J. Moll. Stud. (2000), **66**, 301–311

A NEW SPECIES OF *BERTHELLA* BLAINVILLE, 1824 (OPISTHOBRANCHIA: NOTASPIDEA) FROM THE CANARY ISLANDS (EASTERN ATLANTIC OCEAN), WITH A RE-EXAMINATION OF THE PHYLOGENETIC RELATIONSHIPS OF THE NOTASPIDEA

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(Received 19 January 1998; accepted 15 November 1999)

ABSTRACT

Berthella canariensis is described from Canary Islands. The mantle is smooth and its ground colour is grey, with black and opaque white spots scattered regularly all over the dorsal surface. White spots are less abundant than black ones. The posterior half of the mantle has areas of with a paler ground colour that are variable in size. *Berthella canariensis* has several features that distinguish it from other described members of *Berthella*. It has a broad radula with numerous teeth per half-row. However, other aspects of its anatomy, such as the absence of a medial buccal gland and the presence of a tuberculate gill, distinguish it from other species with a broad radula.

As the present species has two features found in some species of *Pleurobranchus* and several new higher taxa have been described recently, Willan's (1987) phylogenetic hypothesis was re-analysed. This analysis largely supports the hypothesis presented by Willan. The sister-group relationship of *B. canariensis* with *B. californica* is supported by two synapomorphies. The relationship of these two species to other species of *Berthella* is poorly resolved in the present analysis and requires additional study of all members of the genus. Similarly, questions of the monophyly of *Bathyberthella, Policlenidia, Parabathyberthella*, *Tomthompsonia* and *Berthella* require the consideration of additional species and comparison with other members of *Berthella* and *Berthellina*. Despite the need for further study, the monophyly of the clade containing *Bathyberthella, Policlenidia, Parabathyberthella* is well supported. Similarly, numerous synapomorphic features confirm the monophyly of the clade containing *Bathyberthella, Policlenidia, Parabathyberthella, Tomthompsonia, Berthellina* and *Berthella*, and its sister-group relationship with *Pleurobranchus*. The present study reveals that the Notaspidea have three distinct configurations of triaulic reproductive systems, not previously differentiated.

INTRODUCTION

Marcus (1984) indicated that the species of Notaspidea from the eastern Atlantic were not as well known as those from the western Atlantic. Since then, Cervera *et al.* (1996a) described *Pleurobranchus garciagomezi* from the Cape Verde Islands and confirmed the taxonomic identity of *P. reticulatus* Rang, 1832 from Ghana. Few species of notaspideans have been recorded from the Canary Islands and are limited to *Tylodina perversa* (Gmelin, 1791), *Umbraculum umbraculum* (Lightfoot, 1786), *Pleurobranchus testudinarius* Cantraine, 1836, *P. areolatus* Mörch, 1863, *Berthellina quadridens* (Mörch, 1863) (probably not this species) and *Pleurobranchaea meckelii* (Blainville, 1825) (Cervera *et al.*,1988; Pérez-Sánchez and Moreno, 1991; Cervera *et al.*, 1996b).

Field collections along the Isla de Gran Canaria coast yielded a single specimen of an unknown notaspidean. The features present in this species and the description of new higher taxa following Willan's (1987) phylogenetic revision of Notaspidea, have led us to reassess

aspects of the phylogenetic relationships of this order, together with the description of the species.

SYSTEMATIC DESCRIPTION

Order Notaspidea Fischer, 1883
Suborder Pleurobranchacea Férussac, 1822
Family Pleurobranchidae Férussac, 1822
Subfamily Pleurobranchinae Férussac, 1822
Tribe Pleurobranchini Férussac, 1822
Genus *Berthella* Blainville, 1824

Berthella canariensis new species

Material: Holotype: One specimen, 36 mm in length, collected under an isolated stone on a sandy bottom at 8 m depth, Bay of Gando, Isla de Gran Canaria (28º05′27″ N; 15º21′49″ W), Canary Islands, eastern Atlantic, 12th February 1984. This specimen has been deposited at the Museo de Ciencias Naturales de Tenerife (Santa Cruz de Tenerife, Canary Islands, Spain), catalogue number TFMC MO-000184.

Description: Body (Fig. 1A) oval. Mantle without anterior notch or posterior siphonal crenulation. Mantle entirely smooth, covering the broad foot, except at the posterior tip. Rhinophores involute and joined basally. Oral veil straight, grooved at its lateral edges and projecting slightly from the mantle. Foot bilabiate anteriorly. Bipinnate gill (Fig. 1B) with 21 pinnae on each side. Gill axis bearing a double row of alternating and conspicuous tubercles. Gill not visible in living specimen, except at posterior end, as it is covered by the mantle. Anus located immediately behind posterior end of membrane that attaches gill to the body. Genital apertures located anterior to gill and surrounded by a single external flap (Fig. 1B). Penis partially everted in the preserved specimen. Pedal gland not observed at posterior end of the foot.

Ground colour grey, with black and opaque white spots scattered regularly over the entire mantle surface. Opaque white spots fewer than black ones. Posterior half of the mantle having some areas of differing size of a paler ground colour (Fig. 1A). Foot translucent, whitish.

No trace of the shell present, but columellar muscle inserting at the posterior region of the visceral mass, indicating that shell may have been situated posteriorly. Medial buccal gland absent. No spicules found in mantle tissue.

