

THE WESTERN ATLANTIC WARM WATER NOTASPIDEA (GASTROPODA,
OPISTHOBANCHIA), PARTE 2

EVELINE d. B.-R. MARCUS
Caixa Postal 6994 - 01051
- São Paulo - SP - Brazil.
(with 66 figures)
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RESUMO - No Atlântico ocidental os Notaspidea Pleurobranchacea Pleurobranchidae contém sete espécies dos Berthellinae, das quais uma nova, *Berthella tamiu*, e cinco Pleurobranchinae, das quais duas novas, *Pleurobranchus (Oscanius) iouspi* e *Pl. (Susania) emys*.

ABSTRACT - The western Atlantic Notaspidea Pleurobranchacea Pleurobranchidae comprise seven Berthellinae with one new species, *Berthella tamiu*, and five Pleurobranchinae, two of which are new: *Pleurobranchus (Oscanius) iouspi* and *Pl. (Susania) emys*. The Pleurobranchaeidae were treated separately (Marcus & Gosliner, 1984).

INTRODUCTION

In continuation of my Catalogue of the Western Atlantic Warm Water Opisthobranchs (1972a, 1972b, 1974, 1978, 1980, 1983, 1984), the present paper is the second on the Notaspidea of the Western Atlantic. The first (1984) treats the Pleurobranchaeidae of all the world, as this was necessary for their classification.

I now deal with the Pleurobranchidae only from the Western Atlantic.

The Order Notaspidea or Pleurobranchomorpha is easily characterized by the gill under the right mantle border.

The Suborder Pleurobranchacea with an inner or no shell differs from the Umbraculacea with an external shell.

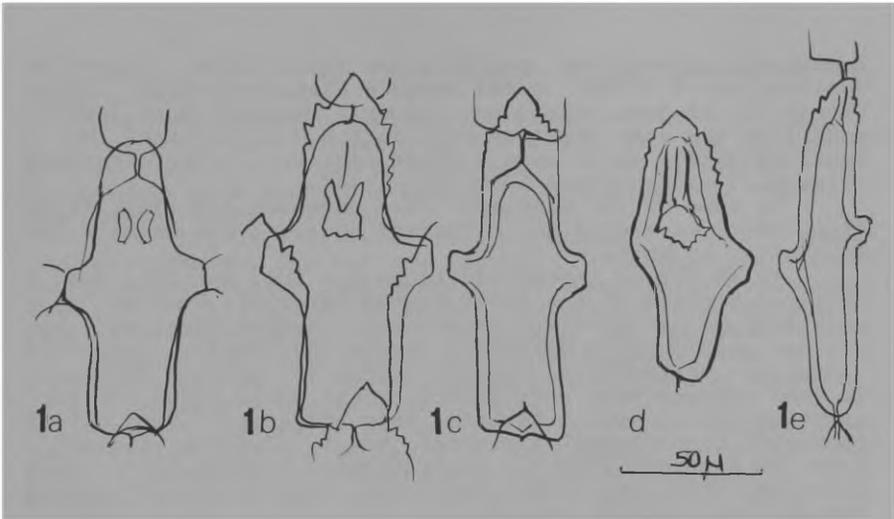
I follow Burn (1962) in considering the Pleurobranchaeidae without shell and the Pleurobranchidae with internal shell as families. The latter are divided into the subfamilies Berthellinae and Pleurobranchinae.

As cited in the introduction of the seventh contribution (1984), on the Pleurobranchaeidae, Vayssière (1885, 1901) indicated the difficulties with the incomplete previous descriptions. One example will do to show how insecure the authors were. Bergh (1900:211) said of a species from the Chatham Islands: "It seems to belong to *Pleurobranchus aurantiacus* Risso, 1818, which occurs in the Atlantic; probably this is again one of the perhaps widely distributed forms of the opisthobranchs". In 1898 (p. 118-120) Bergh had said: "Several of the species indicated here to be new, are perhaps identical with one another or with already described species"

It is difficult to find the right mean between variability, lumping and splitting genera or species. Most authors differ in their opinions.

Willan (letter of 11. VII. 1983) has seen thousands of living and preserved specimens and found so much intra-individual and intraspecific variation, in the cruciform or polygonal mandibular elements, that they cannot serve for taxonomic distinction (Fig. 1).

Vayssière (1898) divided the Pleurobranchidae by what he thought the only safe character, the long denticate teeth for the genus *Berthella* Blainville, 1825, now *Berthellina* Gardiner, 1936, and the hook-shaped teeth for the genus *Pleurobranchus* Cuvier, 1805. The latter included four subge-



Figures 1 a-e - Jaw platelets of *Pleurobranchus areolatus* from different positions in the jaw plate; 1a, old platelet in front of jaw; 1b, from middle of jaw; 1c, young platelet near hind end of jaw; 1d, platelet near inner side of jaw ; 1e, platelet near outer side.

nera, *Bouvieria* Vayssière, 1896, now *Berthella* Blainville, 1825, *Pleurobranchus* s. str., Cuvier 1805, *Oscanius* Leach, Gray, 1847, and *Susania* Gray, 1857.

The Pleurobranchidae are now divided into two Subfamilies, *Berthellinae* with *Berthella* and *Berthellina*, and Pleurobranchinae with *Pleurobranchus* with three subgenera, *P. s.* str., with small shell in front, *Susania* with small shell behind, and *Oscanius*, with large shell in the middle. Many species with undescribed shell have to find their place in *Pleurobranchus* (sensu lato)

The Pleurobranchinae are the most difficult subfamily I have met with, and the state of their literature shows that this is not only my opinion: also Abbott (1949:73) and Pruvot-Fol (1954:217) complain. Bergh (1897-8, 1905), Vayssière (1898), Odhner (1926) and Burn (1962) have given keys by the character: footgland present or absent. Thompson & Slinn (1959:510) found that the footgland depends upon the sexual state of the specimen. It is not specific or generic.

The "type specimen" has to be dissected for the mouth parts and is thereby sometimes destroyed. The paratypes may be good. However, in the case of the Pleurobranchaeid *Koonsia obesa* Verrill, 1822, all paratypes are quite different from Verrill's very good figure of the total animal (1883, f. 107) with its small, round mantle and large, long foot. Bergh (1897:30 fi. 19-21) and Vayssière (1901:72) received paratypes from the TYPE vial and called them *Pleurobranchaea obesa* (Verrill). I received, also from the Type vial, two different species of Pleurobranchacea, which do not correspond to this figure, and cannot accept *Koonsia* as synonym of *Pleuro-*

branchaea. *Koonsia* can possibly be found again. Therefore Gosliner and I (1984) named Bergh's *Pleurobranchaea obesa* Verrill *P. confusa*, spec. nov. Later I received more specimens from the same paratype vial in the U.S. National Museum, n^o 34217, which were a third species, *Pleurobranchus (Oscanius) membranaceus* (Montagu, 1815)

In some of the samples I have received for classification, there were also two different species; the animals are so similar in shape.

It is almost impossible to give a full specific description because of the often scarce material. Even as famous authors as Vayssière synonymized several "species", some, now belonging to different genera, and their indicated characters obviously do not all belong to the same species. As some species have been said to occur world wide, the geographical distribution is not a safe character. Baba (1971) separated *Pleurobranchus hirasei*, now *P. (Susania) hirasei*, from the Japanese *Oscanius testudinarius* Hirase, 1927. Lin Guang-Yu (1975) had several specimens from China and called the species: endemic Chinese.

If we see the discussion of synonymies of the species of Pleurobranchidae by Odhner (1926:15-20) and others, I think it is better to leave many of them as unrecognizable and to make as complete as possible descriptions of the present materials, not only their outer aspect, but also shell, jaw platelets, radular teeth and reproductive organs, and if they do not coincide with one of the older diagnoses, give them a new name.

I try to give a key of the genera with the most simple of the not invalidated characters, and of the species as far as possible. The number of doubtful species is greater than that of completely described ones. Our own descriptions are also often incomplete with respect to the reproductive organs (1955:118)

I restrict the present paper to the Western Atlantic Warm Water species of the family, of which about 130 species are named.

Only about 40 species are sufficiently described to be valid. Even some of our own, including the present paper, are not complete, due to the scarcity of material and the state of contraction of the complicated and entangled reproductive organs.

Several generic names are synonyms to *Pleurobranchus*: *Pleurobranchidium* Blainville, 1826, *Pleurobranchillus* Bergh, 1892, and *Oscaniella* Bergh 1897. *Pleurobranchoides* O'Donoghue, 1929, is synonymous to the Pleurobranchaeid *Pleurobranchella* Thiele, 1925. The genus *Gymnotoplax* Pilsbry, 1896, was characterized by an opening over the shell in the mantle. Pruvot-Fol (1954:218, note) supposed such holes were caused by mutilation during fixation. Bouchet (1977:29) found *Berthellina sideralis* just like Verrill's figure and assumed *Gymnotoplax* to be synonymous with *Berthella*.

Willan (1978:339) examined the type specimen of Verrill's *Pleurobranchus americanus* and found similar open shells in *Pleurobranchus forskali* and *Berthella postrema*. Hence *Gymnotoplax* is invalid, and not synonymous to the other genus.

Abbott (1974) was not right to use *Gymnotoplax* as prior to *Berthellina*.

My Mediterranean *Gymnotoplax barashi* (1977:418, figs. 1, 2) with the mantle open over the shell in two specimens is also evidently a case of mutilation. The characters of the animals show that they belong to *Pleurobranchus* (*Oscanius*) *membranaceus* (Willan, 1977:342)

Verrill, 1900:547 (fig. 5), introduced a new genus *Pleurobranchopsis* for his new species *P. aurantiacus* from the Bermudas. Thiele considered it as subgenus to *Pleurobranchus* (1931:419), and as it is not identical with *Pleurobranchus aurantiacus* Risso, 1818, he gave it the new name *verrilli*. Thompson (1977:106) found Verrill's proposed name "mischievous" Willan, 1978, considers it as a dubious species.

Pleurehdera Marcus (1970c:158, f. 8-12) with naked gill rachis belongs to the Berthellinae. With denticulate jaw platelets and one denticle on the radular teeth it stands between *Berthella* and *Berthellina*. *Gigantonotum album* Lin Guangyu, 1975, is not sufficiently well described. Burn, in a letter, 1981, invalidated his genus *Berthellinops*, 1962, himself.

Of the 20 previously named Western Atlantic species nine are well described, six are synonyms, and four are not recognizable. I describe three new species.

Future researchers should give complete descriptions of their specimens, and not rely upon insufficient older descriptions, it is better to give a new name to a species that can later be recognized and perhaps identified with an old one, than to put old names in lists of synonymy and distribution without justification.

