OPISTHOBRANCHIATE MOLLUSCA FROM GHANA: AEOLIDIIDAE, WITH CONSIDERATION OF SEVERAL CARIBBEAN SPECIES

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Abstract *Descriptions are given of five species of Aeolidiidae from Ghana:* Spurilla neapolitana *and* Berghia columbina *are widespread from the Mediterranean to West Africa,* Berghia benteva *is known from Senegal and the West Atlantic, while* Berghia ghanensis *n. sp. and a single specimen tentatively placed in the genus* Spurilla, *both known only from Ghana, are also described here. Two specimens of* Berghia *from Jamaica and two from North Carolina are also described and assigned to* Berghia marcusi *while a third specimen from Jamaica is assigned to* Berghia rissodominguezi. *The process of speciation in genera with species on both sides of the Atlantic Ocean is discussed in the light of recent DNA profiling.*

Key words *Nudibranchia, Aeolidiidae,* Spurilla, Berghia, *amphiatlantic species*

INTRODUCTION

Until recently the opisthobranchiate molluscan fauna of West Africa has been poorly known (e.g. Pruvot-Fol, 1953) but a large collection of doridoid nudibranchs from Ghana has now been described (Edmunds, 2013, and earlier papers cited therein). The aeolid nudibranchs from Ghana remain relatively unknown with just four species described (Edmunds, 1968a, b).

The main purpose of this paper is to describe the aeolid nudibranchs belonging to the family Aeolidiidae collected in Ghana between 1963 and 1973. Because several of the species from Ghana have sibling or apparently closely related species in the West Atlantic, several aeolids from the West Atlantic are also described with a discussion of how some aeolids cross oceans and undergo speciation.

MATERIAL AND METHODS

All of the material described here was collected near to Accra and Tema in Ghana, close to longitude 0 latitude 5.7 by the author under stones at low tide and by Mr Walter Pople by Scuba diving and dredging. The method of collection, processing and preservation of specimens has been described by Edmunds (2007, 2011). Some of the larger specimens were found under stones etc and collected by hand, but small ones were encouraged to come to the surface of debris in the laboratory by reducing aeration. After examination most specimens were anaesthetized with magnesium chloride and preserved in Bouin's fluid. Body measurements and drawings of entire animals are from life unless otherwise stated.

The material collected and described in this paper (excluding severely damaged specimens) is deposited in the Natural History Museum, London.

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SYSTEMATIC DESCRIPTIONS

Family Aeolidiidae Gray, 1827

Diagnosis (based on Carmona, Pola, Gosliner & Cervera, 2013) Usually large aeolids with anus in cleioproctic position (i.e. amongst the cerata of the posterior digestive gland), uniseriate radula with pectinate teeth, feeding on sea anemones.

A comprehensive phylogenetic analysis of the Aeolidiidae using DNA profiling and morphological characters has validated the two genera described here, *Spurilla* and *Berghia* (Carmona *et al*., 2013).

Genus ***Spurilla*** Bergh, 1864

Type species *Eolis neapolitana* Delle Chiaje, 1841, by monotypy and subsequent designation by Bergh (1864).

Diagnosis (based on Carmona *et al*., 2013) Aeolidiid nudibranchs with wide, bilobed radular teeth; anterior groups of cerata arranged

in arches, cerata cylindrical or flattened, often curved; rhinophores with perfoliate lamellae; oral tentacles short; foot corners usually short; oral glands large.

Spurilla neapolitana (Delle Chiaje, 1841)
Figs 1A–C, E-G.

Eolis neapolitana Delle Chiaje, 1841: Pl. 73, Figs 12–14.
Eolidina neapolitana – Delle Chiaje, 1844: 7.
Eolidia neapolitana – Vérany, 1846: 97.
Facelina neapolitana – Bergh, 1861: 321.
Spurilla neapolitana – Bergh, 1864: 205, Pl. IIB, Figs 1–16.
Eolis alderiana Deshayes & Frédol, 1865, in Frédol, 1865: Pl. XVII, Fig. 7.
Flabellina neapolitana – Costa, 1866: 71, Pl. I, Fig. 1.
Flabellina inornata Costa, 1866: 72, Pl. II, Fig. 6.
Spurilla inornata – Carus, 1889–1893: 209.
Eolis conspersa Fischer, 1869: 7.
Spurilla vayssierei García-Gómez & Cervera, 1985: 154.

Material examined Teshie at low tide 1 spec. 9mm long 1 May 1965; under stone Tema beach collected by W. Pople 3 spec. 18, 18 & 15mm long 18 November 1971, NHMUK Reg. no. 20150025; Prampram beach collected by R. Isaacs 1 spec. 45mm long 24 September 1972, NHMUK Reg. no. 20150026.

External features This species is well-known in the Mediterranean but is described here because of variation in colouration. Foot broad and rounded anteriorly with sharp but not tentaculate corners. In the 9mm specimen (Fig. 1B) rhinophores and oral tentacles 2mm long, cerata 3mm, slender tail projecting 2mm beyond last cerata; rhinophores with 7 lamellae sloping from anterior ridge with 4 partial lamellae alternating with complete ones; first two groups of cerata on left side and first three on right in simple arches, remaining cerata in rows as follows: 7; 6, 3, 3, 2, 1 on left side, 7; 5, 4, 3, 3, 1 on right. (Here, and for subsequent species, ceratal group(s) anterior to heart followed by semicolon, then ceratal groups posterior to heart.)