Jaws (Fig. 2A) with elongate and slightly cruciform elements, with a single central cusp in many of these elements (Figs. 2B,3A). Each element consisting of a central cusp flanked by 1-3 denticles or by 2-4 denticles without a central cusp (Figs. 2B,3A).

The radular formula: 69 X 141.0.141. Radular teeth smooth and hook-shaped (Fig. 3B,C,D). Inner teeth slightly smaller than those from the

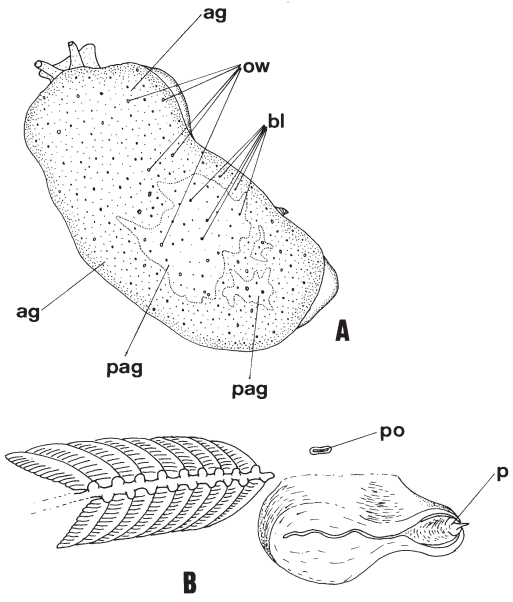

Figure 1. *Berthella canariensis* new species. A, Dorsal view of the holotype. B, Detail of the external flap covering the genital orifices, and anterior part of the gill in the preserved holotype.
Key: ag, ash-gray; bl, black; ow, opaque white; pag, pale ash-gray; po, prebranchial orifice.

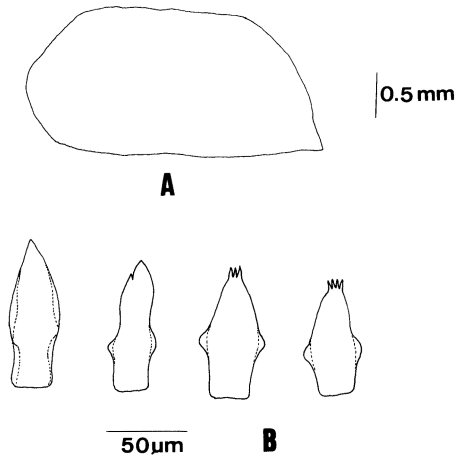

Figure 2. *Berthella canariensis* new species. A, Jaw. B, Detail of different types of jaw elements.

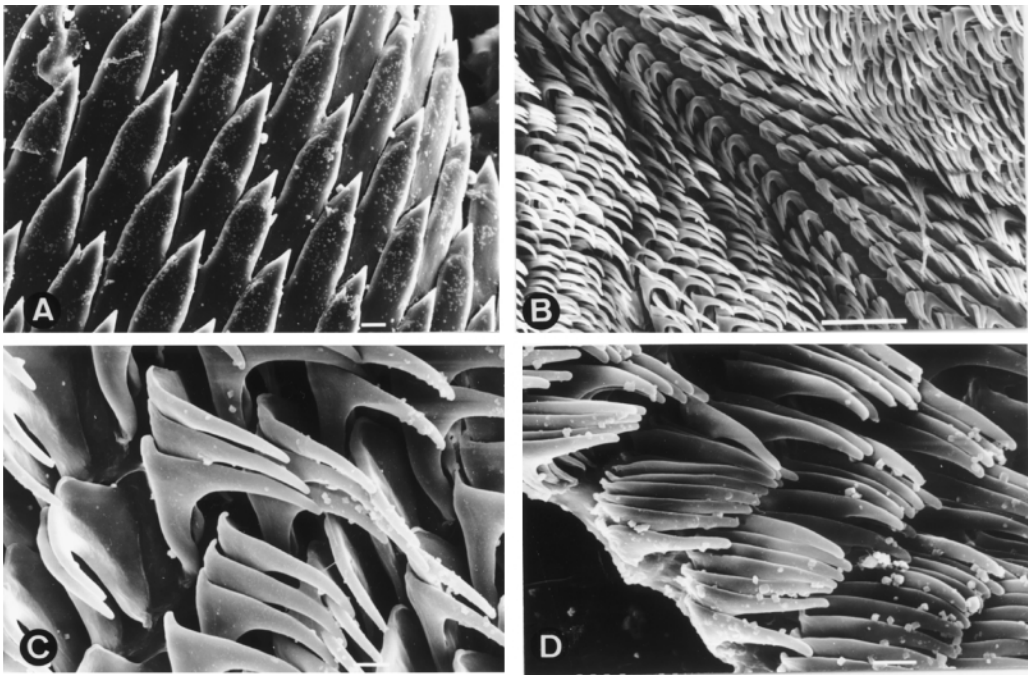

Figure 3. *Berthella canariensis*. A, Jaw elements from the anterior edge. B, general view of radula, showing central region. C, middle region of the half-row, D, outermost radular teeth. Scale bar = 10 μm (A,C,D), scale bar = 100 μm (B)

middle portion of half-row (Fig. 3B,C). No marginal teeth present and outermost teeth are less steeply arched with moderately elongate cusps (Fig. 3D).

