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Description of the Antarctic notaspidean *Polictenidia tomasi* gen.nov. and sp.nov. (Gastropoda, Opisthobranchia) from the Scotia Sea proposing also a new notaspidean tribe

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Abstract During the expedition “ANTARTIDA 9101”, organized by the Spanish Oceanographic Institute, two specimens of an unknown notaspidean species were collected. These differed considerably from other notaspidean species, mainly by the presence of three gills and a prebranchial sac with large external expansions. Since these specimens have three gills, while members of the order Notaspidea have been described as having only one, this feature is doubly interesting: firstly, from the systematic point of view, the definition of the order has to be modified, and secondly, it generates a phylogenetic discussion of the possible affinity between the notaspideans with one gill and doridaceans, which possess several gills.

Introduction

Within the subclass Opisthobranchia, the order Notaspidea shows a great heterogeneity of body form (Willan 1987). Species of this order mainly live in tropical seas, while there are few species in polar waters (Willan and Bertsch 1987; Wägele and Hain 1991). This order has been considered as an intermediate phylogenetic stage between tectibranch opisthobranchs and nudibranchs,

mainly because of the reduction and loss of the shell and to the nervous and reproductive systems (Odhner 1939; Ghiselin 1965; Schmekel 1985; Willan 1987; Gosliner 1994).

With regard to the branchial system, so far, all the known notaspidean species possess a uni- or bipinnate plume-shaped gill on the right side, which lies between the mantle and foot (Burn 1962; Marcus 1985; Willan 1983, 1987). The origin and phylogenetic relation of the side-gilled condition have been discussed, mainly in relation to other opisthobranch orders. Thus, several authors consider the notaspidean gill to be homologous to that of the other opisthobranch orders (Schmekel 1985) and the primitive molluscan ctenidium (Gosliner 1981; Haszprunar 1992); however, the opisthobranch gill is regarded by other authors to be a secondary structure derived from small animals that are in the initial period without gill (Fretter and Graham 1962; Morton 1972; Brace 1977; Haszprunar 1988). Along with this, several morphological and embryological aspects indicate that the gills of doridacean nudibranchs may have originated directly from those of the notaspideans (Evans 1914; Minichev 1970; Tardy 1970; Gosliner 1994).

During the expedition “ANTARTIDA 9101”, organized by the Spanish Oceanographic Institute, in January and February of 1991, two specimens of an unknown notaspidean species were collected. These differed from other notaspidean species, mainly by the presence of three gills, and a prebranchial sac possessing large external expansions.

Since these specimens have three gills, while the order Notaspidea has been described as having only one, this character is doubly interesting; firstly, from the systematic point of view, the definition of the order has to be modified, and secondly, it generates a phylogenetic discussion of the possible affinity between the orders Notaspidea and Nudibranchia.

Willan (1987) reviewed the phylogenetic systematics of the order Notaspidea using Henning's method (1966)

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and carried out a phenetic analysis, thus recognizing the suborder Umbraculacea, with two families (Tyloidinidae and Umbraculidae), and the suborder Pleurobranchacea, with only one family (Pleurobranchinae), which includes two subfamilies, Pleurobranchinae (containing two tribes, Pleurobranchini and Berthellini) and Pleurobranchaeinae (with three genera). These taxonomic ranks have been corroborated, at least partially, by Tsubokawa and Miyazaki (1993), by application of a two-dimensional electrophoresis method.

In the present study the anatomy of this new notaspidean is described and its relationship with other species of the opisthobranchs discussed. These comparisons permit us to assume the need for establishing a new tribe to contain the newly described species, together with the genera *Bathyberthella* Willan 1983 and *Parabathyberthella* García et al. 1994.

Materials and methods

Two specimens were collected during the expedition "ANTARTIDA 9101" at a station in the South Orkney Islands (60°44.10 S 46°15.40 W), between 119 and 125 m in depth, with a semipelagic trawl net. After collection the specimens were frozen and later fixed in 4% formaldehyde in the laboratory. The larger specimen was used for anatomical descriptions, while the smaller was designated as the holotype.