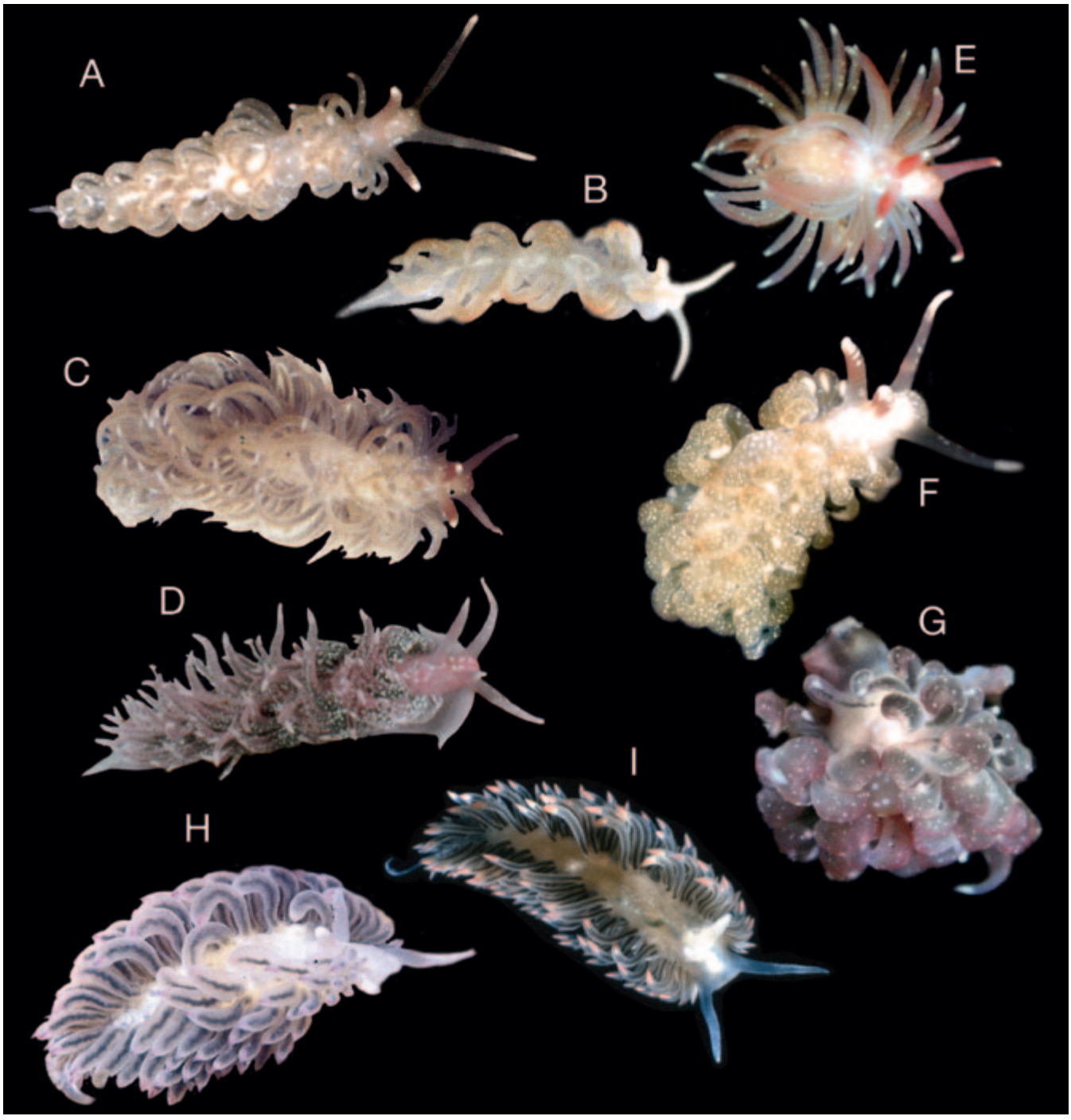
Body translucent grey with orange-yellow suffusion on head, white patches form a broken median line broadest on head and between the ceratal groups but extending to tail tip; oral tentacles tipped white; rhinophore bases grey, middle part suffused orange, tip white; digestive gland ducts in body and cerata olive-brown; larger cerata suffused pale orange, smaller ones grey, most with scattered white spots and white cnidosacs.

The three specimens from 1971 were all the same size (the 15mm animal having a deformed body and broken tail), and were under the same stone with an egg ribbon (Figs 1A, E, F, G). Apart from the larger size with many more cerata and 13 rhinophoral lamellae (alternating large and small ones), they were similar to the small specimen described above but with more numerous white spots on the cerata, white spots rather than patches dorsally on the body, and greenish grey digestive gland ducts. The damaged specimen had bright red instead of pale orange on rhinophores and oral tentacles, and the ceratal epithelium was suffused with pink or mauve (Fig. 1E); the hue of the ceras varies with the degree of contraction (Figs 1A & F).

The much larger 1972 specimen (Fig. 1C) had cerata in arches as follows: 27; 17, 17, 14, 11, 9 on the left and 23; 20, 16, 14, 11, 8 on the right. After the 6th arch the cerata were so close together that the arrangement was impossible to resolve, but there was either one more arch and two rows or 4 rows with about 14 cerata in total on each side. Anus below first arch of posterior digestive gland, gonopore below first (anterior digestive gland) arch. The rhinophores had 24 lamellae, some meeting at the otherwise flat anterior surface, others very incomplete. Dorsal surface with dense circular white spots; pale orange suffusion on head and cerata, brightest on the rhinophores; rhinophores and oral tentacles with conspicuous white tips; digestive gland ducts in cerata greenish grey, cnidosacs white.

Internal morphology The buccal mass of the 9mm specimen was removed: jaws with broad, smooth cutting edge; radula formula 10×0.1.0, each tooth arched, emarginate (i.e. with central cusp and adjacent denticles shorter than middle denticles), 17 to 25 slender denticles on each side of receded cusp.

Behaviour An egg ribbon was found on the stone with the three animals close by: it was a coil of 1½ turns, 7mm diameter, with the eggs in a spiral coil within the ribbon. When the animal is crawling, the cerata are normally held over the



Figures 1A–C, F–G *Spurilla neapolitana* Delle Chiaje, 1841: **A, E, F** & **G** Tema, Ghana, all 18mm long, 1971, **A** & **F** are the same specimen, **E** had a broken tail; **B** Teshie, Ghana, 9mm long, 1965; **C** Prampram, Ghana, 45mm long, 1972. **Fig. 1D** *Spurilla braziliana* McFarland, 1909: Port Royal, Jamaica, 37mm long, December 1961. **Figs 1H–I** *Berghia benteva* (Marcus, 1958): **H** from Ghana; **I** from North Carolina, photo by Rick Fox.

back, each one in a curve (Figs 1A, B). When at rest the cerata are often contracted so are much shorter and thicker (Fig. 1F). When disturbed the cerata can be held upright with the tips projecting upwards (Fig. 1C), while if violently molested the body contracts, the cerata are elongated and violently waved about (Fig. 1E), presumably as a form of deimatic display.

Geographical range Mediterranean and East Atlantic from France to the Canary Islands, Madeira, Azores, Morocco, Senegal and now

Ghana (Schmekel & Portmann, 1982; Bianchi, Haroun, Morri & Wirtz, 2000; Cervera, Calado, Gavaia, Malaquias, Templado, Ballesteros, García-Gómez & Megina, 2006; Carmona *et al*., 2013; Carmona, Lei, Pola, Gosliner, Valdés & Cervera, 2014). Records of this species from the West Atlantic and the Indo-Pacific are now considered to be of the different but closely related species, *S. braziliana* McFarland, 1909 (Carmona *et al*., 2013: Carmona, Lei *et al*., 2014; see below).