Characters for the classification of the present species

The size is only of relative value, as in the living animals it varies according to movement. Under preservation they contract more or less strongly, even if they are anesthetized. The relative size of mantle and foot is often registered, but it may be quite different in specimens in one and the same sample. The structure of the mantle surface serves.

The colours vary in life and are generally lost by preservation. A notch or crenulation in the mantle border in front and one behind (Abbott, 1949:74) depend upon contraction; they have no specific value.

The presence (Fig. 60,k) or absence of tubercles on the gill rachis separates the Pleurobranchinae from the Berthellinae.

The size of the shell in relation to body size is of little use due to the variation of the latter.

The calcareous shell is often dissolved by preservation or lost by old age, and the conchinous shell is also easily lost. The measurements should be taken of the latter.

Unfortunately most diagnoses (also our own) only describe the shell, often in detail; Vayssière (1898:21) said, it can by no means serve for the classification as it shows

great similarities in most of these animals. Its location in the body is rarely mentioned. I found that its size and position are quite good characters for separating the subgenera of *Pleurobranchus*. In *Pleurobranchus* (s. str.) the shell is small and generally lies in front; in *Susania* it is small and lies behind; in *Oscantus* it is large and lies in the middle of the body. However, in one case I called a specimen with a small shell in the middle of the body *Pleurobranchus* (s. str.) *areolatus* (1976b:16).

Spicules are often mentioned, but they may be dissolved by preservation.

The presence or absence of a pedal gland is not a specific character, but depends upon the sexual phase of the specimen.

I found jaw platelets to be useful as specific characters, though their shape varies according to their position in the jaw (Fig. 1a-e). In front the old denticles are often worn; near the sides the shape is frequently asymmetrical. The young platelets are simpler, but those in the middle of the plate have the specific shape of tip and denticles, width of platelet and structure of the inside (Fig. 36-40).

The jaw platelets show two different types, but with a few intermediate forms. In all the known Pleurobranchinae they are square behind and triangular in front (Fig. 1c) and generally have one to more short denticles on each side. In *Berthellina* they have a longish ovoid surface with a slender pointed tip and one or more long, frontal denticles parallel to the tip (Fig. 25-29). They do not serve as subfamily characters, as *Berthella* generally has pleurobranchine platelets (Fig. 6-12). But they provide some specific distinctions, though their aspect varies according to their place in the jaw. The youngest, posterior platelets are thin and transparent, the foremost, old brown ones have often lost their denticles. In the middle, more to the front, are the strongest complete, often light brown, platelets. They may have a round or irregular central mark or a longitudinal streak, which Thompson (1977:108, f. 12 d) considers as diagnostic for *P. areolatus*. But such also occur in other species, e.g., in *Pleurobranchus ovalis* Pease (Pruvot-Fol, 1954a: f. 1), *Berthella agassizii* (MacFarland 1909:61, said slits; Marcus, 1955, f. 74) and *Berthella tupala* Marcus (1957: f. 65). In other species these marks are of different shape, or there are none. In one young specimen of *P. areolatus* I found the first rows of the platelets (Fig. 6) consisting of regular rows of knobs not set off from their basal cuticle.

The radular teeth differ little in shape. The denticulation of lamelliform teeth separates the genus *Berthellina* from the rest. Tiny denticles on the innermost unciform teeth are often not recognizable, but if they are, they should be mentioned in the description.

I specially give the systematically useful characters, as far as they are indicated. The reproductive organs cannot be evaluated as long as there are so few descriptions. I do not treat the digestive, circulatory, excretory and nervous systems, described by some of the previous authors. The nervous system was emphasized by Bergh (1897:11) and Vayssière (1898:223-229). The central nervous system of *Oscantus* Vays-

Pleurobranchacea

Pleurobranchidae

Berthellinae Burn, 1962

Pleurobranchidae without tubercles on the gill rachis

Berthella Blainville, 1824;

synonym *Bouvieria* Vayssière, 1896

Berthellinae generally with pleurobranchine jaw platelets, exceptions: *B. ocellata* (Cheeseman, 1878) Odhner (1924:86) and *B. americana*; unciform or straight teeth without denticles.

Type species *Bulla plumula* Montagu, 1803

Berthella patagonica d'Orbigny, 1837

Figures 2,3

Pleurobranchus patagonicus d'Orbigny, 1847: 204-205, pl. 17, f. 4, 5; Pilsbry, 1896: 201, pl. 74, f. 93; Bergh, 1898a: 496-499, pl. 28, f. 26, pl. 29, f. 10-16; 1898: 146-148.

Bouvieria patagonica Vayssière, 1898: 289-291, pl. 15, f. 32-33.

Distribution. - Southern Atlantic, near Rio Negro, 41° S; Chile, Quiriquina; 20° 19' S.

Description. - The animals were up to 22 mm long. The foot is quadrangular in d'Orbigny's figure. The gill rachis is smooth. The shell is 9.5 mm long. The jaw platelets are of pleurobranchine type (Fig. 2), with 3-5 denticles on either side. The radula has 75 x 55.0.55 hook-shaped teeth without denticles (Fig. 3)

The brain (Bergh, 1898a, pl. 29, f. 12) is knobby like that of *Oscanius membranaceus* (Vayssière, 1898:381, f. 188).

Discussion. - The quadrangular foot seems to be the only distinctive character (Vayssière)



Figures 2-3 - *Berthella patagonica*, from Bergh, 1898 2, Jaw platelet; 3, radular tooth.

Figures 4-5 - *Berthella americana*, from Willan, 1983. 4, jaw platelets; 5, radular teeth.

Berthella americana (Verrill, 1885)

Figures 4, 5

Pleurobranchus americanus Verrill, 1885:429, pl. 44, f. 13 ;
Dall, 1903:90, pl. 46 f. 13.

Gymnotoplax americanus Pilsbry, 1896:210, pl. 74, f. 91; Abbott, 1974:347 f. 4189.

Berthella americana Willan, 1978:339, f. 1 A-C.

Distribution. - Martha's Vineyard, 475 m, one specimen.

Description of the holotype, from Willan, p. 341 :
Length 13.4 mm, shell 12.6 mm; mantle porous; whole body dull brownish; gill rachis smooth; anal opening in front of middle of attached gill. Jaw platelets with 1-5 big denticles. (Fig. 4) Radula 85 x 170.0.170 (Fig. 5) Innermost tooth broad-based and curved, in middle of row larger with only a very slight bend, outermost teeth erect; no denticles.

Discussion. - The radula is very similar in many *Berthella* and *Pleurobranchus* species, so that it does not serve for specific distinction.

I do not accept *Gymnotoplax* as synonym of *Berthella*, as an open mantle occurs as mutilation in several genera (Willan 1978:341) My *Gymnotoplax barashi* (1977) has, apart from the open mantle, all characters of *Oscanus membranaeus*.

Willan compared *americana* from Martha's Vineyard only with *tupala* as west Atlantic, and with north Atlantic *sideralis* (Loven, 1846) of which he only mentioned Dall's specimen from Alaska. He did not compare Mörch's *circularis* (1863) nor MacFarland's *agassizii* (1909) Willan's figure 1 A of the shell of *americana* is identical with Odhner's of *sideralis* (1939, f. 10)

Bergh (1898:120) synonymized *Pleurobranchus americanus* Verrill with *P. aurantiacus* Risso, 1818, and therefore he indicated *aurantiacus* as west and east Atlantic (1900:210)

Berthella agassizii (MacFarland, 1909)

Figures 6-16

Pleurobranchus agassizii MacFarland, 1909:58-64, f. 43-57

Bouvieria agassizii Engel, 1927; 110, f. 26a-c.

Berthella agassizii Marcus, 1955:117-119, f. 66-77; 1957b :
20-21, f. 38-39; 1963:24; 1970:53-54; 1976:133.

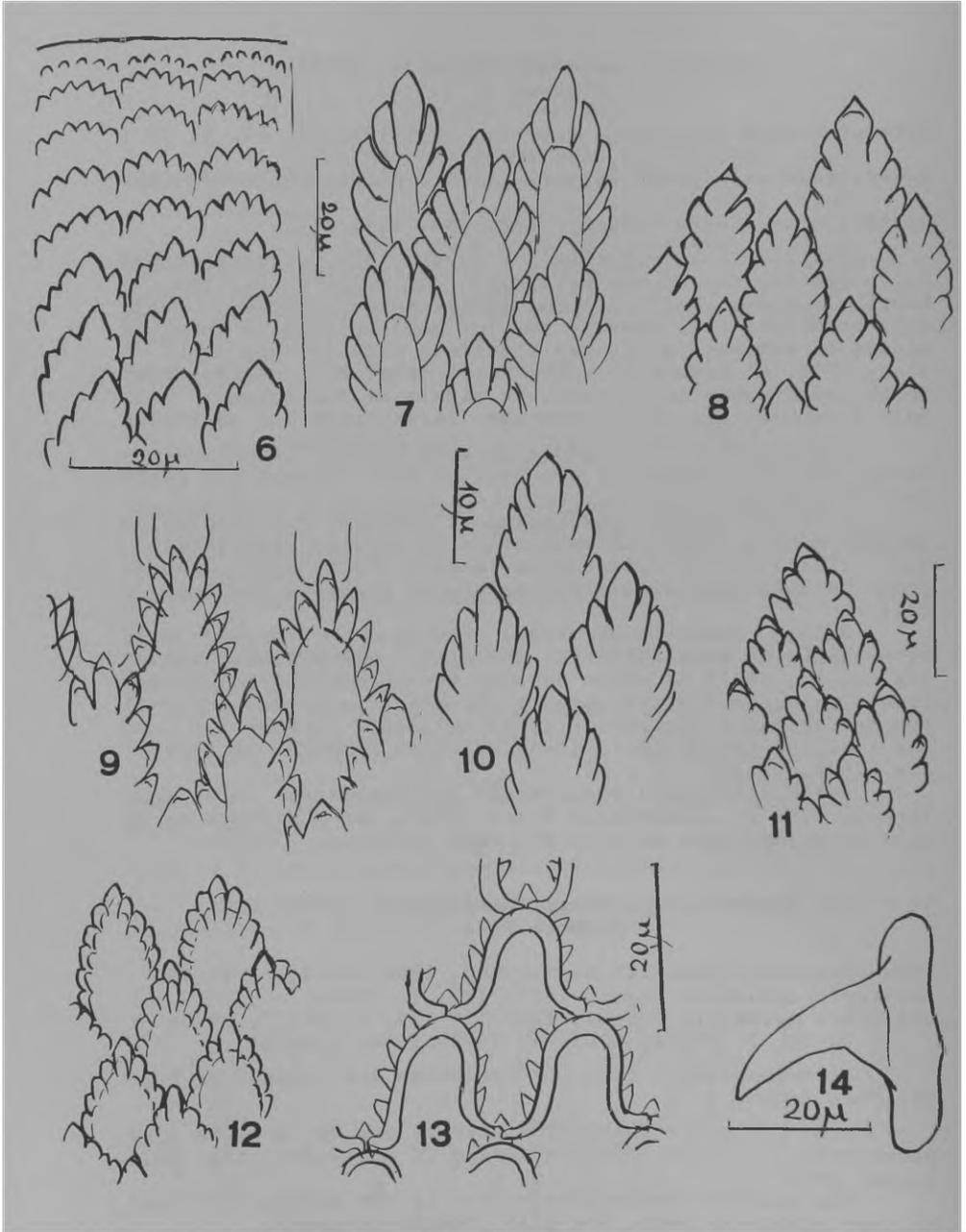
Distribution. - From the Caribbean and Curaçao to Brazil, São Paulo.