Results

Genus *Polictenidia* gen.nov. García et al.

Definition

Three small pinnate gills with branchial membranes attached to the rachis for the greater part of its length, on the right side of the body. Prebranchial sac with great external expansions, some of them pinnate. Anal pore at the end of a short tube behind the gills. Shell internal, large and fragile. Radular teeth narrow, erect and smooth. Mandibular elements oval, with anterior margin irregularly denticulated. Median buccal gland long. Reproductive system triaulic; prostate gland surrounding deferent duct for the greater part of its length. Penis smooth.

Polictenidia tomasi sp.nov. García et al.

External anatomy

Specimens 41 and 80 mm long and 25 and 44 mm wide, respectively. Body wall thick and smooth, without spicules. Mantle margin separated from the foot and oral veil. Rhinophores with bases fused, smooth, rolled open at a lateral slit. Oral veil smooth, with two lateral

and posterolaterally furrowed short oral tentacles (Fig. 1).

Foot, bigger than the mantle, with a transversal groove in its anterior end.

Both specimens have three minute gills at the anterior third of the body attached one over the other to the lateral body wall for almost all the gill's length (Fig. 2). The gills are joined by a common afferent branchial vessel. There, the prebranchial sac opens at the end of an external, smooth and cylindrical cutaneous expansion; an apical hood-shaped sheet covers the

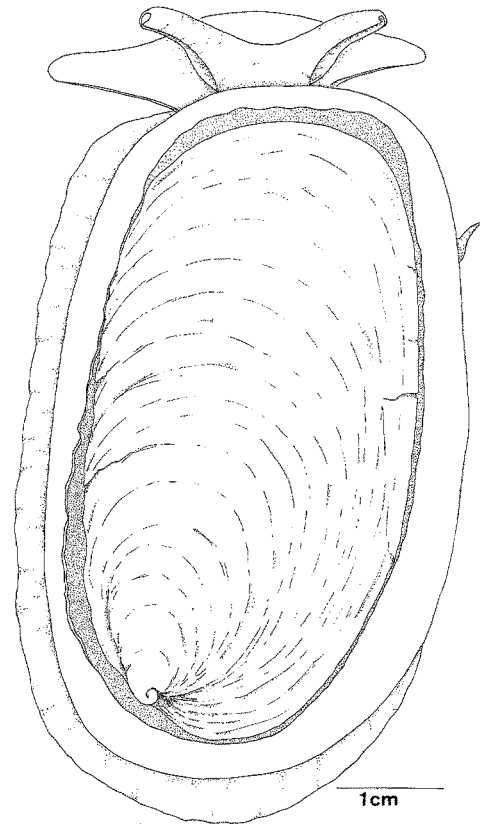


Fig. 1 External view of *Polictenidia tomasi*. The mantle has been removed

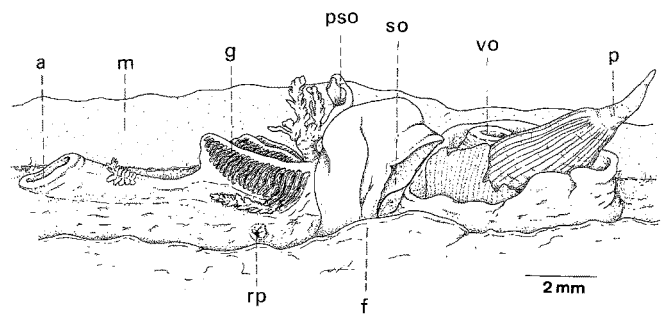


Fig. 2 Detail of the right side of *Polictenidia tomasi* (a anus, f foot, g gill, m mantle, p penis, pso prebranchial orifice, rp renal pore, so spawn orifice, vo vaginal orifice)

prebranchial aperture. At the base of this expansion two smaller pinnate branches merge.