Remarks The anatomy of this species from the Mediterranean and East Atlantic is well-known (see descriptions and reviews by Schmekel & Portmann, 1982; García & Cervera, 1985; & Carmona, Lei *et al*., 2014). The degree of contraction of the cerata is variable (see above), and the body colour varies from more or less colourless with a faint orange tinge to the head and rhinophores to bright orange. The colour of the digestive gland ducts varies with diet as in many other aeolids but is typically greenish grey. The digestive gland ducts are often clearly visible ramifying into the head and body, but they were not seen in Ghanaian specimens (Figs 1A, B, C, E). The white on the dorsum can be in patches and lines or as scattered or dense circular white spots: this variation appears to be related to the age of the animal, the young ones having patches and older ones spots (see above). Lance (1999) followed this change in a single individual of an animal he believed to be *Spurilla neapolitana* but which we now know was the closely related *Spurilla braziliana* (see below). The recently described *Spurilla onubensis* Carmona, Lei, Pola, Gosliner, Valdés & Cervera, 2014 is much brighter red but does not have any white spots. *Spurilla mograbina* Pruvot-Fol, 1953 from Morocco has a colour pattern not reported for *Spurilla neapolitana*, so may be a distinct species rather than an extreme colour form of *neapolitana* (Carmona, Lei *et al*., 2014). However, the two paintings published by Pruvot-Fol (1953 Plate I Fig. 12 and Plate II Fig. 27) differ in colour and in the shape of the foot corners, so their identity must await collection of further specimens.

Spurilla neapolitana has been thought to have an amphiatlantic distribution, with a few recent records from the Indo-Pacific, but studies by Carmona *et al*. (2013) and Carmona, Lei *et al*., (2014) have shown that there are substantial differences in the mitochondrial and nuclear genes of West and East Atlantic *Spurilla* sufficient to justify recognition of three distinct species, *Spurilla neapolitana* (Delle Chiaje, 1841) in the east and *Spurilla braziliana* McFarland, 1909 and *Spurilla sargassicola* Bergh, 1871 in the west. In *S. neapolitana* the foot has angled corners whereas in *S. braziliana* and *S. sargassicola* there are short digitiform projections (clearly shown in Fig. 1D). *Spurilla neapolitana* and *Spurilla sargassicola* have a reticulate digestive gland usually easily visible in the head and body of the living animal whereas in *S. braziliana* it is rarely visible in dorsal view. This difference appears to depend on whether the animal has fed on actinians containing zooxanthellae which it has sequestered into its digestive gland (Rudman, 1999). *S. sargassicola* further differs from the other species in the shape and disposition of the cerata and in its ecological habitat of living on floating *Sargassum muticum* seaweed where it feeds on epizootic sea anemones.

Carmona, Lei *et al*. (2014) have recently described two further species of *Spurilla* from the Atlantic: *Spurilla onubensis* from France, Spain and Morocco, and *S. dupontae* from the Bahamas. Living specimens of these two species can be easily distinguished from *S. neapolitana* by their colouration. DNA profiling has shown that *S. neapolitana* and *S. sargassicola* are sister species in one subclade while the other three species form a separate subclade in which *S. onubensis* and *S. dupontae* are sister species (Carmona, Lei *et al*., 2014). Thus, subject to more comprehensive DNA profiling, the evolutionary relationships of these five species is clear.

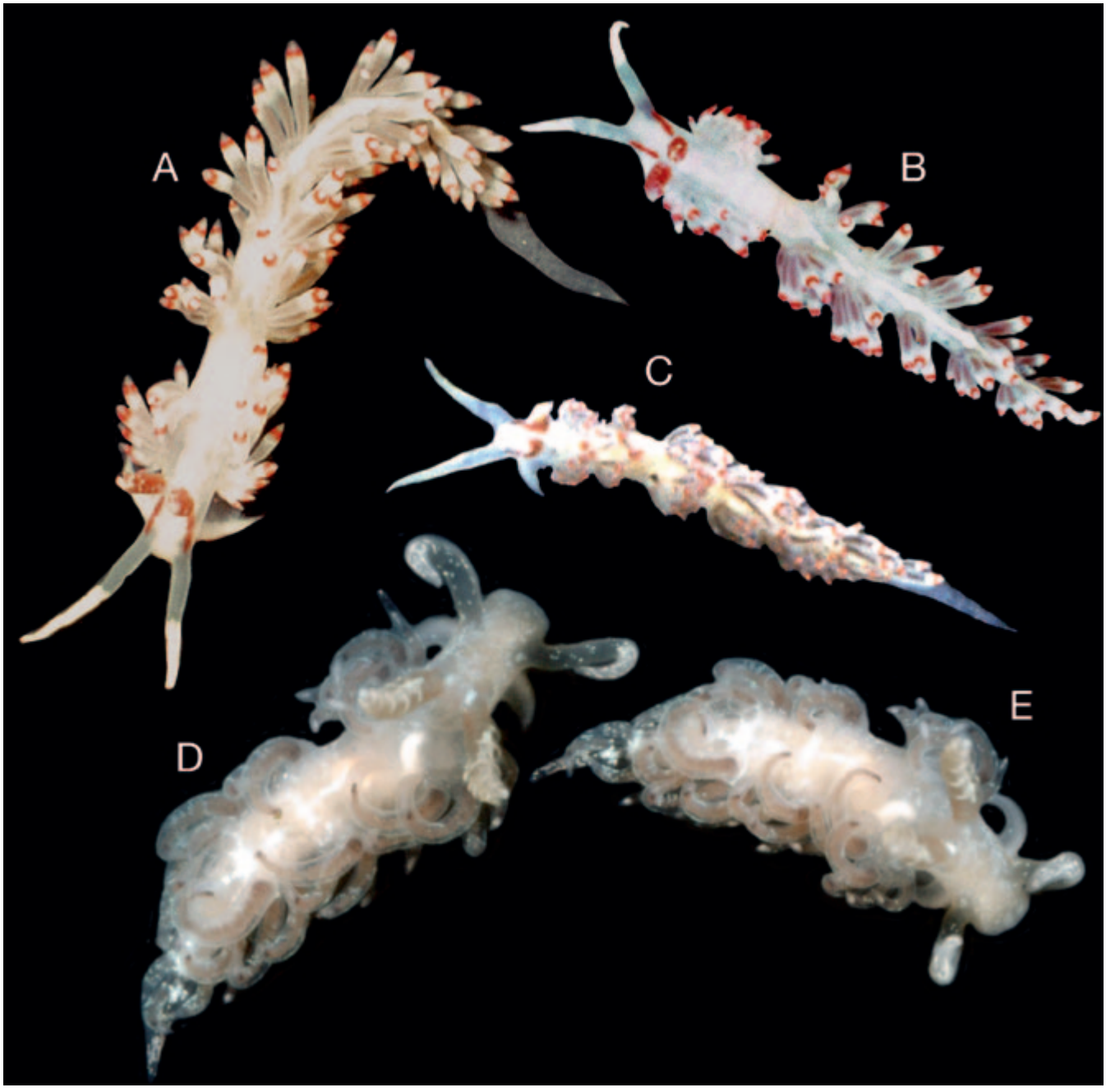
The date of authorship of *Spurilla neapolitana* is given as 1823 and 1841 by different authors, but I can find just two references to this species in Delle Chiaje's monograph dated 1841 and 1844 (as listed in the synonymy above). Gary McDonald has kindly provided the following information from his invaluable bibliography: 30 authors of systematic/taxonomic publications have used the date 1823, 6 have used 1824, 4 have used 1828, 5 have used 1830 and 9 have used 1841. He adds: "My gut feeling is that Delle Chiaje, 1841 is the source for *S. neapolitana*, and because of the 1822–1830 date in the title, various authors have used various dates…. I've also looked through Delle Chiaje 1822, 1823–1824, 1825–1827, 1828 & 1830 and found no *Eolis neapolitana*." Carmona, Lei *et al*. (2014) have also reviewed the date for this species and arrived at