Description. - The living animals are up to 25 mm long, preserved, in life the mantle is dirty red, the sole bluish green.

The slightly reticulate mantle is not notched in front. No foot gland was seen. The gill rachis is smooth.

The shell is up to 6 mm long and 3 mm wide, with distinct growth lines. It is located near the anterior end of its cavity. There are no spicules.

The jaw platelets bear 3-5 longish denticles on either side of their free margin (Fig. 7-12) Number and size vary



Figures 6-14 - *Berthella agassizii*. 6, anterior border of jaw plate; 7-13, jaw platelets; 7, old and dry; 8-9, young; 10-11, from São Paulo; 12, from Colombia; 13, under side; 14, radular tooth.

greatly in one and the same specimen. The radular formula is 44-49 x 42-52.0.42-52. The teeth are all very short and broadly hook-shaped (Fig. 14).

The anal opening lies in front of the gill membrane. The gonopores are close together (Fig. 16) in front of the gill. The spermoviduct widens to serve as ampulla (a), and then divides. The oviduct (u) enters the albumen and mucus gland mass (w), which opens independent from the vagina (v) into the common atrium. The sperm duct (e) is in the greater part of its course lined with prostatic cells (x) and receives a tubular accessory prostate (b) near its entrance into the short, muscular penis (p). The latter is protruded in MacFarland's figure 54, retracted in the present Fig. 16. The vagina leaves the common atrium and goes to the stalked spermatheca (t) and the spermatocyst (s), which has rings of black pigment. Then a short uterine duct opens into the female gland mass.

Bandel described the egg mass (1976:103, f. 16)

Discussion. - *Berthella agassizii* differs clearly from *B. patagonica* d'Orbigny, 1837, redescribed by Bergh (1898a), by its smooth nervous system. This was figured by Bergh (pl. 29, f. 12) for *patagonica* with knobby ganglia like *Oscantius membranaceus*, and quite smooth in MacFarland's figure 55 of *agassizii*. Bergh did not figure the under side of the base of radular teeth of *patagonica*, so the broad upper end of the base in *agassizii* might be a further difference to *patagonica*.

Berthella tupala Marcus, 1957
Figures 17-19

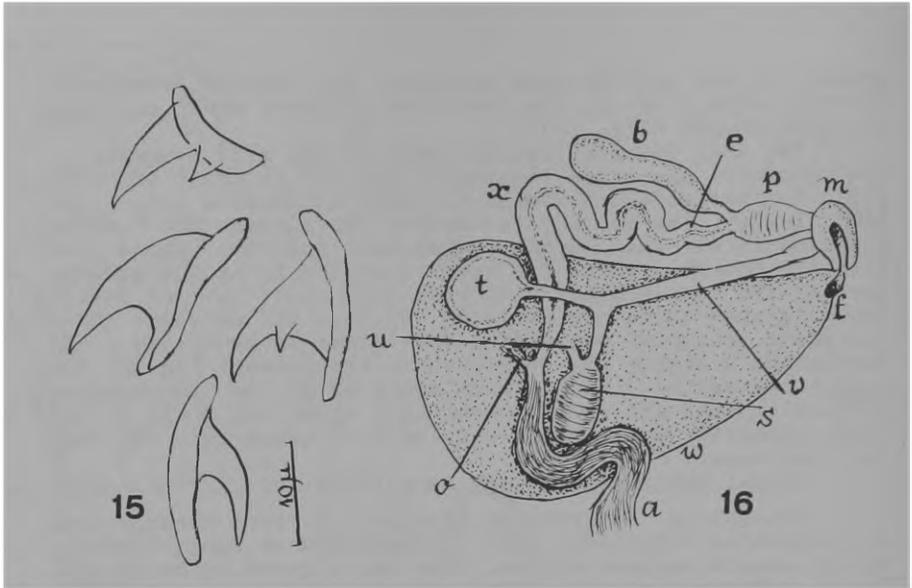
Berthella tupala Marcus, 1957a:416-419, f. 58-69; ;1967 : 43; 1970:54, f. 102
not *Berthella tupala* Bertsch, 1975:124-126, f. 1-7

Distribution. - From Brazil, coast of São Paulo, to Curaçao, Puerto Rico, and Florida.

Description. - A living specimen was 17 mm long; preserved ones are 4.5 - 7 mm. The mantle was light ochre with bright white marks and contained stellate spicules. The gill was about one fourth of the preserved body length. It has about 12 pinnules on each side of the smooth rachis. The shell is 5 mm long and covers all the inner organs.

The jaw platelets have 5-6 more or less blunt denticles on either side and a longitudinal mark between them (Fig. 17). The radular formula is 55 x 50.0.50. The innermost 1-3 teeth have a small basal denticle. They are hook-shaped and get erect farther outward, and some have a small secondary cusp (Fig. 18).

The animal from Panama (Bertsch, 1975) has the same colour pattern as ours, but the jaw platelets without denticles and the radula teeth are so different from the original description, that it certainly is a different species. The reproductive organs (Fig. 19) were described (1957a:418, f. 69).



Figures 15, 16 - *Berthella agassizii*. 15, teeth of specimen from São Paulo; 16, diagram of reproductive organs: a - ampulla of spermoviduct; b, accessory prostate; e, efferent duct; f, nidamental opening; m, male opening; o, oviduct; p, penis; s, spermatocyst; t, spermatheca; u, uterine duct; v, vagina; w, female gland mass; x, prostatic part of efferent duct.

Berthella tamiu, spec. nov.
Figures 20-24

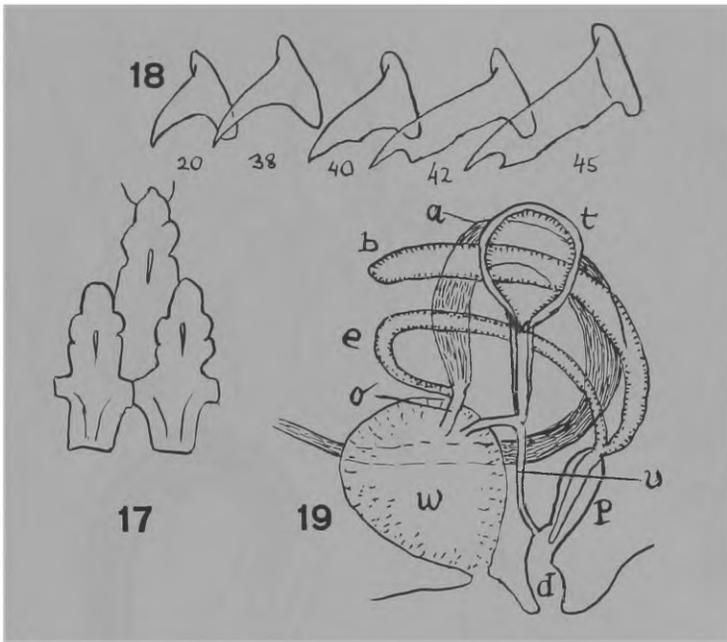
Material. - John Elliott Pillsbury Cruise 6701, P 518, 21° 05' N, 86° 23' W, 146-265 m; May 4, 1967; two specimens.

Description. - The specimens are 9 and 10 mm long, 6 and 6.5 mm broad and 2.5 mm thick. The brownish mantle is almost smooth with very slight tubercles. The gill has a smooth rachis and 26 pairs of alternate pinnules. The anal opening lies slightly in front over the gill membrane. No spicules are preserved. In one of the specimens there were traces of a conchinous shell in the middle of the body.

The jaw platelets are of the berthelline type and have no denticles (Fig. 21, 22). They are 65-75 μ m long. In their middle they have a small refractive circling, not present in the young ones. The anterior pointed half is narrow, 16 μ m, the posterior square one is about 22 μ m broad.

The radula measures 2 mm long and 1 mm broad. There are about 72 rows of 50 strong, hook-shaped teeth per half-row without any denticles (Fig. 23). The genital openings have a ring-fold but no flaps. Part of the male atrium is extended around the slender protruded penis (Fig. 24).

Discussion. - The species belongs to *Berthella* due to the smooth gill rachis and the radular teeth without denti-



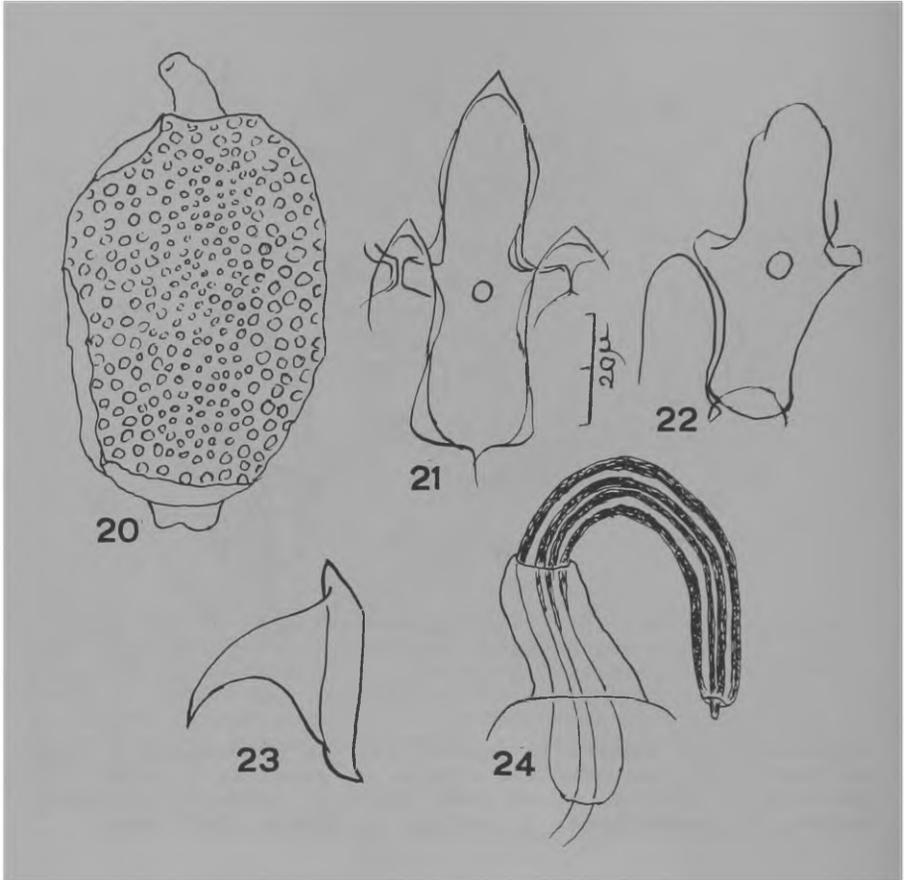
Figures 17-19 - *Berthella tupala*. 17, jaw platelets; 18 radular teeth; 19, reproductive organs: a, ampulla; b, accessory prostate; c, atrium; e, efferent duct; o, oviduct; s, spermatocyst; t, spermatheca; v, vagina; w, female gland mass.