Reproductive system triaulic (Fig. 4). Wide ampulla elongate and sausage-shaped. Ampulla dividing into the prostate and oviduct. Connection present from the base of the ampulla directly to the female gland mass, although it had been broken during the examination of the reproductive system. Prostate thin and highly convoluted. Connective to elongate, highly convoluted penial gland extending from the base of the vas deferens. Remaining portion of the vas deferens relatively straight and narrow including the distal part of vas deferens and the penis. These two portions not clearly demarcated from each other. Bursa copulatrix large and rounded receptaclum seminis elongate and slightly convoluted. Vagina relatively long and without convolutions, emerging from bursa and exiting between vas deferns and nidamental openings. Elongate duct of the receptaculum seminis joining vagina near the base of vaginal duct. Female gland mass large and adjacent to remaining genital organs. Nidamental opening with its own orifice at genital atrium.

DISCUSSION

Berthella canariensis can be distinguished externally from the other Atlantic species of the genus, *B. sideralis* Lovén, 1846, *B. plumula* (Montagu, 1803), *B. stellata* (Risso, 1826), *B. ocellata* (Delle Chiaje, 1828), *B. aurantiaca* (Risso, 1818), *B. agassizii* (MacFarland, 1909), *B. platei* (Bergh, 1898), *B. patagonica* d'Orbigny, 1837, *B. tamiu* Marcus, 1984 and *B. americana* (Verrill, 1885), by its coloration, lack of any kind of protuberances, intersecting ridges or folds on the mantle. Moreover, the all the above species, except *B. canariensis*, have a smooth gill axis. The presence of a single external flap surrounding the genital apertures in *B. canariensis* is similar to *B. platei***.** With respect to its internal anatomy, the absence of the shell has been observed occasionally in some species of Pleurobranchinae (i.e. species of *Pleurobranchus*, *Berthellina*) (Willan, 1987; personal observations). The single specimen has no trace of a shell, not even the periostracum. It is not clear whether the shell is typically entirely absent in this species, whether its presence or absence represents a variable feature of the species, or whether its absence is merely a

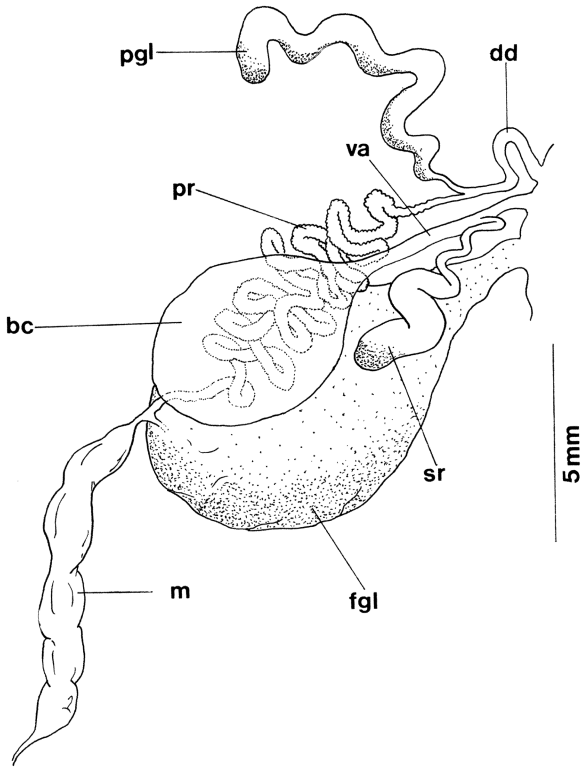

Figure 4. *Berthella canariensis*. Reproductive system.
Key: am, ampulla; bc, bursa copulatrix; dd, vas deferens; fgl, female gland; hd, hermaphroditic duct; pgl, penial gland; pr, prostate; sr, receptaculum seminis; va, vagina

preservational artefact. However, we have observed that in different specimens of a single species of *Berthellina*, a shell may be calcified**,** uncalcified or entirely absent. Regardless of the explanation for the absence of a shell, it is probably placed at the rear part of the animal, as the columellar muscle inserts posteriorly. We have found that the position of the columellar muscle is a reliable indicator of shell location, and that this feature does not vary intraspecifically in other species of Pleurobranchinae.

A comparison among different features (medial buccal gland, jaws, radula and reproductive system) of all the Atlantic species of *Berthella* are presented in Table 1. From data presented in this table, several differences are apparent. Four of the twelve Atlantic species of *Berthella*, including *B. canariensis*, have a radular formula with more than 140 teeth on either side of the radular rachis. The remaining species have between 42 and 88 teeth per half row. All the species in the first group have elongate outer lateral teeth. Of these four species with a wide radula, *B. canariensis* is unique in lacking a medial buccal gland. The gland has not been studied in *B. americana*. *Berthella sideralis* and *B. americana* are both known only depths greater than 100 m and very similar in all aspects of their anatomy. The reproductive system of *B. americana* has not been described by Willan (1978), but the other similarities suggest that the two species may be synonymous. *Berthella canariensis* differs from the other three species with a wide radula in that it has a tuberculate gill surface while the others have a smooth rachis. *Berthella canariensis* and *B. sideralis* have a convoluted receptaculum seminis and penial gland , while both organs are straight in *B. platei* and undescribed for *B. americana*. These characteristics clearly distinguish *B. canariensis* from other members of the genus known from Atlantic waters.

Pruvot-Fol (1953) erroneously erected the name *Berthellina africana* from Moroccan

Table 1. Comparison of the medial buccal gland, jaws, radula and reproductive system of the Atlantic species of the genus *Berthella*.