The renal pore opens below and at the middle of the ventral-most gill. The anus opens at the end of a short tube behind the gills. In one specimen a small pinnate cutaneous expansion is present on that tube.

The three genital apertures are in front of the gills. The penial and vaginal apertures are surrounded by cutaneous sheets and the spawn orifice is covered by a hood-shaped flap (Fig. 2).

There was no visible pedal gland in the specimens collected.

Because the specimens were fixed in formaldehyde before this study, the colouration could not be determined.

The internal shell is auriculate and not calcified, covering dorsally almost all the visceral cavity (Fig. 1). The protoconch is of one whorl, barely set off from the teleoconch. The columellar muscle fits into the ventral surface of the protoconch.

Internal anatomy

Digestive system The large oral tube connects directly to the posterior region of the buccal apparatus, which has a notable asymmetry in the specimen dissected, perhaps due to the large size of the reproductive organs that fill almost all the anterior third of the visceral cavity, displacing the buccal apparatus toward the left side (Figs. 3, 4).

The columellar muscle is attached to the subjacent tegument of the shell, extending forward and, after bifurcating, each branch goes to the buccal apparatus inserting at both sides of the radular sac. Due to the asymmetry of the buccal apparatus, the insertion of the right and left columellar buccal branches are ventral and dorsal to the buccal apparatus, respectively.

The median buccal gland connects mid-dorsally with the buccal apparatus at the transition from oral tube to buccal posterior region. This gland is tubular and long, extending between the organs through the visceral cavity (Fig. 3). The length of this gland is more than 4 times the body length.

Salivary glands extend on the frontal side of the digestive gland. From there, the tubular and long salivary ducts leave and extend between the median buccal gland, entering the buccal apparatus at its transition into the oesophagus (Fig. 4). Due to the asymmetry of the buccal apparatus the left and right salivary duct dilates to a small ampulla.

The two jaws are large, elongate and thin. The length is 12 mm and the width is 6 mm. Mandibular elements are narrow, elongated and without lateral processes. Their anterior end bears usually two or three conical denticles (sometimes one, four or five denticles) (Fig. 5).

The radular formula of the biggest specimen was $67 \times 190 - 270.0.190 - 270$. All the teeth are alike