cles. By the jaw platelets of berthelline type it is separated from the Western Atlantic *Berthella agassizii* MacFarland, 1909, (Marcus, 1957b, f. 39) and from *Berthella tupala* Marcus (1957a, fig. 65), whose platelets are of the pleurobranchine type. The platelets are similar to those of *Berthella kaniae* (Sphon, 1972) from the Pacific side of Panama, but those were evidently drawn from the under side, and their spot in the middle (fig. 5) is quite different from the circlet of *B. tamiu*. Also *Berthella ocellata* Delle Chiaje, 1828, from the Mediterranean has Berthelline jaw plates, but their tip is different (Vayssière, 1898, f. 93)
Tamiu is the name of an Egyptian cat.

Berthellina Gardiner, 1936

Synonym *Berthella* Vayssière, 1896

Berthellinae with forward denticles of the jaw platelets, and with one to more denticles on the radular teeth.
Type species *Berthellina engeli* Gardiner, 1936:198



Figures 20-24 - *Berthella tamiu*. 20, preserved specimen; 21, young jaw platelet; 22, old jaw platelet; 23, radular tooth; 24, protruded penis.

Berthellina quadridens (Mörch, 1863)
Figures 25-27

Berthella quadridens Mörch, 1863:29-31.

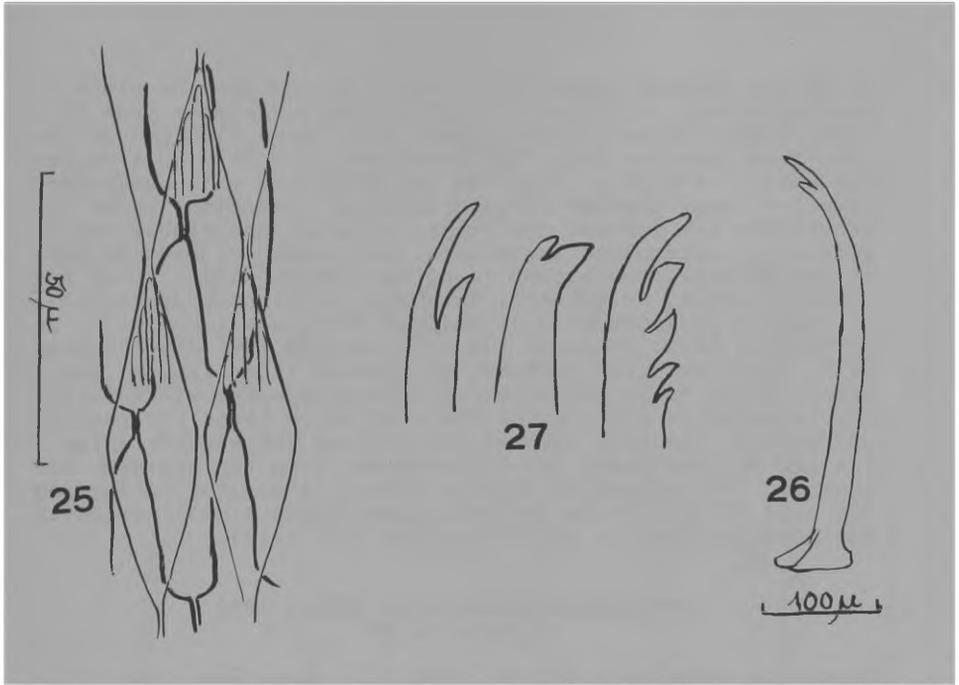
Pleurobranchus quadridens Bergh, 1898:136-138, pl. 10, f. 12-19.

Berthellina quadridens Marcus, 1962:463-466, f. 9-13; 1967 : 43, f. 53; p. 163; 1970a:53; Marcus & Hughes, 1974 : 516, f. 33, 34. Keen, 1971:812, pl.19, f. 5; Thompson, 1977:105, f. 11, 12a, b.

Gymnotoplas quadridens Abbott, 1974:347

non *Berthellina quadridens* Marcus, 1969:12, f. 4; and Marcus, 1976:132; it is *B. circularis* Mörch, 1863.

Material. - One slide with jaw plates and radula from Barbados.



Figures 25-27 - *Berthellina quadridens*. 25, jaw platelets ; 26, radular tooth; 27, tips of radular teeth.

Distribution. - In the Caribbean area from Jamaica, St. Thomas (type locality) and Barbados. It was also recorded from the Pacific coast of Panama (Marcus, 1967:163). The specimen from Recife, Brazil, was misclassified (1969:12); it now turned out to be *B. circularis* Mörch, 1863.

Description. - The living animals were 30 (Bergh) to 45 mm (Thompson) long. The mantle is covered with densely distributed papillae of 0.2 mm diameter, interspersed with larger ones, 0.4 mm in diameter; these are up to 0.8 mm high. The shell measures 4.5-6.2 x 2.75 mm. It lies near the middle of the body, slanting towards the left side. The narrow jaw platelets have on their tip up to 8 long and slender denticles directed forward; their base is 66 μ m long (Fig. 25). They have no refractive circling. The radula has 70 x 150.0. 150 teeth to 98 x 300.0. 300 in larger specimens. Their length is 140-350 μ m. They have 1-4 small denticles immediately behind the tip (Fig. 27), most have only one. Bandel (1976:102, f. 15) described the egg mass.

Discussion. - It is useless to give a detailed anatomical description, as the species was frequently confounded with *B. circularis*. Bergh also had material of *circularis* among his *quadridens*, as he found 7 denticles on the radular teeth. In my f

10 of our Florida paper (1962:146) I united the jaw platelets with many denticles of *Berthellina quadridens* from St John, Virgin Islands, Europa Bay, with those with few denticles from Lameshur Bay. The former are evidently *B. circularis* Mörch, 1863 (Fig. 31) The jaw platelets of *quadridens* have 3-8 long, slender forward directed denticles, those of *circularis* 1-4 forward denticles, of which the middle one is generally larger than the others. The number of radular denticles differs from author to author (Mörch, 1863: three denticles; Marcus, 1976: five; Thompson, 1977: four denticles). *B. amarillia*, synonym of *circularis* Mörch was given with 10 by Mattox, 1953. Thompson (1977:106) doubts the distinctness of *B. quadridens* and presumes *B. citrina* (Rüppell & Leuckart, 1828) to be the only, world-wide species of *Berthellina*. I prefer to distinguish the species by their specific characters. The type species *engeli* from the eastern Atlantic and Mediterranean was not recorded from the western Atlantic. Its subspecies *ilisima* Marcus (1967:160, f. 18) from the Gulf of California and Galapagos (Sphon & Mulliner, 1972) was accorded species degree by Keen (1971:812).

Berthellina circularis Mörch, 1863
Figures 28-33

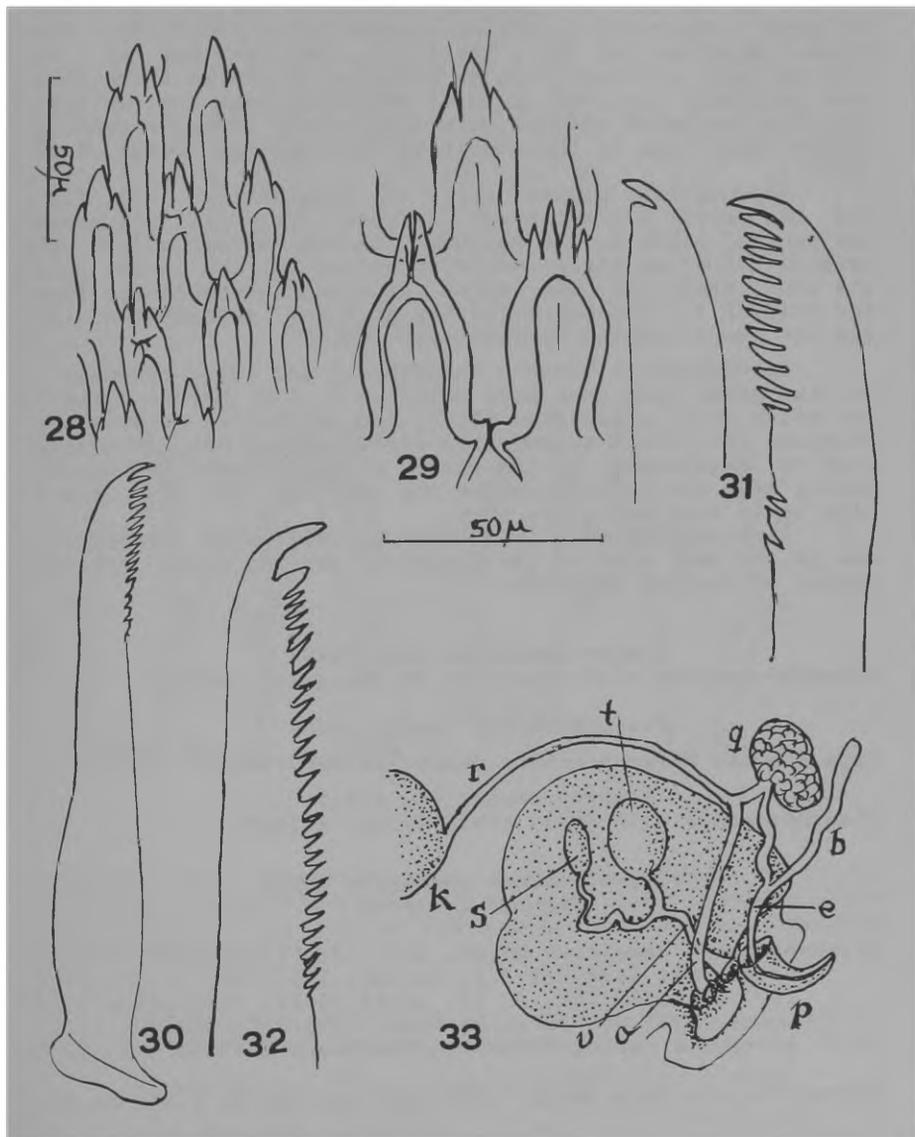
- Berthella circularis* (Mörch, 1863:31). Vayssière, 1898:277.
Pleurobranchus circularis Pilsbry, 1896:200; Bergh, 1897:134-135, pl. 10, f. 31-37.
Berthellina circularis E. & E. Marcus, 1962:465.
synonyms *Pleurobranchus (Oscanius) amarillius* Mattox, 1953 : 110, figs. 1-10.
Berthellina amarillia Marcus, 1957b:21; 1962:466; 1967:163 ; 1969:12
Berthellina quadridens Ev. Marcus, 1962: f. 10, part.; 1976: 132-133.
Pleurobranchus amarillius syn. to *Berthellina quadridens* Thompson, 1977:105.