the same conclusion. In this paper I have therefore cited 1841 as the date, as have several other recent authors (e.g. Valdés, Hamann, Behrens & DuPont, 2006; Gosliner, Behrens & Valdés, 2008).

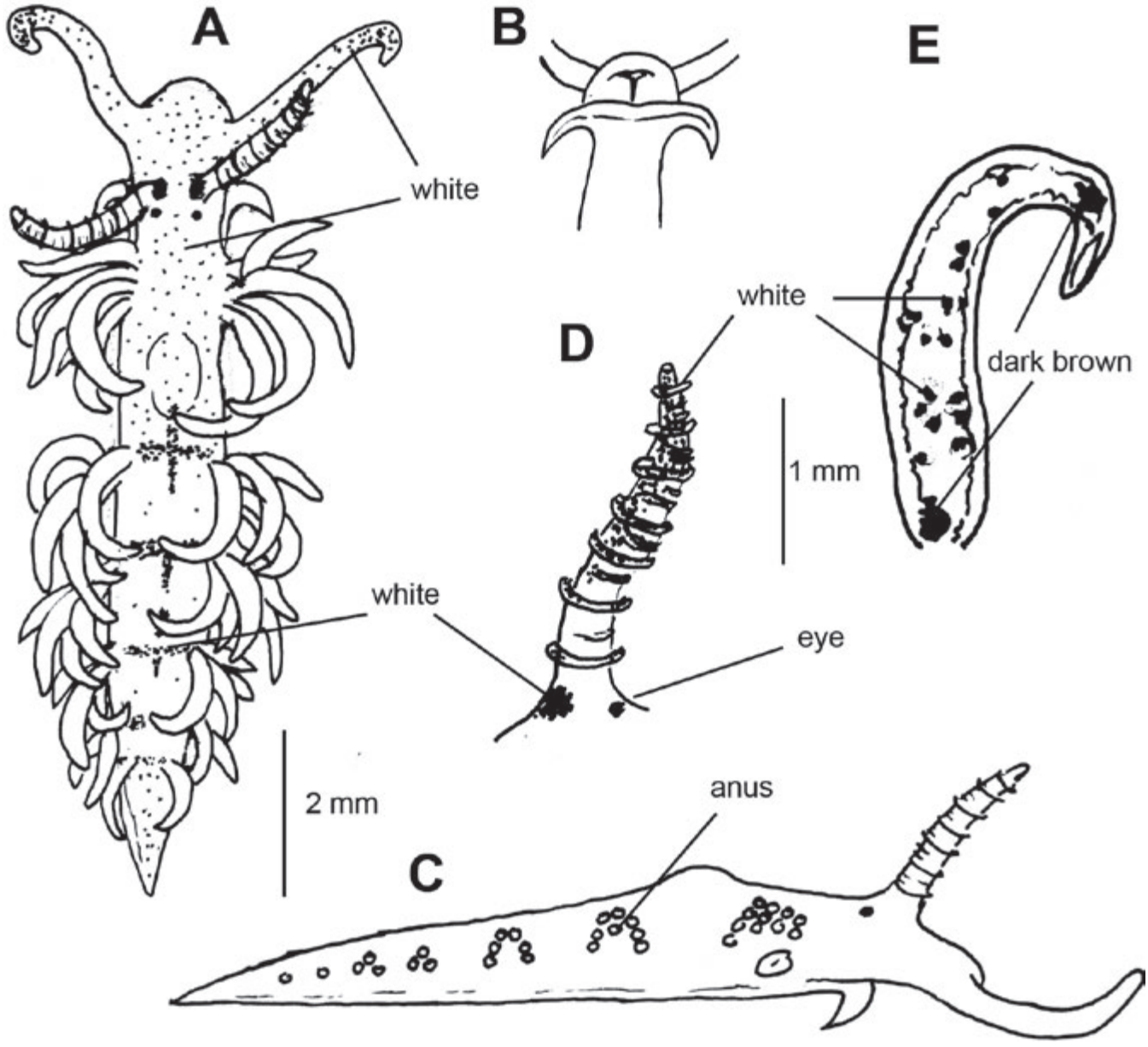
Spurilla species A
Figs 2D, E; 3

Material examined Dredged from 40m south of Tema 1 spec. 10mm long 23 February 1970, NHMUK Reg. no. 20150032.

External features Body broad with large eyes and very short pointed tail, foot slightly broader than body (Fig. 3B), rounded anteriorly with slight notch, bilabiate with slender, almost tentaculiform, pointed corners; oral tentacles arising from behind the front of the oral veil, often held in a curve; rhinophores lamellate from just above base with 7 complete sloping rings and about 10 partial rings (Fig. 3D); anterior cerata in rows, posterior cerata in arches as follows: 2, 2, 3, 2, 2; 7, 7, 4, 2, 2, 1 on the left, 2, 2, 3, 4; 7, 6, 3, 3, 1, 1 on



Figures 2A–C *Berghia ghanensis* n. sp.: **A** holotype, 19mm long, 1970; **B** 11mm long, 1970; **C** 15mm long, 1965. **Figs 2D–E** *Spurilla* species A: two views of same specimen, 10mm long.



Figures 3A–E *Spurilla* species A: **A** dorsal view; **B** ventral view of head; **C** side view of living animal, semi-diagrammatic to show ceratal arrangement; **D** left side view of right rhinophore; **E** ceras.

the right. Cerata long, curved, pointed (Fig. 3E), anus below first arch of posterior digestive gland, gonopore below first three rows of first group of cerata (anterior digestive gland) (Fig. 3C).

