Zoologie'. (Ed. E. Rüppell.) pp. 1–47. (Brönner: Frankfurt am Main.) Dates of publication: pp. 1–22 [1828], pp. 23–47 [probably 1830].
- Thompson, T. E. (1972). Observations on *Hexabranchnus* from the Australian Great Barrier Reef (Gastropoda: Opisthobranchia). *Veliger* **15**, 1–5.
- Thompson, T. E. (1976). 'Biology of Opisthobranch Mollusks,' Vol. 1. (The Ray Society: London.)
- Valdés, A. (2001). Depth-related adaptations, speciation processes and evolution of color in the genus *Phyllidiopsis* (Mollusca, Nudibranchia). *Marine Biology* **139**, 485–496.
- Wägele, H., and Willan, R. C. (2000). Phylogeny of the Nudibranchia. *Zoological Journal of the Linnean Society* **130**, 83–181.
- Winckworth, R. (1941). A note on Rang, Leuckart and Ehrenberg. *Proceedings of the Malacological Society of London* **24**, 290.