Material. - Brazil, Recife, one specimen (Marcus, 1972) of which jaw plates and radula were preserved.

Distribution. - St. Thomas, Virgin Islands, type locality; Jamaica; St. John, Lameshur Bay (not Europa Bay); Puer to Rico (Mattox, 1953); Brazil, Recife.

The description of the animal is shortened from Mattox' description (1953) The living animals were up to 37.5 mm long, the preserved one 36 mm. The colour was a bright yellowish orange. The preserved specimen was "museum-brown" (term used by Libbie Hyman). The mantle is covered with microscopic papillae. The shell is small, about one third of the animal's length, located about one fifth from the posterior end of the dorsum. The gill rhachis is smooth; the up to 22 pinules on either side arise from swollen areas of the rhachis. The anal opening is located at the end of the gill membrane, at the beginning of the free third of the gill.

The jaw platelets (Fig. 28) are of the Berthelline type, of narrow oval shape with 1-5 slender denticles pointing



Figures 28-33 - *Berthellina circularis*. 28, 29, jaw platelets; 30, radular tooth; 31-32, tips of radular teeth; 33, reproductive organs b, accessory prostate; d, atrium; e, efferent duct; f, nidamental aperture; k, ovotestis; m, male aperture; o, oviduct; p, penis; q, free prostate; r, spermoviduct; s, spermatocyst; t, spermatheca; v, vagina; w, female gland mass.

forward on the tip. The radular formula is 130 x 200.0.200 in Bergh's description, Mattox counted 180 x 200.0.200. The present specimen has 140 x 190.0.190. The teeth are up to 0.35 mm long and flat, 0.21 mm broad and 0.004 mm thick. They have generally two, but up to 25 denticles near the tip (Fig. 32). The innermost and the outermost have a stronger denticulation than those in the middle of the half-row (Bergh, f. 33-37)

Reproductive organs, (Fig. 33, from Mattox, 1953, fig. 19) The Bourne's gland opens in front of the gill and above the genital papilla. The male duct passes through a free prostate (q), receives the accessory prostate (b) and enters into the short penis (p) The vagina (v) opens independently from the oviduct (o) and bears the big globular spermatheca (t) and the small longish spermatocyst (s)

Discussion. - Mörch's description was quite incomplete, but Bergh gave some more details. E. & E. Marcus compared these to *B. quadridens* Mörch, and maintained *circularis*. Thompson (1977:105) synonymized *circularis* as well as *amarillius* to *quadridens*. In the radula of *quadridens* the teeth mostly have one denticle under the tip (Fig. 26) and those with up to four are quite rare.

I synonymize *amarillia* (Mattox, 1953) with *circularis* due to the very similar jaw platelets and the much greater number of radular denticles.

Pleurobranchinae Burn, 1962

Pleurobranchidae with tubercles on the gill rachis

Pleurobranchus Cuvier, 1804

Type species *Pleurobranchus peroni* Cuvier. 1805

Pleurobranchus (s. str.)

Pleurobranchus with small shell lying in front.

Pleurobranchus areolatus Mörch

Figures 1, 34-43

Pleurobranchus areolatus Mörch, 1863:28; Pilsbry, 1896:199; Vayssière, 1898:338-339; Marcus, 1962:466, f. 14, 15; 1963:25; 1967:163, f. 19; 1976a:16-18; discussion); Edmunds, 1968:85, f. 2, 3; Keen, 1971:811, pl. 19, f. 6; Bertsch & Smith, 1973:169; Thompson, 1977:108, f. 12, c, d, f. 13, a, b.

Oscaniella areolata Bergh, 1897:111-113, pl. 9, f. 31-41, pl. 10, f. 34.

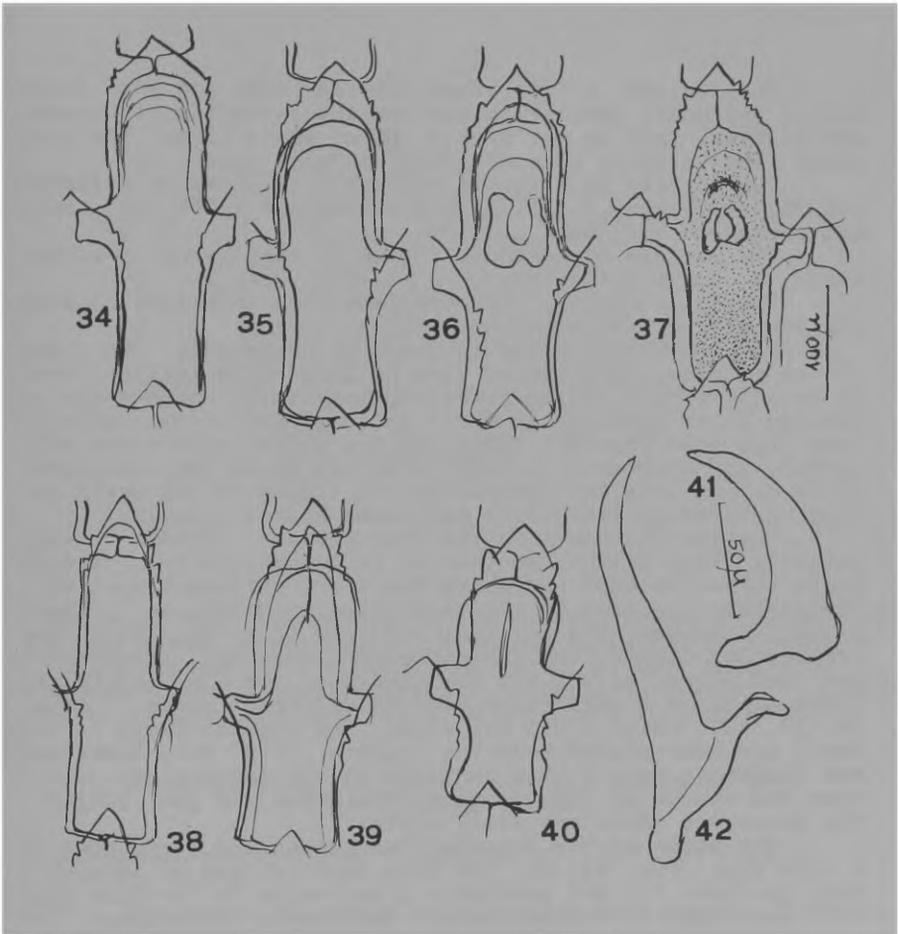
Synonym. - *Pleurobranchus digueti* Rochebrune, 1895:240; MacFarland, 1966:75, pl. 14, f. 1-6, pl. 16, f. 10, 11.

Pleurobranchus crossei Vayssière, 1896:353; 1898:332-334, f. 148-154.

Pleurobranchus (Susania) atlanticus Abbott, 1949:73, pl. 5.

Susania gardineri White, 1952:106, text-f. 2-5, pl. 6, f. 1.

Material. - Brazil, 02° 22' S, 44° 28' W, 35 m, M. Kempf leg. 1973; and some old slides.



Figures 34-42 - *Pleurobranchus* (s.str.) *areolatus*. 33-36, young to old jaw platelets; 37-40, same, other specimen from same locality; 41, radular tooth near rachis; 42, largest radular tooth.

Distribution. - From Florida to Cabo Frio; Panama; East Pacific, Gulf of California; Galapagos; East Atlantic, Ghana.

Description. - The living animals attain 120 mm in length. On a slide from Cabo Frio (Marc Kempf phot.) of a living 85 mm specimen (preserved, 65 mm) the mantle is covered with tubercles of different sizes and colours, giving it a lively pattern, red to crimson in the mid-line, surrounded by some larger dark knobs between groups of small white ones and towards the border dense brown spots.

In the centre of the large tubercles there is a glandular pore.

The gill is red, and the upper side of the foot red sprinkled with white.

The colour slides from Florida (Pat and Rog Armes phot.) are quite similar in pattern and intensity of colours, but lighter. They do not have a net of white lines. The specimen from Colombia (Bandel phot.) is much paler.

The pattern is a little different in Thompson's figure 13a (1977) Bergh (1897:111) and MacFarland (1966:76) only had preserved specimens.

The pattern of Edmunds' figure of the living animal (1968, f. 2) is different.

The gill rachis is tuberculate. The anus lies over the end of the gill membrane.

The small shell lies in front of the middle. In the 120 mm specimen it attained 9 mm in length, in smaller ones it is 1/10 to 1/5 of the preserved length; in Mörch's contracted 21 mm specimen it was 6 mm long. In the two animals from Cabo Frio (Marcus, 1976a:16) the shells were quite different, one shattered; in the preserved 85 mm long specimen, it is 6.5 mm long and located in the middle of the shell cavity. Only Bergh (1897:112) mentioned scarce spicules.

The jaw platelets in the four present slides vary slightly (Fig. 34-40), so that it is impossible to decide where variation ends and where there are different species. The platelets differ in size and shape according to their place in the jaw; the anterior old ones (Fig. 36, 40) are smaller and denser than the posterior large and transparent new ones (Fig. 34, 38). In the middle of the old platelets there is often a refractive body of different shape (Fig. 36, 37, 40), which I did not study. The radular teeth are small and hook-shaped near the rachis (Fig. 41). Sometimes the innermost bear a tiny denticle on the outer side. Towards the middle of the row they straighten and get longer. The outermost teeth are small again.