Body suffused pale orange, palest posteriorly, scattered white spots on head and dorsal surface concentrated in a broken medial line and transverse lines between each ceratal group (Figs 2D, E; 3A); basal half of oral tentacles pale orange with scattered white spots, densest distally, but tip clear; rhinophores suffused pale orange, brightest proximally, large white spot at base on medial side, dense white dots and patches in distal half on lamellae at front and rear, and at tip; digestive gland in cerata brown with dark brown spots at base and just below cnidosac, white spots scattered over surface, cnidosac pale cream; foot pale greyish.

Internal morphology Not examined so as not to damage the single specimen.

Geographical range Known only from this record from Ghana.

Remarks Although I have not examined the radula, the broad body and foot together with the

sloping lamellae on the rhinophores and curved cerata indicate that this specimen is probably an aeolidiid rather than a facelinid, and these characters are shared with species of *Spurilla* (see above). However, the anterior cerata on each side arranged in multiple rows rather than in an arch, and the slender, almost tentaculate foot corners are not found in the five species of *Spurilla*. This specimen therefore remains enigmatic, but it appears from my experience to resemble *Spurilla*, so I have placed it provisionally in this genus.

Genus ***Berghia*** Trinchese, 1877

Type species *Eolidia coerulescens*, Laurillard 1832, by monotypy and subsequent designation by Trinchese (1877).

Diagnosis (based on Carmona, Pola, Gosliner & Cervera, 2014) Aeolidiid nudibranchs usually with elongate, slender body; foot corners short, slender; rhinophores usually papillate; oral tentacles longer than rhinophores; cerata usually arranged in arches, cerata long, slender, cylindrical, more or less uniform diameter throughout their length, with rounded apices; genital aperture below anterior group of cerata, reproductive system diaulic; oral glands composite, large and tubular; radular teeth bilobed, deeply indented; jaws varying intraspecifically with or without denticles on masticatory edge.

The species of *Berghia* from the East Atlantic

The genus *Berghia* is only known from the Atlantic Ocean with species described from both east and west coasts (Carmona, Pola *et al*., 2014). The number of European species has been the subject of confusion for a great many years with uncertainty as to whether the two names *Berghia coerulescens* (Laurillard, 1832) and *B. verrucicornis* (Costa, 1867) refer to the same or to different species. Using material from the Atlantic coast of France, Tardy's (1962) careful study showed that these two names refer to distinct species both of which also occur in the Mediterranean. (Another species, *Berghia norvegica* Odhner, 1939, a cold water species from northern Norway, is very different in colouration and in other features and will not be considered further here.) Tardy's conclusion has been supported by more recent workers (e.g. Schmekel & Portmann, 1982; Cervera *et al*., 2006), but a third species has since been described from southern Europe, *B. columbina* (García-Gómez & Thompson, 1990) (initially placed in the genus *Spurilla*) which has different colour markings from both *B. coerulescens* and *B. verrucicornis*. All three species occur on the Atlantic coast of the Iberian peninsula, the Mediterranean and south to the Canary Islands (Muniain & Ortea, 1999; Cervera *et al*., 2006), while *B. verrucicornis* has also been found on the West African coast in Senegal (Poddubetskaia, 2003). Reports of *B. verrucicornis* from Ghana and Príncipe (Edmunds, 1968a; Muniain & Ortea, 1999) are more controversial and will be discussed further below. A fourth warm-water species has recently been described from Senegal, *Berghia marinae* Carmona, Pola, Gosliner & Cervera, 2014.

Tardy (1962) followed by Edmunds (1968a), García-Gómez & Thompson (1990) and Domínguez, Troncoso & García (2008) attempted to clarify the differences between the species which they recognised in tables but some of the characters which they used are not useful without qualification: thus number of ceratal groups, number of cerata and number of denticles on radular teeth all increase with the size of the animal, so quoting them without reference to body length is of limited value. For this reason I have omitted these characters from Tables 1 and 2. Tardy also noted a difference in the ratio of body width to body length in live animals of *B. coerulescens* and *B. verrucicornis*, but he did not specify the precise way in which the measurements were made, whether the animals were crawling or stationary and whether the width was that of the body or of the foot. In Tables 1 & 2 I have taken measurements from photographs of crawling animals: body length from front of head to tail tip and width of the body (not of the foot) in the pericardial region between the first two groups of cerata which can often be seen in a fully extended animal. Where I have more than one photo of a specimen I give the measurements from different photos. I have also attempted to measure this ratio in published photos and drawings of some other species although this is less reliable if the animal was not fully extended or if cerata hide the body width. Further problems are that small specimens of many species of aeolid often have paler colouration than larger ones, and the colour of the digestive gland in the cerata varies depending on the food eaten. The general configuration of the reproductive system

is very similar in all species of *Berghia*: there are differences in the dimensions of the various structures (Carmona, Pola *et al*., 2014), but how much weight should be placed on these without dissections of several individuals of each species of different sizes is not known.

I conclude that in the absence of more precise information on these characters, the most reliable characters for distinguishing the species of *Berghia* are maximum body length, body width as a proportion of length, shape of cerata and details of colouration. In some species there are also important differences in arrangement of preanal cerata and shape of the egg ribbon.

A further problem with species of *Berghia* is that collectors usually find just one or two specimens on each occasion and the next specimens found may not have identical colouration so that it is difficult to be sure if they are the same species. Documenting intraspecific colour variation is thus not easy. Observing copulation between animals with different colour patterns can be successful if there is a large collection as occurred with *Eubranchus farrani* (Edmunds & Kress, 1969), but with just one or a few specimens found on each occasion molecular studies are required to confirm whether or not they belong to the same species.

Berghia benteva (Er. Marcus, 1958)
Figs 1H, I; 4A–F

Baeolidia benteva Er. Marcus, 1958: 65–69, Figs 105–111.
Berghia benteva – Ev. Marcus, 1976: 9.
Antaeolidiella benteva – Miller, 2001: 633.
Aeolidiella benteva – García García *et al*., 2008: 189.
Berghia dakariensis – Caballer & Ortea, 2013: 440, Figs 1–2.
non Spurilla dakariensis Pruvot-Fol, 1953: 55–57, Fig. XVIII.
non Aeolidiella benteva – Valdés *et al*., 2006: 274–5.

Material examined Under stone on Tema breakwater 1 spec. 19mm long 8 February 1973, NHMUK Reg. no. 20150031.