	Jaws denticles	Primary cusp of jaw elements	Radular formula	Inner lateral teeth	Outer radular teeth	Medial buccal gland	Seminal receptacle	Prostate	Penial gland	References
B. platei	2-8	Equal to denticles	55-66 X 93-155.0.93-155	Short cusp	Elongate cusp	Long, convoluted and unbranched	Pyriform	Well developed	Straight	Schrödl (1999)
B. sideralis	3-15	Longer than denticles	92-95 X 163-200.0.163-200	Short cusp	Elongate cusp	Long, convoluted and unbranched	Convoluted	Well developed	Convoluted	Bergh (1898), Odhner (1939), this study
B. plumula	2-4	Equal to denticles	40-75 X 49-75.0.49-75	Short cusp	Short cusp	Absent	Pyriform	Short	Convoluted	Vayssière (1898), Cattaneo-Vietti (1986), this study
B. stellata	0-6	Equal to denticles	50-80 X 55-80.0.55-80	Short cusp	Elongate cusp, more or less denticulate	Absent	Pyriform	Little developed	Slightly convolute	Vayssière (1898),Gosliner and Bertsch (1988), this study
B. ocellata	0	—-	60-107 X 65-88.0.65-88	Short cusp	Short cusp, but very wide base	Absent	Elongate	Well developed	Convolute	Cattaneo-Vietti (1986), this study
B. aurantiaca	3-5	Slightly larger than denticles	50-70 X 50-80.0.50-80	Short cusp	Short cusp	Absent	Elongate	?	Straight	Vayssière (1898), Cattaneo-Vietti (1986), this study
B. agassizii	1-6	Slightly larger than denticles	42-52 X 42-53.0.42-53	Short cusp	Short cusp	Absent	Pyriform	Short	Straight	Gosliner and Bertsch (1988), this study
B. americana	1-5	Equal than denticles	85 X 170.0.170	Short cusp	Elongate	?	?	?	?	Willan (1978)
B. patagonica	3-5	*	65-75 x 45-55.0.45-55	*	*	Present, but 'not well developed'	?	?	?	Bergh (1898), Marcus (1984)
B. tamiu	0	—-	72 X50.0.50	Short cusp	Short cusp	?	?	?	?	Marcus (1984)
B. africana	2-3	?	?	?	?	?	?	?	?	Gantès (1956)
B. canariensis **n.sp.**	0-2	Moderately elongate	69 X 141.0.141	Short cusp	Moderately elongate	Absent	Convoluted	Highly elongate, convoluted	Long, convolute	This study

* The Bergh's (1898) description of these features is not suficiently detailed.

material. It was later transferred to *Berthella* by Gantès (1956), who explained the counfusion surrounding the colour plates that she had sent to Pruvot-Fol and the subsequent errors that were published by Pruvot-Fol. Thus, figures 49, 50 and 51 of Pruvot-Fol's plate III actually belong to *Berthella africana*. This species lacks genital flaps and tubercles on the gill rachis and figures 49 and 50 show its ground colour varies from light beige to light reddish brown. Well separated white punctuations can be seen in the specimen shown in figure 49, but they are not mentioned in by either Pruvot-Fol or Gantès. According to Pruvot-Fol (fig. 51), 'a la loupe, la coloration est due à un pointillé roux, disposé en petits cercles entourant les faibles varicosités de la peau'. The correct details of the internal anatomy given by Pruvot-Fol are those that she attibuted to '*B. aurantiaca*' or a similar species and that Gantès explained a little better later (shell, jaws and radula). On the other hand, those that Pruvot-Fol originally attributed to *africana* correspond to *Berthellina*. The description of the internal anatomy is incomplete and does not permit a correct taxonomic placement of this species nor a detailed comparison with other species. It cannot be stated with any certainty that the specimens depicted in figure 49 and 50 of Pruvot-Fol's paper are conspecific. Moreover, Pruvot-Fol stated that her specimens had a smooth gill axis and lack genital flaps. The above facts leads us to consider *B. canariensis* distinct from *B. africana*.

Etymology: The specific name, *canariensis,* refers to the Canary Islands.

RE-EXAMINATION OF THE PHYLOGENETIC RELATIONSHIPS OF THE NOTASPIDEA

To compare the anatomy of *Berthella canariensis* with other described species and to re-evaluate phylogenetic relationships of the Notaspidea, it has been necessary to examine additional material of several other species. A list of that material is provided below:

Pleurobranchus areolatus Mörch, 1863: one specimen from San Clemente Island (California, USA), 25 February 1995, California Academy of Sciences (CAS) (CASIZ 105739).

Berthella sideralis (Lovén, 1846): two specimens from Trondheimsfjorden (Norway), 30 June 1936, at 200–350 m depth, Swedish Museum of Natural History (catalogue numbers 1731 and 1732).

Berthella plumula (Montagu, 1803): four specimens from Cádiz (southwestern Spain), June 1984, intertidally.

Berthella aurantiaca (Risso, 1818): three specimens from Punta Carnero (strait of Gibraltar, Spain), July 1981, intertidally.

Berthella stellata (Risso, 1826): four specimens from Cádiz (southwestern Spain), August 1985, intertidally.

Berthella ocellata (Delle Chiaje, 1828): one specimen from Isla de Tarifa (Strait of Gibraltar, Spain), June 1985, at 15 m depth.

Berthella martensi (Pilsbry, 1896): one specimen from Batangas, Luzón Island (Philippines), 6 March 1992, CAS (CASIZ 083771).

Berthella agassizii (MacFarland, 1909): one specimen from Bahía Sebastián Vizcaíno, southern Baja California (Mexico), 30 June 1984, CAS (CASIZ 063276).