The pores of the reproductive organs are surrounded by a wide flap (Fig. 43, n). The male duct (e) has an independent prostate (q) and prostatic gland cells in the male duct (x), and a short, not cuticular, penis (p). The oviduct (o) passes over the female gland mass (w) and unites with the vagina (v) near the spermateca (t) and spermatocyst (s). It opens together with the albumen and mucus glands.

Remarks. - The unusual thickening in the jaw platelets that Thompson (1977, f. 12 d) considered as diagnostic, occurs in several species, but not in all specimens and in all platelets. It was not drawn by Bergh (1897, pl. 9, f. 34) nor by Edmunds (1968, f. 2A) for *areolatus*; Bergh did figure it for *Susania testudinaria* (1897, pl. 9, f. 7); Vayssière (1898, f. 39 and f. 93) showed it in *Berthellina edwardsi* and *B. ocellata*.

In the descriptions of the animals classified as, or synonymized to *areolatus*, there are contradictions, e.g., the shell lies in front (Bergh, 1897:111; Bertsch & Smith: 172; White, 1952:107, *gardineri*), or in the middle (Vayssière, 1898:345, *digueti*). The synonymy of the latter is justified by Bertsch & Smith, 1973. Bergh (1897:111) said: no prostate for *areolatus*, but MacFarland (1966:81, pl. 16, fig. 10) and Marcus (1967:165 f. 19) gave a large prostate.

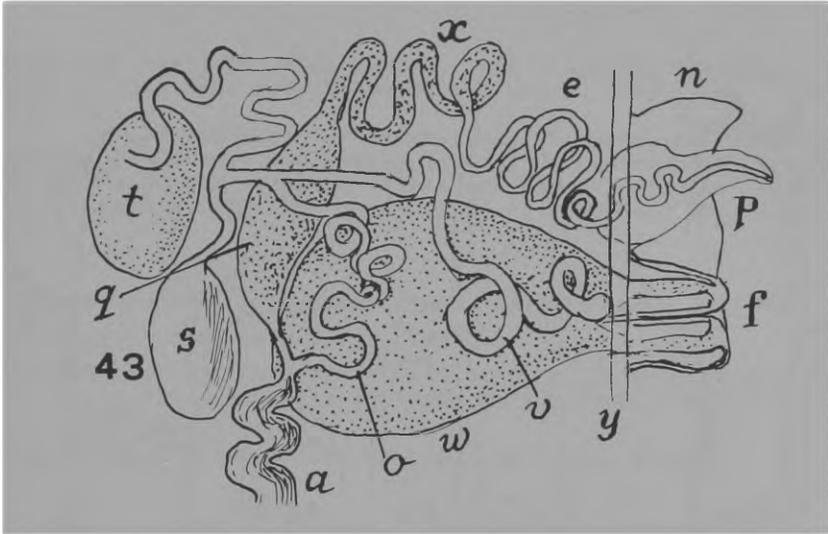


Figure 43 - *Pleurobranchus* (s. str.) *areolatus*. Reproductive organs (from Marcus, 1967) a, ampulla; e, efferent duct; f, female aperture; o, oviduct; p, penis; q, free prostate; s, spermatocyst; t, spermatheca; v, vagina; w, female gland mass; x, prostatic part of efferent duct; y, body wall.

Pleurobranchus (s. str.) *evelinae* Thompson, 1967
Figures 44-50

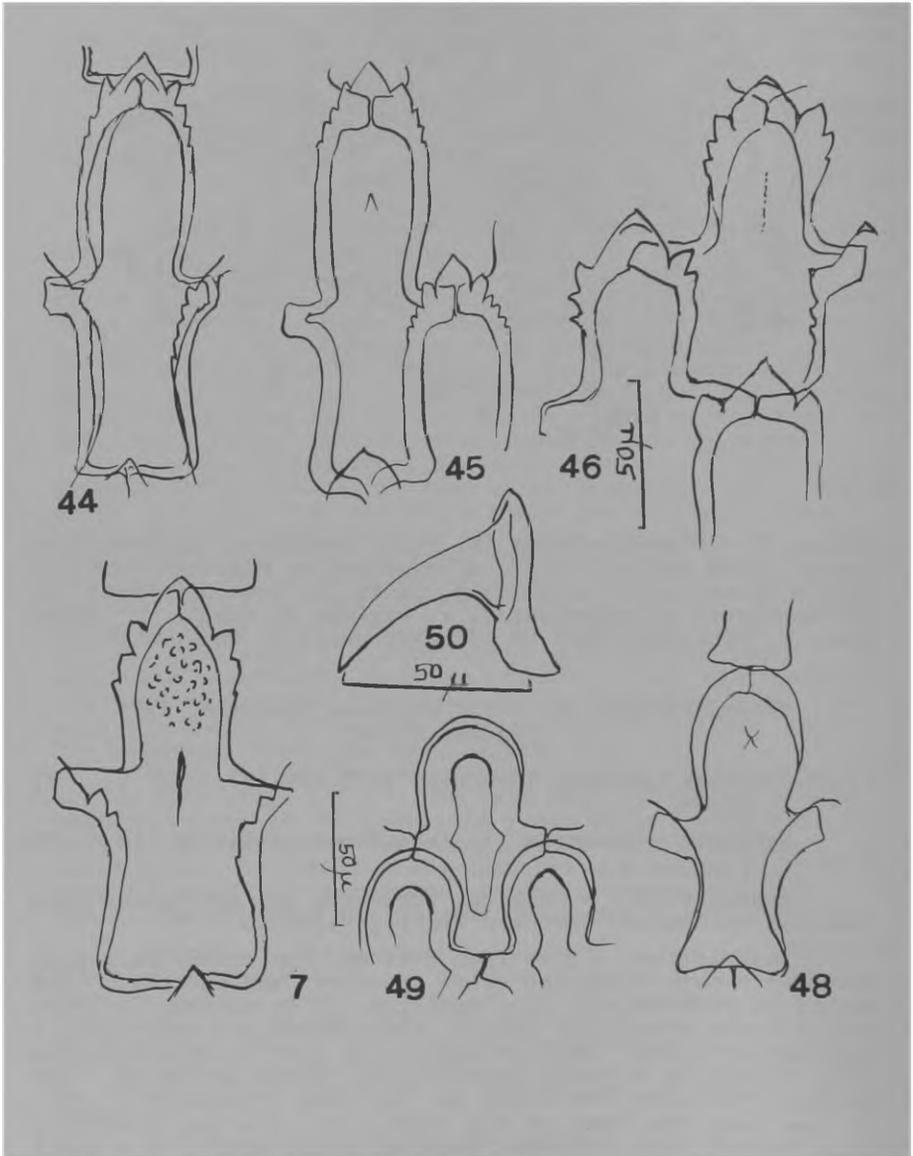
Pleurobranchus evelinae Thompson, 1977:108-110, f.12 e, f, f. 13c-e.

Synonym. - *Oscanius* (?) *testudinarius* Marcus, 1970:939, f.30.

Distribution. - Jamaica, Discovery Bay and Maiden Cay, numerous specimens. Northern Brazil, Maranhao.

Description. - Size from 6-60 mm. The colour is a pale brown with dark brown and white speckles and patches. The mantle is covered with tiny mamillae. It is notched in front and slightly emarginate behind. Rhinophores and oral tentacles are inrolled. The fore end of the foot is bilabiate. The gill rachis is strongly tuberculated, there are up to 22 pairs of pinnules. The shell is 5 mm long (Thompson, f.13d). It lies near the front on the right side. The jaw platelets (Fig. 44-49) have a central terminal point with 1 to 4 denticles on either side. The radular formula is 130 x 223.0.223. The teeth have simple hooks lacking sub-denticles (Fig. 50). The extreme marginal ones are more slender and their basal plate is less substantial than in the middle of the row. The penis has a flap-like ridge on its anterior face and a slender recurved tip.

Remarks. - Thompson was right to separate the present species from my *Oscanius testudinarius*, (now *P. (S.) emys*) in



Figures 44-50 - *Pleurobranchus* (s. str.) *evelinae*. 44-49, jaw platelets; 44, young; 45-47, older; 48, very old; 49, under side; 50, radular tooth.

which the shell is lying behind. This character distinguishes it also from *Susania gardineri* White, 1952, from Dry Tortugas.

In old platelets of *P. evelinae* Thompson the posterior part is relatively wider than in most *Pleurobranchus*, but the sides of the young platelets are almost straight from tip to bottom (Fig. 44) contrary to *P. (Susania) emys* (Fig 65)

Pleurobranchus (Oscanius) (Gray, 1847) (Leach, 1819;MS)

Synonym *Susania* Bergh, 1898:62

Pleurobranchus with large shell covering the greater part of the body; a single denticle on the inner teeth of the radula.

Type species *Oscanius membranaceus* (Montagu, 1815)

Pleurobranchus (Oscanius) membranaceus (Montagu, 1815)
Figures 51-56

Oscanius membranaceus Mazzarelli, 1891:240, f 5; Bergh, 1897: 66-81 (synonyms), pl. 4 f. 18-31, pl. 5 f. 1-18; 1899: 22, pl. 2 f. 24-34; Vayssi re, 1898:382-388, f. 165 - 176, 188-189.

Pleurobranchus (Oscanius) membranaceus Odhner, 1926:23; Gardiner, 1936:195; Willan, 1978:342.

Pleurobranchus membranaceus Thompson & Slinn, 1959:507

Synonyms. - *Pleurobranchus tuberculatus* Meckel, 1808 ; Pruvot-Fol, 1954:220; non *Oscanius tuberculatus* Mazzarelli , 1891:238, f. 4.

Gymnotoplax barashi d.B.-R. Marcus, 1977:418, text-f 1-7, pl. 1.

I do not consider all the synonyms listed in the literature as certain, and do not mention them.