External features Foot slightly broader than body when actively crawling, rounded and transversely grooved anteriorly with short, pointed but not tentacular foot corners and a short tail (Figs 4A, B); oral tentacles 4mm long; rhinophores 3mm long with about 50 papillae on posterior surface (Fig. 4E); cerata in front of anus arranged in 10 or 11 rows with up to 8 cerata in each row and about 50 in total (Fig. 4F), posterior cerata in about 12 groups, first 7 as arches, posterior ones in rows, but so close together that they are impossible to count without detaching them with about 80 in total on each side.

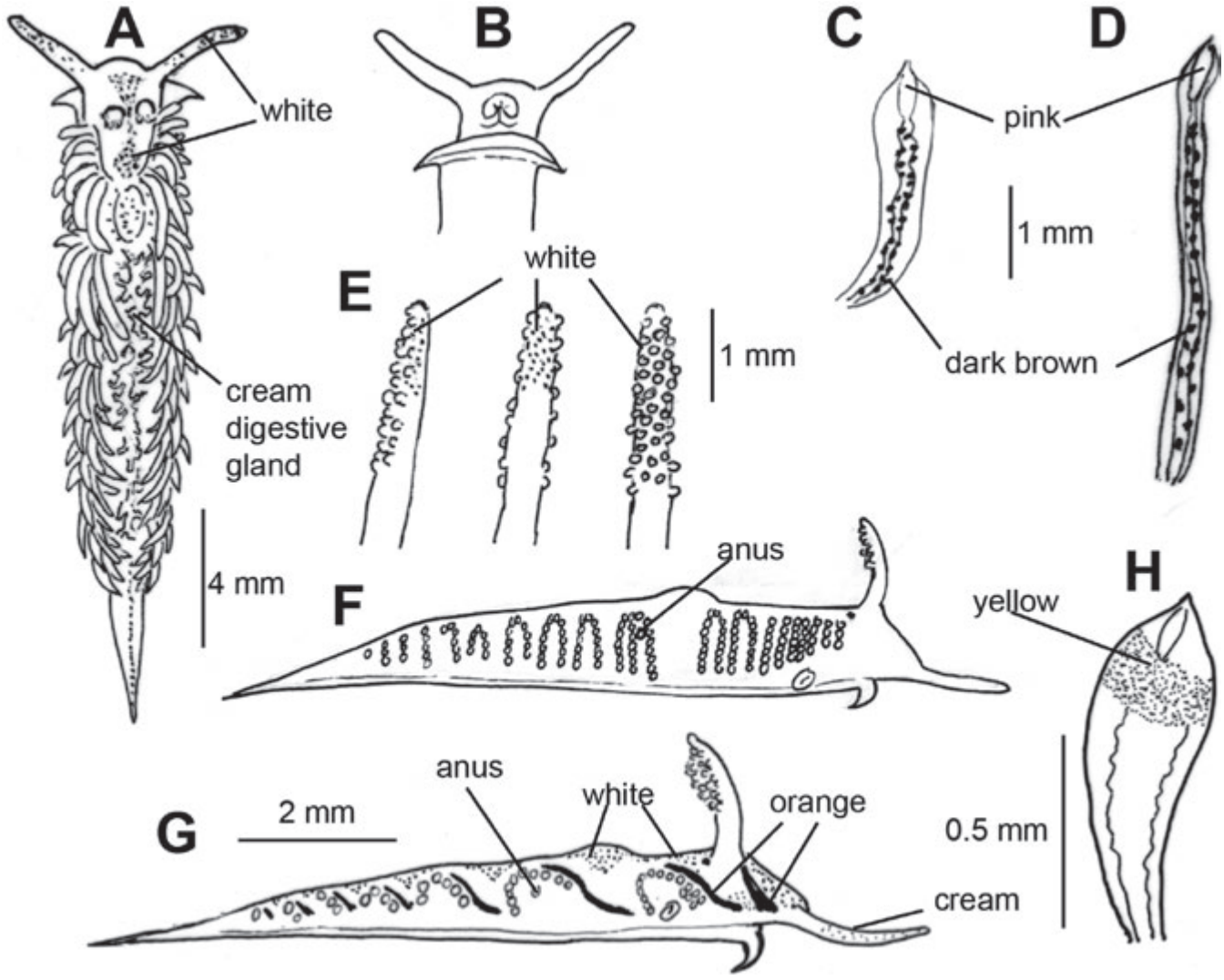
Cerata broad, often held curled over back as in *Spurilla neapolitana* (see Fig. 1H), often slightly broader just below cnidosac then abruptly tapering to a mucronate tip. They can be extended when the animal is disturbed to up to 5mm (Fig. 4D) or very much retracted (Fig. 4C).

Body grey with white dots dorsally dense enough to form a line between rhinophores and on tail, irregular elsewhere, but with some cream digestive gland branches visible where not obscured by white pigment (Figs 1H, 4A); oral tentacles white distally; rhinophores grey with white distal third and white tubercles Fig. 4E); ceratal epithelium pearly grey partly obscuring brown digestive gland ducts with darker brown tubercles, cnidosac bright pink (Figs 1H, 4C, D).

Internal morphology Not examined so as not to damage the single specimen.

Geographical range West Atlantic: Brazil (Marcus, 1958; Domínguez *et al*., 2008), South Carolina (Eyster, 1980), North Carolina (Marcus, 1961; Fox, personal communication, this paper); East Atlantic: Senegal (Caballer & Ortea, 2013) and Ghana (this paper).

Remarks The original description of *Baeolidia benteva* Marcus, 1958 from Brazil gave no indication of the colouration alive. It was found again in Brazil and described with colour illustrations of the living animal by Domínguez *et al*. (2008) and by Carmona, Pola *et al*. (2014). The cerata arising from the anterior digestive gland are described as being in rows by Marcus (1958) but in arches by Carmona, Pola *et al*. (2014). This difference may be a function of age: Marcus's specimens were 12 and 15mm long preserved compared with 9 and 10mm for Carmona's animals. The specimens studied by Domínguez *et al*. were 10–19mm alive and my own animal was also 19mm alive (probably similar in size to Marcus's specimens), and the illustrations of both of these show several anterior rows of cerata followed by one or more arches.



Figures 4A–F *Berghia benteva* (Marcus, 1958), 19mm long: **A** dorsal view; **B** ventral view of head, **C** contracted ceras; **D** extended ceras; **E** side, front and rear views of rhinophore; **F** side view of animal, semi-diagrammatic to show arrangement of cerata. **Figs 4G–H** *Berghia columbina* (García-Gómez & Thompson, 1990), 9mm long: **G** side view of living animal, semi-diagrammatic to show ceratal arrangement and colour markings; **H** contracted ceras.

The body colour has been described as 'whitish to cream' (Domínguez *et al*., 2008), 'translucent white' (Carmona, Pola *et al*., 2014) and 'grey' (this paper). In most aeolids the body is translucent (i.e. semi-transparent) and it may be coloured (e.g. orange or violet) or colourless where its appearance may be described by different authors as whitish or greyish.