Berthella californica (Dall, 1900): three specimens from Great Tide Pool, Pacific Grove, California (USA), 1 June 1973, CAS (CASIZ 069858).

Berthellina edwardsi (Vayssière, 1896): four specimens from Cádiz, southwestern Spain, December 1985, intertidally.

Pleurehdera haraldi Marcus and Marcus, 1970: one specimen from Batangas, Luzón Island, Philippines, 25 February 1995, CAS (CASIZ 105739).

Willan (1987) conducted the first phylogenetic analysis of the Notaspidea, but did not use parsimony analysis to produce his hand-constructed tree. A second tree was based on phenetic rather than cladistic analysis. Within the Pleurobranchidae, he noted certain synapomorphies shared by members of *Pleurobranchus*, including a cleft anterior border of the mantle, a tuberculate rachis of the gill, external flaps surrounding the genital aperture, and rhinophores that pulsate in the living animal. Other features, such as the texture of the mantle, mantle spicules, a denticle at the base of the radular teeth, number of allosperm storage organs and form of the prostate, vary within *Pleurobranchus*. Willan also determined that the sister group of *Pleurobranchus* was the clade containing *Berthella, Bathyberthella, Pleurehdera* and *Berthellina*. He stated that all members of this clade have a triaulic reproductive system with a distinct uterine duct that joins the receptaculum seminis to the female gland mass and a branch from the ampulla directly to female gland mass. Members of this clade have a penial gland with the exception of *Bathyberthella antarctica* Willan and Bertsch, 1987 (Willan & Bertsch, 1987; Wägele & Willan, 1994). Willan and Bertsch and Willan suggested that absence of a penial gland in this species was due to secondary loss rather than plesiomorphic absence.

Following Willan's review of the Notaspidea, three additional genera have been described. *Parabathyberthella* García, García-Gómez, Troncoso and Cervera, 1994, differs from *Bathyberthella* in that it lacks mandibular elements. *Polictenidia* García, Troncoso, Cervera and García-Gómez, 1996, is also similar to *Bathyberthella* and *Parabathyberthella*, but has three minute, but distinct gills. *Tomthompsonia* Wägele and Hain, 1991, is unique among notaspideans in having a spirally coiled shell.

In view of the fact that several new higher taxa have been described, it is appropriate to re-examine aspects of the phylogenetic relationships of the Notaspidea originally examined by Willan (1987). In addition, the present species possesses a mixture of plesiomorphic and apomorphic characteristics and two apomorphic characteristics in common with species of *Pleurobranchus* (tuberculate gill and genital flaps) which further necessitates phylogenetic analysis. In order to reassess the phylogeny of the Notaspidea, 19 taxa were examined. These included species within the five genera of the Pleurobranchinae (*Pleurobranchus, Bathyberthella, Berthella, Pleurehdera and Berthellina*) considered by Willan, the three genera recently described montypic genera (*Parabathyberthella*, *Polictenidia* and *Tomthompsonia*), two members of the Pleurobranchaeinae (*Pleurobranchaea* and *Euselenops*) and *Tylodina* as the outgroup. Since the two species of *Bathyberthella* differ in the presence or absence of the penial gland, both species were included in the analysis. Finally, several species of *Berthella* were included to compare with *B. canariensis*. This comparison was made to test the monophyly of *Berthella* and the relative position of *B. canariensis* to other members of the genus. Thirty-two morphological characters were chosen for the analysis (Table 2). Most of these were utilized previously by Willan (1987), but characters such

Table 2. Characters and states used for the phylogenetic analysis of Notaspidea. 0 = plesiomorphic condition; 1,2,3 = apomorphic conditions.

CHARACTER	STATES
1. Shell size	0: large; 1: small; 2: absent
2. Shell position	0: external; 1: internal
3. Columellar muscle	0: present; 1: absent
4. Shell coiling	0: few whorls; 1: many whols
5. Shell calcification	0: present; 1: reduced or absent
6. Shell shape	0: circular; 1: rectangular; 2: spiral
7. Shell height	0: conical; 1: flat
8. Mantle texture	0: smooth; 1: pustulose; 2: puckered
9. Spicules	0: absent; 1: stellate; 2: linear
10. Anterior border of mantle	0: entire; 1: cleft
11. Mantle separation	0: present; 1: absent
12. Oral veil	0: smooth; 1: papillate
13. Rhinophores	0: well separated; 1: close together
14. Pedal gland	0: absent; 1: present
15. Gill size	0: large; 1: small
16. Gill branching	0: single; 1: divided
17. Gill texture	0: smooth; 1: tuberculate
18. Medial buccal gland	0: absent; 1: present; 2: vestigial or lost
19. Medial buccal grand branching	0: absent; 1: branched; 2: unbranched; 3: highly ramified
20. Rachidian row	0: present; 1: absent
21. Inner radular teeth	0: hooked; 1: denticulate
22. Outer radular teeth	0: hooked; 1: elongate
23. Jaw elements	0: present; 1: absent; 2: lost
24. Jaw elements shape	0: oval; 1: cruciform
25. Reproductive system	0: monaulic; 1: triaulic
26. Oviduct	0: enters receptaculum seminis; 1: enters female gland mass
27. Penial gland	0: present; 1: absent
28. Receptaculum seminis	0: semiserial; 1: serial or absent
29. Receptaculum seminis shape	0: pyriform; 1: filiform
30. Uterine duct	0: absent; 1: present
31. Prostate	0: absent; 1: tubular; 2: massive
32. Tubular prostate	0: narrow; 1: wide