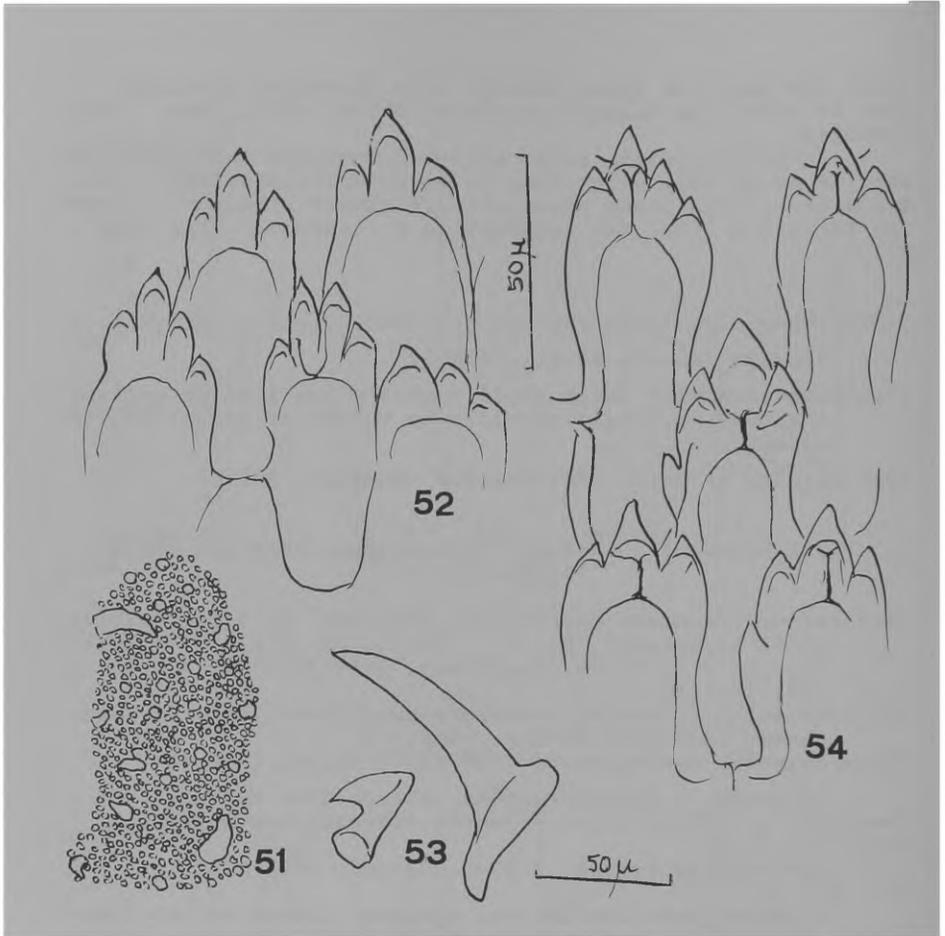
Material. - West Atlantic, off Delaware Bay, 38^o 35'N, 73^o 13' W, 400 m; 10.10.1881. Four specimens, "paratypes" from the vial of *Koonsia obesa* Verrill, 1882, Smithsonian USNM 34217; Nudi-collection, alcohol n^o 6484.

Description. - The present preserved specimens are 18-50 mm long. The largest recorded alive measured 120 mm (Vaysi re, 1898) The colour is museum-greyish brown. In one specimen a little dark pigment was preserved on the back of the foot. The mantle has longish elevations separated by furrows and is covered with very small tubercles; some larger ones reach 2 mm in diameter. (Fig. 51) There are many radial brown spicules with about five spines in all directions in the mantle. Where a spine touches the mantle epithelium, it lifts the skin to form a small papilla.

The grooved sides of the velum are much thickened and stand out over the front like ears.

The shell is 20-43 mm long, only the conchinous part is preserved; it shows growth lines.

The nervous system is knobby.

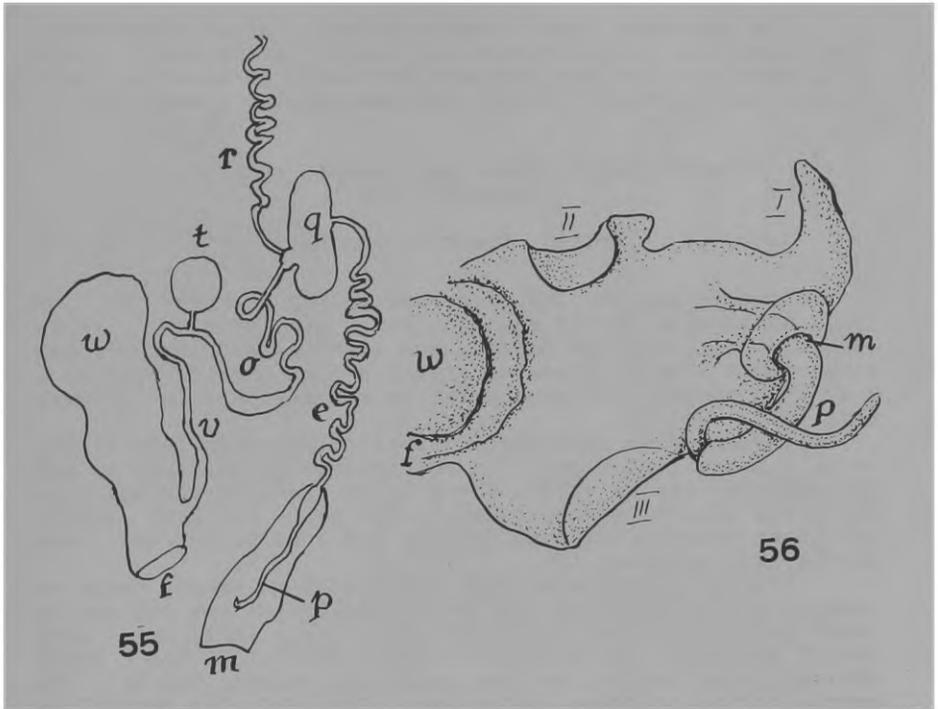


Figures 51-54. *Pleurobranchus (Oscanius) membranaceus*. 51, mantle surface; 52, 53, jaw platelets from Marthas Vineyard; 54, radular teeth.

The oral canal is very long (Thompson & Slinn, 1959, fig. 6), and the pharynx rather small, 4 mm long. The jaw platelets are of intermediate type. They have a large tip and one to three broad denticles on either side, almost as large as the tip and directed forward (Fig. 52, 53). They are often asymmetrical.

The radular teeth are hook-shaped near the rachis and straighten outwards. The innermost have a single basal denticle on the outer side (Fig. 54). Their length is 52 μ m near the rachis, 100 μ m in the middle of the half-row, and 50 μ m on the outer side. Their basal plates are large (60 μ m).

There are three genital pores (Vayssière, 1898, f.176), surrounded by three flaps (Fig. 56). The male atrium is protruded from the pore, and the membranous, 20 mm long, thin penis stands out. The efferent duct winds slightly in the pe



Figures 55, 56 - *Pleurobranchus (Oscanius) membranaceus*, reproductive organs. 55, from Mattox, 1953; 56, from Delaware Bay.

nis, and inwards it coils strongly (Fig. 55)

Of the inner ducts I could only follow the male duct to near its separation from the hermaphrodite duct, where it passes through a free prostate. Behind the flaps follows the large female opening, from which in the present specimen the female gland mass is extruded (Fig. 56, w)

Discussion. - The present specimens have all characters of *Oscanius membranaceus*. As a number of opisthobranch species occur on both sides of the Atlantic, I consider my material as *membranaceus*. My classification of *Gymnotoplax barashi* (1977:418-421) from the Mediterranean was based upon the open mantle, which showed the shell in the two specimens I had; this was the typical character of *Gymnotoplax*. Willan (1978:339-343) studied the type specimen of *Gymnotoplax pleurobranchus americanus* Verrill, 1885, and found that its notum was mutilated, and its other characters correspond to *Berthella*. My specimens with a knobby gill rachis are pleurobranchine. Their large shell and their jaw platelets belong to *Oscanius*, as do the present ones, and there is no specific difference.

The specimens from Colombia which I called *Pleurobranchus (Oscanius) testudinarius* (1976:133) have a small shell lying near the hind end and must be placed in *Susania*. Their unusual jaw platelets justify the new species *S. emys* (Fig. 64-66)

Pleurobranchus (Oscanius) iouspi, spec. nov.
Figures 57-61

Material. - Brazil, coast of São Paulo, 24° 47' S, 45° 15' W.

Description. - The preserved animal measured 60 mm long, 40 mm wide and 25 mm high. It is greyish with small tubercles all over the mantle, and eight protruding whitish rings about 7 mm in diameter around a flat whitish papilla, 4 mm in diameter, and some a little smaller ones in between (Fig. 57)

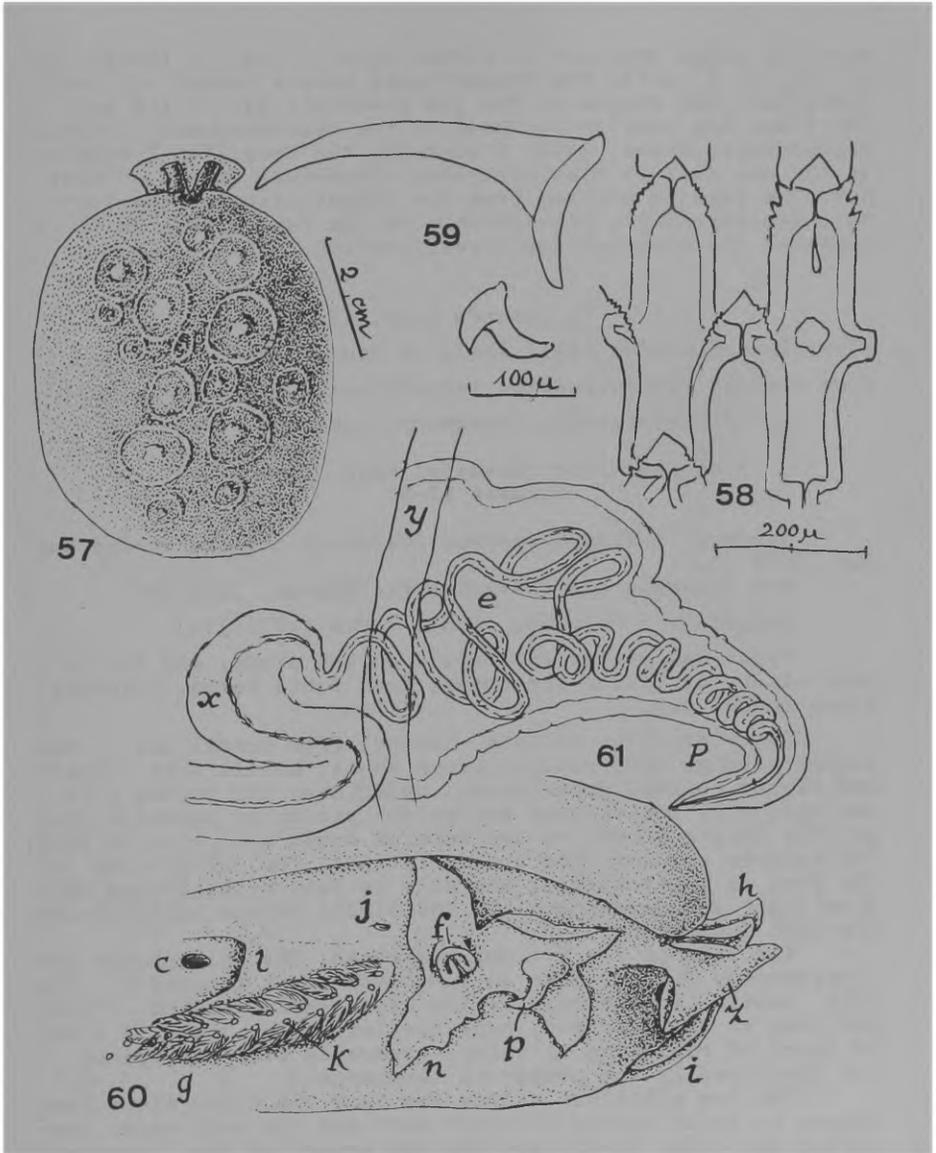
The anterior foot border is bilabiate (Fig. 60, i). There is a large foot gland. The rhinophores (tentacles, h) and the veil (z) are as usual. There is no trace of a shell in the shell cavity, nor spicules in the skin. The gill rachis is almost smooth. The anal opening (c) lies behind the end of the gill membrane (l)

The jaw plates are 15 mm long and 9 mm broad, their elements, 0.4 mm long and 0.09 mm broad. Beside the tip are several small denticles (Fig. 58) The radula is 15 mm long and 15 mm broad. Its formula is 100 x 250.0.250. The teeth are simple unicuspid, at the rachis 65 µm long and in the middle of the half-row 350 µm long (Fig. 59) The genital apertures are surrounded by three large flaps (n).