A history of the generic placement of this species is summarised by Carmona, Pola *et al*. (2014) whose DNA profiling and phylogenetic analysis confirm that it belongs to the genus *Berghia*. Although originally described from Brazil it has recently been reported from Senegal by Caballer & Ortea (2013) under the earlier name *Berghia dakariensis* (Pruvot-Fol, 1953). However, Carmona *et al*. (2013) have pointed out that Pruvot-Fol's description is so inadequate that her specimen could equally be a species of *Spurilla*, so they conclude that *Spurilla dakariensis* Pruvot-Fol, 1953 should be considered a *nomen dubium*. I have accepted this conclusion so the name of this amphiatlantic species is *Berghia benteva*. Caballer & Ortea (2013) also consider that the specimen identified by Pruvot-Fol (1953) as *Baeolidia moebbi* is *Berghia dakariensis* (= *benteva*), but Pruvot-Fol gives no information on the colouration of this specimen so I consider that it should remain simply as an unidentified species of *Berghia*.

A photograph of a *Berghia* from North Carolina taken by Dr R Fox has similar external morphology to *Berghia benteva* with characteristic pink

cnidosacs so must surely belong to this species, but the specimen illustrated by Valdés *et al.* (2006) under the name *Aeolidiella benteva* has orange tipped cerata so may be a different species (*B. marcusi* has been suggested by a referee). *Berghia benteva* always seems to have pink cnidosacs which are very noticeable in life and particularly in Dr Fox's photograph (Fig. 1I), but not always easily seen in other photographs, e.g. Fig. 1H.

***Berghia ghanensis* n. sp.**
Figs 2A–C

Berghia verrucicornis – Edmunds, 1968a: 212–214, Figs 7, 9A-C.

Material examined 10m reef Kpone Bay 1 spec. 15mm long 22 January 1965, NHMUK Reg. no. 20150028; rock pool at Teshie 1 spec. 11mm long 30 December 1970, NHMUK Reg. no. 20150030; under stone at low tide West Tema 1 spec. 19mm long 31 December 1970, NHMUK Reg. no. 20150029.

Holotype NHMUK Reg. no. 20150029 from under stone low tide, West Tema, Ghana, 31 December 1970, collected by M. Edmunds.

External features The 15mm specimen has already been described (Edmunds, 1968a Fig. 7) but a photo is published here for the first time (Fig. 2C). The 19mm holotype has the foot slightly broader than the body (2.5mm) when actively crawling (Fig. 2A), rounded anteriorly with short, pointed but not tentacular foot corners and a slender tail; oral tentacles long; rhinophores with numerous papillae on posterior surface; first five groups of cerata on each side arranged in arches, the last three groups in rows, first two arches on the right with two rows of cerata at base of each arm of the arch (as illustrated by Edmunds, 1968a): 21; 14, 12, 7, 5, 3, 2, 1 on the left, 22; 14, 8, 7, 5, 4, 3, 2 on the right. Cerata slender, straight, broadest just below cnidosac. Anus below first arch of cerata of posterior digestive gland.

Body translucent grey with head very faintly tinged orange, pair of orange-red patches between rhinophores and bases of oral tentacles (Fig. 2A); broad cream line mid-dorsally from front of head to last cerata, narrower between ceras insertions, with a few spots on tail; oral tentacles cream in distal half; rhinophores with transparent stalk and tip with a few cream dots, papillae bright orange to orange-red; cerata transparent grey with broad white ring distally followed by bright orange-red ring, another white ring and clear tip, cnidosac whitish, digestive gland ducts brown.

The 11mm specimen was similar but with foot 1.75mm broad and 15; 9, 7, 4, 3, 1, 1, 1 cerata on the left side and 13; 9, 6, 4, 3, 1, 2, 1 on the right. No orange tinge on head but marks on head and cerata almost red instead of orange-red (Fig. 2B); mid-dorsal cream line broken on head and heart and absent from tail; rhinophores with orange-red basal papillae, cream distal papillae and tip; orange-red ceratal ring often incomplete posteriorly and usually with cream just below tip.

For the three specimens the ratios of body width to length (as percentages) are: 19mm specimen: (6.8, 7.0, 8.1) mean 7.3%; 15mm specimen: (6.4, 7.7) mean 7.1%; 11mm specimen: (7.6, 8.8) mean 8.2%. The principal characters of this species compared with similar species of east Atlantic *Berghia* are summarised in Table 1.

Internal morphology The radula and jaws of the 15mm specimen have been described and illustrated previously under the name *Berghia verrucicornis* (Edmunds, 1968a Fig. 9 A–C). There are small pointed denticles on the cutting edge of the jaw and the radula has 13 complete teeth each of which is bilobed with up to 24 needle-like denticles on each side of the receded cusp.

Behaviour The two larger specimens immediately ejected nematocysts when poked with forceps. The 19 and 11mm specimens from December 1970 were placed together and were found copulating the next day, so the two are clearly conspecific and they mature at a relatively small size.

Geographical range Known from the present records from Ghana and also from Príncipe in the Gulf of Guinea (Muniain & Ortea, 1999, who identified it as *B. verrucicornis*; see also below).

Etymology The species is named from its occurrence in Ghana.

Remarks The 1965 specimen was compared with European *Berghia* as distinguished by Tardy (1962) and was initially identified as *B. verrucicornis* (Edmunds, 1968a). However, many photos of *B. verrucicornis* have now been published (e.g. Sea Slug Forum, 2001–2003; Nudipixel, 2014; Mediterranean Opisthobranchs, 2014) from

which it is clear that European specimens as well as some from Senegal are greyish white with bright orange-yellow cheek stripes, rhinophoral papillae and rings round the cnidosac region of the cerata; the digestive gland is usually pale brown (occasionally dark brown), and there is a white line mid-dorsally, often expanded in the cardiac region. The specimens from Ghana differ in three characters:

1. the hue of the orange markings on the head, rhinophores and cerata which are orange-red, not orange-yellow;
2. the body width as a percentage of length (see Table 1);
3. pointed denticles on the masticatory border of the jaw (Edmunds, 1968a Fig. 9C) compared to the finely pectinate border of *B. verrucicornis* (described but not illustrated by Tardy, 1962, and recently illustrated by Carmona, Pola *et al*., 2014).