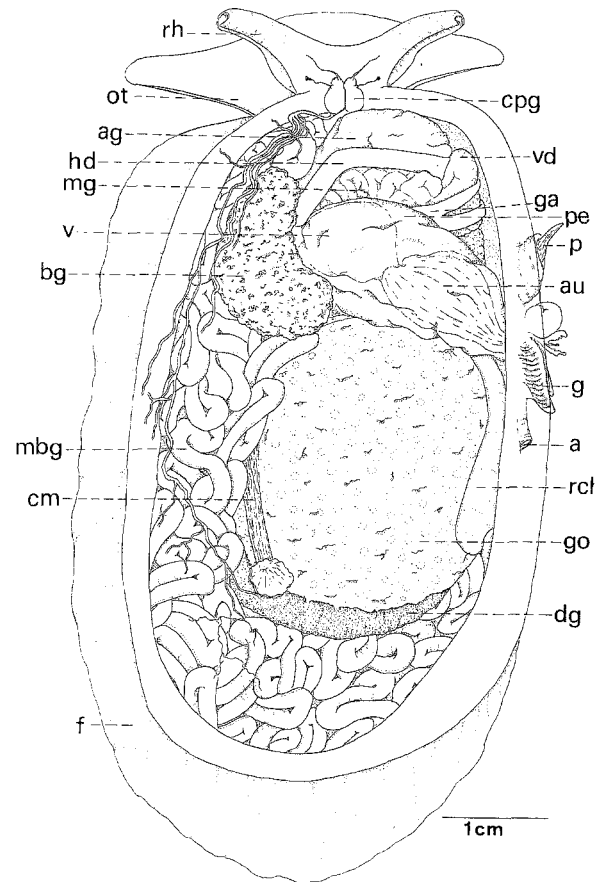


Fig. 3 Dorsal dissection of *Polictenidia tomasi* showing its internal morphology (a anus, ag albumen gland, au auricle, bg blood gland, cm columellar muscle, cp cerebropleural ganglion, dg digestive gland, f foot, g gill, ga genital artery, go gonad, hd hermaphroditic duct, mbg median buccal gland, mg mucous gland, ot oral tentacle, p penis, pe pericardium, rch renal chamber, rh rhinophore, v ventricle, vd vaginal duct)

erect, tall and with a recurved sharp-pointed apex (Fig. 6).

The oesophagus, leaving the buccal apparatus latero-dorsally, turns immediately forward on the right side, and at the level of the oral tube turns backward, entering a common gastric cavity with the digestive gland ventrally; there is no separate stomach.

The intestine leaves from the right anterior side of the digestive gland and passes directly to the anus, which opens at the end of a short duct behind the gills.

Circulatory and excretory system (Fig. 3) The pericardium is a spacious cavity lying on the reproductive organs in the anterior third of the animal. Ventrally, it connects with the renal chamber, which opens externally through a pore located below the ventral gill, at the middle of the gill membrane. In the pericardium are a thin-walled auricle and a muscular ventricle.

Blood coming from the gills enters the auricle through a common efferent branchial vessel that also connects with the prebranchial sac.

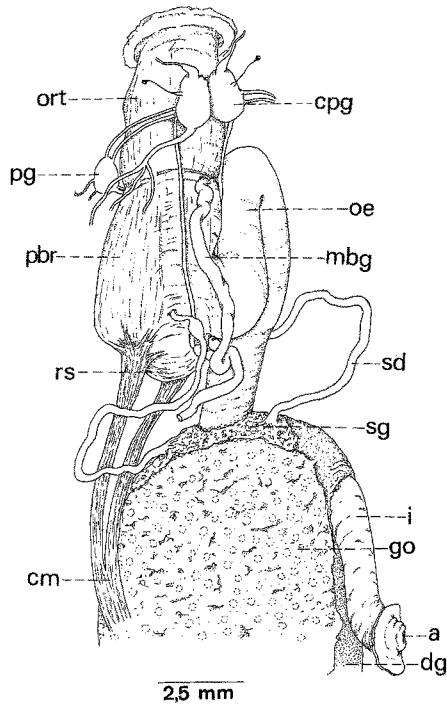


Fig. 4 Dorsal view of the digestive system of *Polictenidia tomasi* (a anus, cm columellar muscle, cpg cerebropleural ganglion, dg digestive gland, go gonad, i intestine, mbg median buccal gland, oe oesophagus, ort oral tube, pbr posterior buccal region, pg pedal ganglion, rs radular sac, sd salivary duct, sg salivary gland)

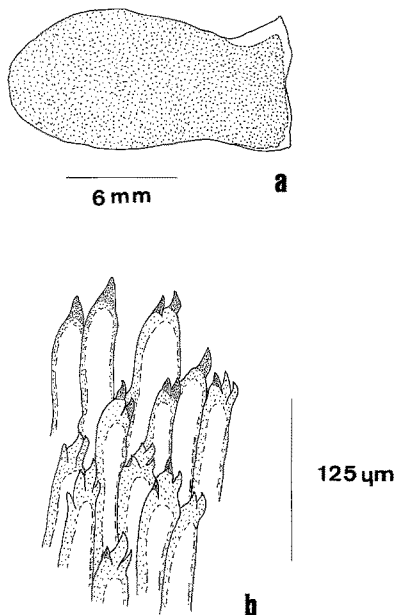


Fig. 5 a) Jaw of *Polictenidia tomasi* b) Detail of the mandibular elements

The ventricle connects to a large aortic trunk from which several vessels branch off toward different organs. Near the ventricle, a vessel passes into a voluminous blood gland and continues toward the digestive gland, where it branches.