as the position of the columellar muscle have been added. Other characters and character states have been added such as the presence of an undivided or divided gills and the presence of a spiral shell. Characters that were used by Willan that were autapomorphic, not relevant to the present taxa or highly variable within taxa were excluded from the present analysis. Specimens of *Pleurobranchus areolatus* Mörch, 1863, *Berthella sideralis* Lovén, 1846, *B. plumula* (Montagu, 1803), *B. aurantiaca* (Risso, 1818), B. *stellata* (Risso, 1826), *B. ocellata* (Delle Chiaje, 1828), *B. martensi* (Pilsbry, 1896), *B. agassizii* (MacFarland, 1909), *B. californica* (Dall, 1900), *Berthellina edwardsi* (Vayssière, 1896) and *Pleurehdera haraldi* Marcus and Marcus, 1970, were examined by us to provide morphological data. Information about the anatomy of *Berthella platei* (Bergh, 1898) has been recently provided by Schrödl (1999). Data for the remaining taxa were derived mainly from published papers. The data for the 32 characters are presented in Table 3**.**

Willan (1987) discussed differences in the arrangement of the reproductive system of various of notaspideans. He indicated that the organs have a androdiaulic arrangement in *Pleurobranchaea*, *Pleurobranchella*, *Euselenops*, *Anidolyta* and *Pleurobranchus*, while *Berthella*, *Berthellina*, *Pleurehdera* and *Bathyberthella* have

Table 3. Data matrix for the characters of Table 2.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	*Tylodina fungina*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	*Pleurobranchus areolatus*	0	1	0	0	0	1	1	1	1	1	0	0	1	1	0	0
3	*Pleurobranchus membranaceus*	0	1	0	0	0	1	1	1	1	1	0	0	1	1	0	0
4	*Polictenidia tomasi*	0	1	0	0	1	1	1	0	?	0	0	0	1	0	1	1
5	*Tomthompsonia antarctica*	0	1	0	1	0	2	1	0	1	0	0	0	1	0	1	0
6	*Parabathyberthella orcadensis*	0	1	0	0	1	1	1	0	2	0	0	0	1	0	0	0
7	*Bathyberthella zelandiae*	0	1	0	0	1	1	1	0	?	0	0	0	1	1	0	0
8	*Bathyberthella antarctica*	0	1	0	0	1	1	1	0	2	0	0	0	1	1	0	0
9	*Bertherlla californica*	0	1	0	0	0	1	1	0	1	0	0	0	1	1	0	0
10	*Berthella plumula*	0	1	0	0	0	1	1	0	1	0	0	0	1	1	0	0
11	*Berthella* ***canariensis***	?	1	0	0	?	?	1	0	0	0	0	0	1	0	0	0
12	Berthella stellata	0	1	0	0	0	1	1	0	1	0	0	0	1	1	0	0
13	*Berthella sideralis*	0	1	0	0	0	1	1	0	?	0	0	0	1	1	0	0
14	*Berthella platei*	0	1	0	0	0	1	1	0	?	0	0	0	1	0	0	0
15	*Berthella martensi*	0	1	0	0	0	1	1	0	?	0	0	0	1	0	0	0
16	*Pleurehdera haraldi*	0	1	0	0	0	1	1	0	?	0	0	0	1	0	0	0
17	*Berthellina edwardsi*	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0
18	*Pleurobranchaea californica*	2	?	1	?	?	?	?	2	0	0	1	1	0	1	0	0
19	*Euselenops luniceps*	2	?	1	?	?	?	?	2	0	0	1	1	0	1	0	0

		17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	*Tylodina fungina*	0	0	0	0	0	0	1	?	0	0	0	0	0	0	0	?
2	*Pleurobranchus areolatus*	1	1	1	1	0	0	0	1	1	0	0	0	0	0	2	?
3	Pleurobranchus membranaceus	1	1	1	1	0	0	0	1	1	0	0	0	0	0	2	?
4	*Polictenidia tomasi*	0	1	2	1	1	1	0	1	1	1	0	0	1	1	1	1
5	*Tomthompsonia antarctica*	0	2	?	1	0	0	0	1	1	1	1	0	0	0	1	0
6	*Parabathyberthella orcadensis*	0	1	2	1	1	1	2	1	1	1	0	0	1	1	1	1
7	*Bathyberthella zelandiae*	0	1	2	1	1	1	0	1	1	1	1	0	1	1	1	1
8	*Bathyberthella antarctica*	0	1	2	1	1	1	0	1	1	1	0	0	1	1	1	1
9	*Bertherlla californica*	1	2	?	1	1	1	0	1	1	1	1	0	0	0	1	0
10	*Berthella plumula*	0	2	?	1	0	0	0	1	1	1	1	0	0	0	1	0
11	*Berthella* ***canariensis***	1	2	?	1	1	1	0	1	1	1	1	0	0	0	1	0
12	Berthella stellata	0	2	?	1	0	1	0	1	1	1	1	0	0	0	1	0
13	*Berthella sideralis*	0	1	2	1	0	1	0	1	1	1	1	0	0	0	1	0
14	*Berthella platei*	0	1	2	1	0	1	0	1	1	1	1	0	0	0	1	0
15	*Berthella martensi*	0	2	?	1	0	1	0	1	1	1	1	0	0	0	1	0
16	*Pleurehdera haraldi*	0	2	?	1	0	1	0	1	1	1	1	0	0	0	1	0
17	*Berthellina edwardsi*	0	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0
18	*Pleurobranchaea californica*	0	1	3	1	1	1	0	0	1	0	0	1	?	0	2	?
19	*Euselenops luniceps*	0	1	3	1	1	1	0	0	1	0	0	1	?	0	2	?