I did not succeed to disentangle the tightly winding genital ducts. The male duct (Fig. 61) has a long stretch with high prostatic epithelium (x), 1 mm in diameter, and then narrows to 0.25-0.3 mm, always looping (e), and then it spirals into the conical smooth, muscular penis (p), protruding from the male aperture about 5 mm; at its base it is 2.5 mm thick.

The recognizable contents of the stomach were a piece of a sponge with asters like *Chondrilla*, a stem of a bryozoan, *Cellaria* spec., and several others, a 4 mm long molluscan shell, and a 7.5 mm gastropod, the arm of an ophiurid, a scale of a fish, and some fragments, probably of tunicates.

Discussion. - In the preserved specimen it was not easy to decide whether the gill rachis has tubercles or not. It was not quite smooth. Moreover, the similarity of the mantle sculpture with that of the preserved Malayan *Pleurobranchus (Oscanius) weberi* Bergh, 1905 (p.53, pl. 2, fig. 1) with whitish rings and central papillae (p. 53) and the more pleurobranchid jaw platelets (pl. 11, fig. 1) made me decide for *Oscanius*. The radular formula of *weberi*, 140 x 280.0.280 in an 8.5 cm long preserved specimen and 100 x 200.0.200 in a 7 cm long one correspond. However, the jaw platelets of *weberi*



Figures 57-61 - *Pleurobranchus iouspi*. 57, preserved specimen; 58, jaw platelets; 59, radular teeth; 60, right side with male and female apertures and gill with tubercles (k) c, anus; e, efferent duct; f, female aperture; g, gill; h, rhizophore; i, anterior foot border; j, pore of Bourne's gland; l, gill membrane; n, flap; p, penis; x, prostatic part of efferent duct; y, body wall.

have one large denticle on either side of the tip (Bergh, 1905, pl. 11, f. 1) while the present ones have a number of small denticles. The shapes of the jaw platelets and of the genital flaps are similar to those of the Mediterranean *Susania testudinaria* Adams, 1858. I consider the Brazilian species as new and call it *Pleurobranchus (Oscanius) iouspi*, spec. nov. The name is derived from the abbreviation of the Instituto Oceanográfico, Universidade de São Paulo, from which I received the material for classification.

Susania Gray, 1857

Pleurobranchus with small shell in hind part.

Type species *Pleurobranchus testudinarius* Cantraine, 1840;

Pleurobranchus (Susania) Vayssière, 1898

Pleurobranchus (Susania) emys, spec. nov.

Figures 62-66

Synonym. - *Pleurobranchus (Oscanius) testudinarius* Marcus, 1976:133.

Not *Oscanius (?) testudinarius* Marcus, 1970:939

Material. - Colombia, Santa Marta (1976:133).

Type: Jaw plates and radula on one slide, and two colour slides of living specimens, from Santa Marta, Colombia, Klaus Bandel leg.

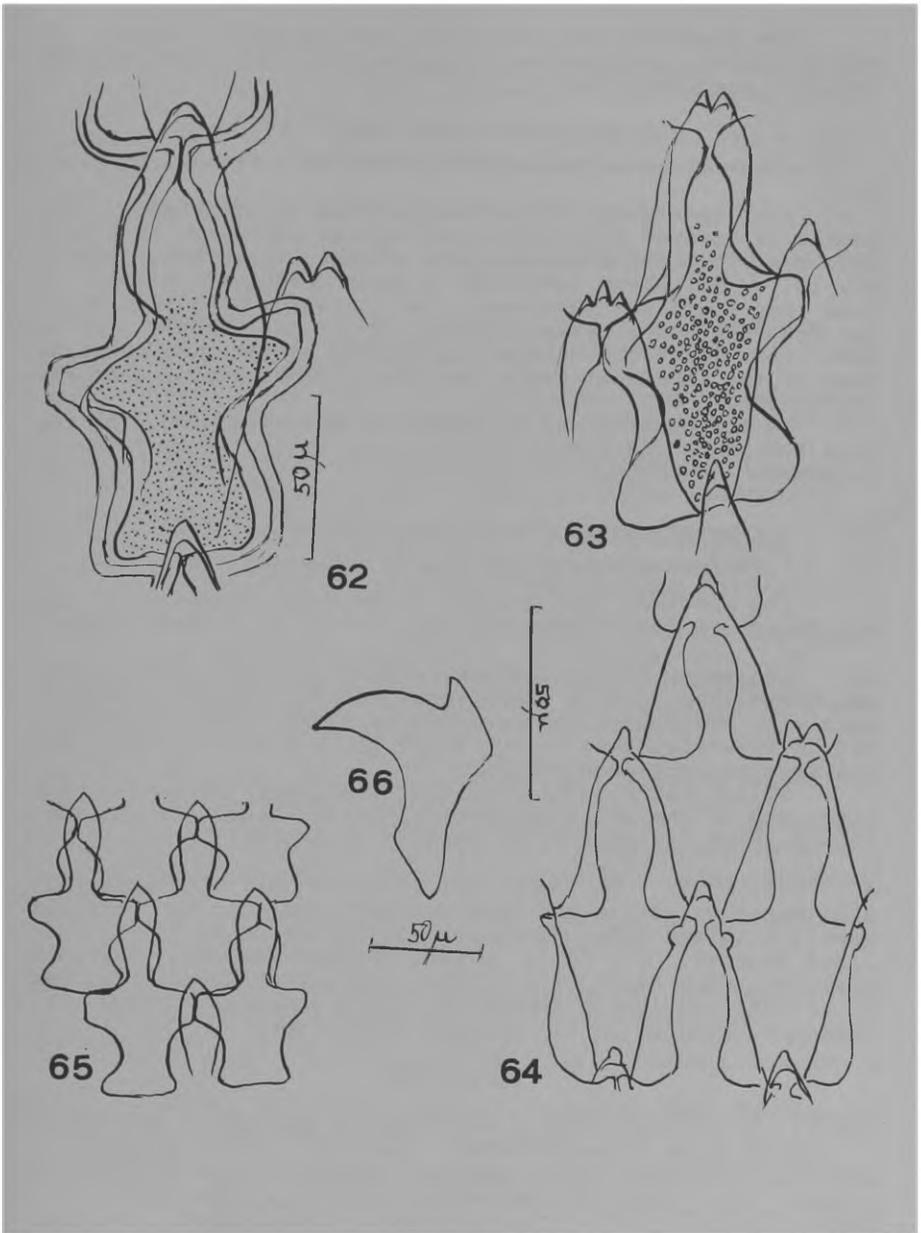
Description. - Colours, living, from Bandel and the slides: orange with reddish brown spots; mantle with small and larger pointed prominences, which near the border glisten opaquely. Inside they are golden yellow to brownish orange. The larger tubercles are reddish brown with a white spot; the sutures between them are indistinct. The dorsal side of the foot is tuberculated; the sole is very wide, orange with fine light and dark spots: in the middle of the tail appears the dark foot gland.

The size is 2 - 2.5 cm, preserved. The rhinophores are transversely folded, like an elephants trunk (Bandel) The gill rachis is tuberculate. The brown shell is 5 mm long and lies at the hind end, near the left side. There is a dense layer of radiating spicules, generally with six spikes, but dissolved in the preserved specimens.

The jaw platelets differ far from the other *Pleurobranchines* by their narrow anterior part and the much wider posterior one (Fig. 62-65) and the odd aspect of the youngest plates (Fig. 64), which in most *Pleurobranchinae* are of one width from tip to bottom and have straight sides (Fig. 38) The radular teeth are all hook-shaped (Fig. 66)

Species dubiae

Pleurobranchus lacteus Dall, 1901:367, pl. 56, f 6 - shell.



Figures 62-66 - *Pleurobranchus (Susania) emys*. 62-65, jaw platelets, 64, very young; 65, pattern of old platelets; 66, radular tooth.

One specimen from Porto Rico. As the gill rachis is not mentioned, the species cannot be classified beyond the Family Pleurobranchidae.

Pleurobranchus reesi White, 1952

Pleurobranchus reesi White, 1952:107, text-f. 6, pl.6, f.6.

Four specimens, (24 mm long), from Dry Tortugas. The mantle is covered with soft, rectangular papillae. Such were also described for *Pleurobranchus peroni* (Vayssière, 1898, pl. 13, f. 7). Large tubercles on gill rachis. Position of 5 mm long shell not mentioned. Jaw platelets with one lateral denticle and a heavy mid-line (f. 6, 1A). Radula 68 x 151.0.151. Teeth hook-shaped, gradually lengthening outwards. Some of the innermost teeth have one slight lateral denticle (f. 6, 2A)

As the position of the shell is not indicated, the species cannot be classified farther than to the genus *Pleurobranchus*.

Pleurobranchus gigas Sawaya & Grepel, 1972.

Pleurobranchus gigas Sawaya & Grepel, 1972: N 31.

The specimen from Brazil, 35 mm long, preserved, was not described nor figured not kept. So it is a nomen nudum

The genus *Pleurobranchopsis* Verrill, 1900, from Bermuda, whose type species *aurantiaca* Verrill, 1900, is homonymous with *Pleurobranchus aurantiacus* Risso, 1818, was annexed to *Pleurobranchus* as sub-genus by Thiele (1931-419) and the species renamed *verrilli*.

Willan (1978:339) found that the type specimen was lost, and as the original description is inadequate, he considers genus and species as invalid or dubious.

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