Nervous system (Fig. 7) The cerebral and pleural ganglia, located on the oral tube, are completely fused into a cerebropleural ganglion, without visible grooves. The rhinophoral and optical ganglia lie dorsally on the cerebropleural ganglia. The well-developed eyes are located on top of the long optical nerves, which merge from the cerebropleural ganglia, where the optic ganglia are located.

A well-developed visceral ganglion lies on the ventral surface of the right cerebropleural ganglion. From there, two nervous trunks start, one of which bifurcates.

The pedal ganglia are located ventrolaterally to the oral tube and separated from the cerebropleural ganglia with long connectives. Pedal commissures are also long.

The buccal ganglia lie at the posterior end of the buccal apparatus, behind the point of transition of that into the oesophagus. The buccal commissure is short although the buccal connectives are long. The gastroesophageal ganglion is attached to the buccal apparatus with short connectives.

Reproductive system (Fig. 8) The gonad lies in the posterior half of the body, enveloping the digestive gland dorsally. The long hermaphroditic duct, flattened and pressed against the female gland, has no anatomically differentiated ampulla. It constricts abruptly and penetrates the female gland complex; before penetration, the deferent duct differentiates.

The proximal deferent duct enlarges to an elongate, tubular and spongy prostate gland, which entwines itself and compresses onto the gametolytic gland, which it ensheathes. The distal deferent duct is long, narrow and entwined and passes into a conical penial sheath.

The vagina is long, enlarged and coiled, and provided with a vaginal muscle. It connects with a round and thin-walled gametolytic gland and a digitiform, narrow and long seminal receptacle. From there it continues to a narrow and coiled uterine duct, which goes into the female gland complex; just before this, it enlarges slightly and coils abruptly.

The albumen gland is smooth and covers the mucous gland, which opens to the exterior through a spawn aperture covered by a cutaneous hood-shaped flap (Fig. 2).

Holotype

The specimen of 41 mm long was designated as holotype and deposited in the Museo Nacional de Ciencias Naturales in Madrid (Spain) with code number 15.05/15820.

Origin of the name

The name of the genus *Polictenidia* was chosen because the specimens have several gills or ctenidia. The

Fig. 6 Radula of *Polictenidia tomasi*

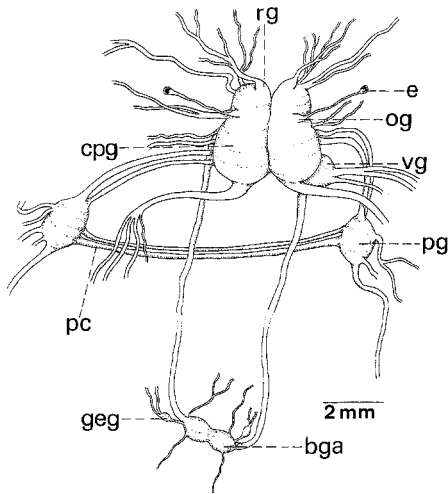
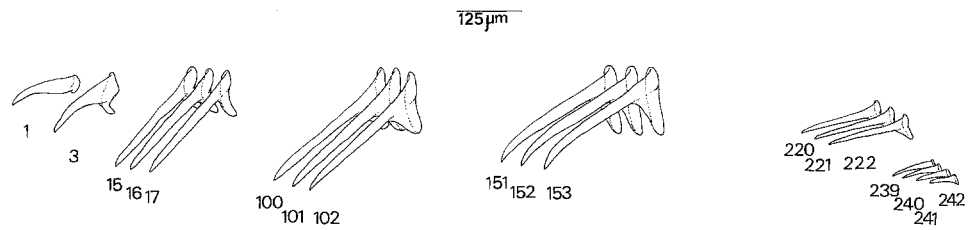