a triaulic condition. Ghiselin (1966) distinguished androdiaulic and triaulic systems on the basis of the number of branches of the reproductive ducts. Within the notaspideans we examined there are three distinct patterns of division of reproductive systems. In *Pleurobranchaea*, *Pleurobranchella*, *Euselenops*, *Anidolyta* and *Pleurobranchus* the hermaphroditic duct divides into the vas deferens and an oviduct that is connected to the receptaculum seminis and bursa copulatrix (Fig. 5A). These sperm storage organs are connected with the female gland mass only at the common genital atrium. While this is technically a triaulic system, it is very different from that found in other notaspideans. In *Berthella*, *Berthellina*, *Pleurehdera* and *Tomthompsonia*, the oviduct enters the female gland mass, which then exits at the nidamental gonopore (Fig. 5B). Here it meets the opening of a separate vaginal duct that joins with a distinct bursa copulatrix and receptaculum seminis. In *Polictenidia*, *Bathyberthella* and *Parabathyberthella* the oviduct also enters directly into the female gland mass, but an additional uterine duct joins the receptaculum seminis and bursa copulatrix with the female gland mass in addition to having a vaginal opening adjacent to the nidamental gonopore (Fig. 5C). The last condition is identical to the triaulic arrangement found in dorid nudibranchs. García-Gómez *et al.* (1990) distinguished two types of diauly in aeolid nudibranchs, based on the position of the receptaculum seminis relative to the oviduct and nidamental glands. In the notaspideans described above, there are three different kinds of triauly. The situation in *Pleurobranchaea*, *Pleurobranchella*, *Euselenops*, and *Pleurobranchus*, where the oviduct joins the receptaulum and oviduct, can be distinguished from the other genera where the oviduct directly enters the female gland mass. This condition is probably plesiomorphic, since it is more similar to the monaulic arrangement found in the outgroup, *Tylodina*. The modification of this system where the oviduct directly enters the female gland mass represents an apomorphy

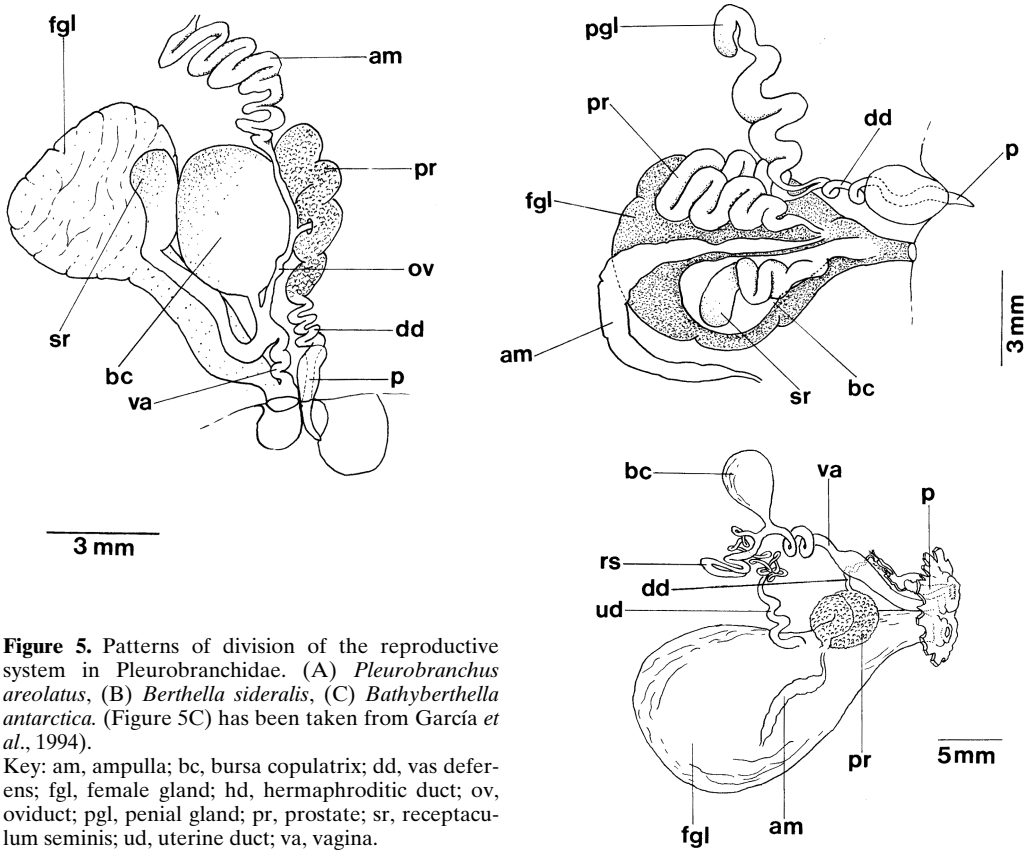

Figure 5. Patterns of division of the reproductive system in Pleurobranchidae. (A) *Pleurobranchus areolatus*, (B) *Berthella sideralis*, (C) *Bathyberthella antarctica.* (Figure 5C) has been taken from García *et al*., 1994).
Key: am, ampulla; bc, bursa copulatrix; dd, vas deferens; fgl, female gland; hd, hermaphroditic duct; ov, oviduct; pgl, penial gland; pr, prostate; sr, receptaculum seminis; ud, uterine duct; va, vagina.

within the remaining notaspideans. In *Policteni-dia*, *Bathyberthella* and *Parabathyberthella* a distinct uterine duct connects the receptaculum seminis directly with the proximal portion of the female gland mass. This is also considered apomorphic, since a uterine duct is absent in the outgroup. This described variation in reproductive anatomy is treated as two distinct characters. Oviduct: 0 = connects to receptaculum seminis, 1 = connects to female gland mass. Uterine duct: 0 = absent, 1 = present.