Fig. 7 Dorsal view of the central nervous system of *Polictenidia tomasi* (bga buccal ganglion, cpg cerebropleural ganglion, e eye, geg gastroesophagic ganglion, og optic ganglion, pc pedal commissure, pg pedal ganglion, rg rhizophoral ganglion, vg visceral ganglion)

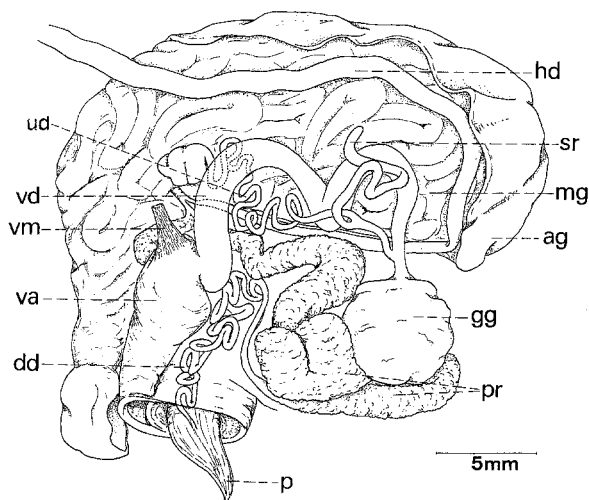


Fig. 8 Reproductive system of *Polictenidia tomasi* (ag albumen gland, dd deferent duct, gg gametolytic gland, hd hermaphroditic duct, mg mucous gland, p penis, pr prostate, sr seminal receptacle, ud uterine duct, va vagina, vd vaginal duct, vm vaginal muscle)

species was named *tomasi* in honour of Tomás García Delgado, father of the first author of this paper.

Discussion

P. tomasi is a significant notaspidean species, possessing some characteristic features. One of its most unique features is the presence of three diminutive gills on the right anterior side joined together at the basis. All three have the typical notaspidean ctenidium structure, i.e. each one has a rachis with pinnæ on both sides and a membrane attaching the ventral surface of the rachis to the body (Burn 1962; Morton 1972; Willan 1983, 1987). Wägele and Hain (1991) described a very small gill in *Tomthompsonia antarctica* Thiele 1912 and established that this situation could be due to less oxygen being necessary in cold water. However, in *P. tomasi* the smaller branchial size is compensated for by a higher number of pinnate gills. Willan and Bertsch (1987) described a specimen of *Bathyberthella antarctica* with several forked pinnæ on the upper side of the rachis, like a bifurcation of the gill. These authors considered this aspect to be the result of a mutation. However, a possible mutation or an injury in *P. tomasi* is not easy to explain because both specimens have almost identical organization of the pallear structures (gills, anal pore and prebranchial sac).

This feature is considered as apomorphic in *Polictenidia* because, according to several authors, in opisthobranchs the presence of only one gill is primitive (Brace 1977; Schmekel 1985); besides, this situation is shown for the origin of the Pentaganglionata Heterobranchia Gastropoda (Thompson 1976; Gosliner 1981; Haszprunar 1985, 1988). Therefore, we think that *P. tomasi* could be in a similar situation as the origin and the evolution of the branchial ring of doridaceans (Potts 1981; Jonas 1985).

Another typical feature of *P. tomasi* is the presence of a prebranchial sac opening to the exterior at the end of a ramified tube, with a hood-shaped flap covering the aperture. Generally, the prebranchial sac aperture is a simple pore in front of the gill, as occurs in the subfamily Pleurobranchinae (Vayssière 1898; Willan

1983) or opens at the end of a more or less developed papilla, as in the subfamily Pleurobranchaeinae (Marcus and Gosliner 1984). It is not clear what the function and origins of the prebranchial sac in Notaspidea are, but a possible homology with the opaline gland of the Anaspidea has been proposed (Morton, 1972). However, according to Lacaze-Duthiers (1859) and Pruvot-Fol (1954) and with its connection with the efferent branchial vessel and the presence of some pinnate branches, we think it could have, at least, a supplementary respiratory function.