The matrix contained in Table 2 was analyzed using PAUP 3.1. All characters were treated as unordered and subjected to a heuristic search. This analysis yielded 278 trees with a length of 54 steps, a consistency index of 0.759 and a retention index of 0.822. The strict consensus of these trees is shown in Fig. 6. Synapomorphic characters as indicated in Table 2 are shown in this figure.

In the above analysis, *Berthella canariensis* and *B. californica* are sister species. They share two synapomorphies, the presence of elongate radular teeth and a tuberculate gill. *Berthella canariensis* and *B. californica* are included within a clade containing the other species of *Berthella* examined, *Tomthompsonia, Pleurehdera*, *Berthellina, Policteni*dia, *Parabathyberthella* and *Bathyberthella.* This clade is the sister group to *Pleurobranchus*. Within the large clade to which *B. canariensis* and B. *californica* belong, there is little resolution. *Policteni*dia, *Parabathyberthella* and *Bathyberthella* form a monophyletic subclade within this group. There is no further resolution witinin this large polytomy. Further studies examining other species of *Berthella* and

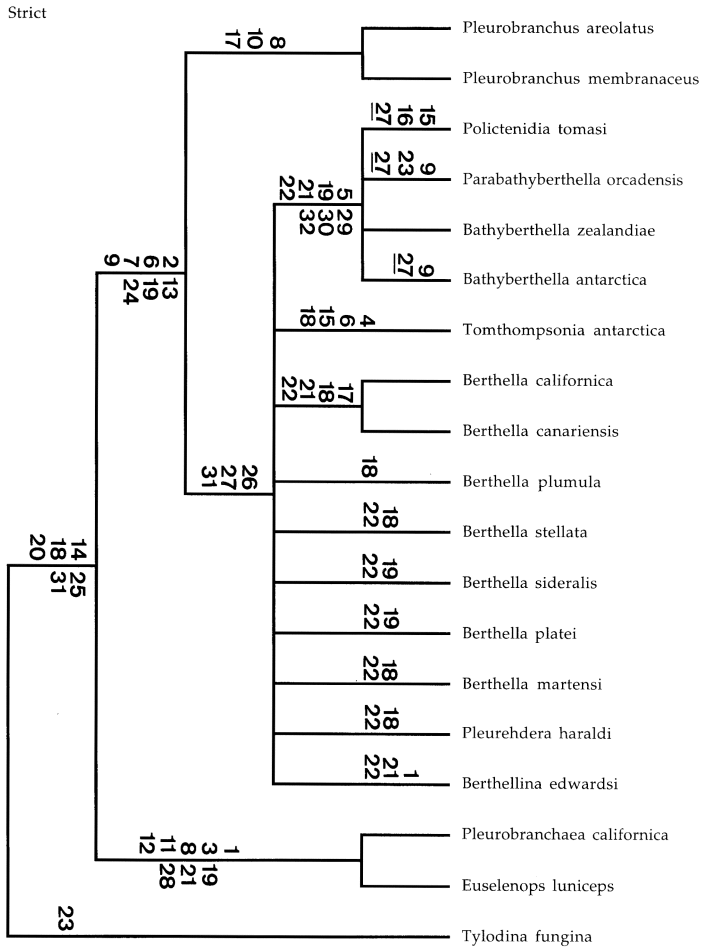

Figure 6. Strict consensus tree of the phylogenetic analysis of Notaspidea. Numbers refer to characters present in Tables 2 and 3. Reversals are indicated by underlining.

Berthellina are required to further establish the monophyly of *Berthella* and the relationships of other members of this large clade. *Berthella canariensis* has a tuberculate gill and the presence of external flaps surrounding the genital aperture that are present in species of *Pleurobranchus*. However, *Berthella californica* also has a tuberculate gill and *B. platei* has large genital flaps. These facts further support the current placement of *B. canariensis* in *Berthella* rather than *Pleurobranchus*.

The present parsimony-based analysis of the phylogeny of the Pleurobranchidae largely supports the phenetic analysis previously undertaken by Willan (1987). However, greater resolution of polychotomies requires further study of additional members of this clade.

ACKNOWLEDGEMENTS

Our sincere gratitude is extended to Mr. José Miguel Pérez Sánchez for his help during the field collections of the PBC and to Dr. Anders Warén (Swedish Museum of Natural History, Stockholm) for sending the specimens of *B. sideralis*. Dr. Richard Willan provided many suggestions for improving the manuscript. We also thank Mr. Agustín Santos his help during the preparation of the manuscript and Mr. José María Geraldía from the Electron Microscopy Service of the University of Cádiz for supplying facilities to take the Scanning Electron Microscope photographs. This paper has been partially supported by the Spanish project 'FAUNA IBERICA IV' SEUI-DGICYT PB95-0235.

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