The anal pore opening at the end of a short tube has only been found in the genus *Umbraculum* (Marcus 1985; Willan 1987). According to Willan (1987), this feature is apomorphic, although in regard to *P. tomasi* it could be a homoplasy.

The genus *Polictenidia* coincides with *Bathyberthella* and *Parabathyberthella* with the presence of a large auriculate internal shell, a long, tubular, apparently not branched, median buccal gland, the presence of a uterine duct connecting the vaginal duct to the female gland complex, the narrow, erect and elongated radular teeth and mandibular elements provided with irregular denticulation on the anterior blade but without lateral projections, except *Parabathyberthella*, which lacks mandibular elements (García et al. 1994). Although, according to Willan (1987), a large shell is plesiomorphic, the rest of the features are apomorphies. With regard to the type of mandibular elements that shows *Bathyberthella* (similar to *Polictenidia*), Willan (1987) established that the absence of lateral projections are lost secondary and constitute a convergence with those of the ancestor. In spite of this, the total absence of mandibular elements in *Parabathyberthella* could be a final stage in the reduction of these structures.

According to these features we propose that the genera *Bathyberthella*, *Parabathyberthella* and *Polictenidia* constitute a new tribe, different from the Berthellini, which we name Bathyberthellini new tribe, defined as follows:

Mantle smooth. Rhinophores with bases fused. Oral veil broad with two short oral tentacles. Foot with an anterior transversal groove. Internal cuticular shell, large and flexible, covering dorsally almost all the visceral cavity. Mantle smaller than foot and separated from it. Anal pore behind the gill. The prebranchial sac is in front of the gill. The genital apertures are located in front of the gill. Median buccal gland long, apparently not branched. Two salivary glands. Jaws composed of distinct plates, the mandibular elements are absent or they are oval with denticulate anterior margins. Radula broad, with narrow, erect and elongate simple lateral teeth; there are no rachidian teeth. Reproductive system triaulic, with seminal receptacle and gametolytic gland, and a prostate gland surrounding deferent duct; uterine duct present. Penis smooth.

Remarks on relationships of the order Notaspidea with Doridacea Nudibranchia

Several authors have stated that the notaspidean gill is a homologue to that of other opisthobranch orders (Schmekel 1985) and the primitive molluscan ctenidium (Gosliner 1981; Haszprunar 1992). Besides, according to their innervation, position of the gill relative to the anus and renal pore, embryological development and the occurrence of a raphe, the gills of Doridacea have originated directly from those of the Notaspidea (Evans 1914; Minichev 1970; Tardy 1970). Thus, from a lateral position in notaspideans, the gills are placed dorsally in doridaceans forming a ring around the anus (Potts 1981). In primitive species and genera, such as the genus *Bathydoris*, there is an intermediate situation since the gills are placed asymmetrically on the right side (Evans 1914; Marcus and Marcus 1962). The gill organization of *P. tomasi* could support a possible phylogenetic relationship between Doridacea and Notaspidea; however, it is not possible to establish a direct phylogenetic relationship between this species and the Doridacea species. This is because of the different connection of the branchial efferent vessel with the auricle, since in primitive doridaceans this vessel connects with the auricle through a circular sinus surrounding the heart (Evans 1914; Minichev 1970; García and García-Gómez 1990). Doridaceans have no prebranchial sac, while *P. tomasi* has external ramified expansions associated with the common efferent branchial vessel. These features can be autapomorphies in *Polictenidia* and the presence of several gills be a homoplasy with doridacean gills, due to an independent evolution of similar characters, which offer a selective advantage to closely related organisms (Gosliner 1985).

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