The apparent difference in the masticatory teeth may be due to comparing a camera lucida drawing with an SEM image: the denticles are of similar size in the two preparations: 40 in a 50µm strip of jaw edge for *B. ghanensis* compared with 37 for *B. verrucicornis*. However, the light microscope preparation of the former with the masticatory border flattened showed each denticle separated from its neighbour by a clear trough while the SEM of the latter shows overlapping triangular denticles. It would be useful to see this structure in two specimens from the same locality with one drawn and the other as an SEM image so as to check how different they appear yet still belong to the same species.

Some *B. verrucicornis* from the Mediterranean have bright red mid-dorsally over the heart and dark digestive gland ducts (Trinchese, 1881, as *B. coerulescens*; Mediterranean Opisthobranchs, 2014) but this was not observed in any of the Ghanaian animals. García-Gómez & Thompson (1990) describe the cerata of *B. verrucicornis* as being 'globular', and their drawing shows a broad ceras widest just below the cnidosac. However, Tardy (1962) describes the cerata of this species as being similar to those of *B. coerulescens* i.e. cylindrical and slightly obtuse at the tip. In numerous photos of live *B. verrucicornis* on the Internet none of the cerata have the shape depicted by García-Gómez & Thompson, but cerata do vary in shape depending on their degree of contraction: the one illustrated by Edmunds (1968a Fig, 7D) was contracted and broadest distally very like the one drawn by García-Gómez & Thompson (1990 Fig. 5C). Finally the material described here does not appear to be part of a cline from Europe round the coast of West Africa to Ghana because specimens from Senegal are identical with those from the Mediterranean (photos by Poddubetskaia, 2003, 2006; Mediterranean Opisthobranchs, 2014). My Ghanaian specimens also differ from *Berghia columbina* and *Berghia marinae* in colouration (notably absence of orange line marking ceratal insertions) and denticulate jaws (see Table 1). I conclude that my Ghanaian specimens belong to a hitherto undescribed species, *B. ghanensis*, which differs from *B. verrucicornis* in body shape, colouration and cutting edge of jaw. Muniain & Ortea (1999) report that a specimen from Príncipe identified as *Berghia verrucicornis* is very similar to and conspecific with the specimen described by Edmunds (1968a) from Ghana, so this specimen is probably also *B. ghanensis*.

Berghia columbina (García-Gómez & Thompson, 1990)
Figs 4G-H; 5A

Spurilla columbina García-Gómez & Thompson, 1990: 323–330, Pl. 2, Figs 1–4.
Berghia columbina – Muniain & Ortea, 1999: 148.

Material examined 10m reef Kpone Bay 1 spec. 9mm long 16 April 1969, NHMUK Reg. no. 20150027.

External features Foot slightly broader than body (1.5mm) when actively crawling, rounded anteriorly with short, pointed but not tentacular foot corners and a slender 3mm tail; oral tentacles 2.5mm long; rhinophores 2.5mm long with numerous papillae on posterior surface; first four groups of cerata on each side arranged in arches, the last three in rows (Fig. 4G), anterior arm of first arch with two rows of cerata at base: 16; 10, 6, 4, 3, 2, 1 on the left and 16; 10, 6, 4, 3, 2, 1 on the right. Cerata slender, straight or slightly curved, broadest just below cnidosac but tapering to a pointed tip. Anus below first arch of posterior digestive gland; gonopore below arch of right anterior digestive gland. Ratio of body width to length: 12%

Body (Figs 4G, 5A) grey with faint orange tinge at base of oral tentacles, just behind eyes and over heart, orange line on side of head running from

rhinophore diagonally to just lateral to base of oral tentacle ('cheek stripe' in Table 1), orange lines on body on dorsal side of each ceratal group, each line running from highest ceras in group anteroventrally along insertions of other cerata and continuing laterally for a short distance in front of most anterior ceras; patches of white dorsally between orange lines on head, laterally between orange line on head and orange line from first ceratal group, and medially behind rhinophores, continuing back as broad white line mid-dorsally to last cerata, narrower between ceras insertions, with a few spots on tail; oral tentacles with dense cream spots in distal half; rhinophores with basal half orange, distal half creamy yellow, tip clear; cerata (Fig. 4H) grey with broad ring of dense yellow dots just below pale whitish cnidosac, tip clear, digestive gland ducts pale brown but not granular.

Internal morphology Not examined.

Geographical range Mediterranean coast of Spain, Atlantic coast of Spain & Portugal, Morocco, Canary Islands, Senegal (García-Gómez & Thompson, 1990; Cervera *et al*., 2006; Domínguez *et al*., 2008; Carmona, Pola *et al*., 2014) and now Ghana (this paper).

Remarks García-Gómez & Thompson (1990) state that there are up to 11 rows of cerata in *B. columbina*, but most *Berghia* have the cerata arranged in arches anteriorly and rows further back; furthermore their Plate 2D appears to show the anterior cerata in an arch rather than a simple row, so I consider this to be an error in their description. My specimen from Ghana agrees with *B. columbina* as described by García-Gómez & Thompson in most characters but has much less orange on the body and ceratal epithelia (see Table 1). However there is considerable variation in the amount of orange in *B. columbina*: specimens illustrated by García-Gómez & Thompson (1990, Plate 2D) and by Domínguez *et al*. (2008, Fig. 8C) have more orange than the two in García-Gómez & Thompson (Plate 2C). Furthermore, the Ghanaian specimen was smaller than the ones described by García-Gómez & Thompson (1990), and young specimens of many nudibranchs often have less marked colouration than mature ones.

The Ghanaian specimen has two other differences from the type description: the rhinophores are large and distinctly clavate rather than of uniform diameter or slightly tapering, and the superficial pigment in the cnidosac region is distinctly yellow rather than white. Nevertheless it is so similar in most characters to *B. columbina* from Spain (Table 1) that I consider it to belong to this species.

The species of *Berghia* from the West Atlantic

In the West Atlantic specimens having orange-red stripes marking the ceratal bases were initially identified as *Berghia coerulescens* (Marcus Er, 1957, 1961; Marcus & Marcus, 1959), but following Tardy's 1962 paper Eveline Marcus decided that these were really *B. verrucicornis* (Marcus Ev, 1972). However, these specimens do not agree in colouration and other characters with either *B. coerulescens* or *B. verrucicornis*, so Muniain & Ortea (1999) assigned them to a new species which they described from Argentina: *Berghia rissodominguezi* Muniain & Ortea, 1999. A few years later another new species was described from Brazil, *Berghia marcusi* Domínguez, Troncoso & García, 2008, and these workers decided that the earlier material of Ernst and Eveline Marcus belonged to this species rather than to *B. rissodominguezi*, a view which has been supported by Carmona, Pola *et al*. (2014). *B. rissodominguezi* is a large species while *B. marcusi* is much smaller, and there are clear differences between these two species in the shape and colour of the orange cheek stripe, and the colouration of the rhinophores and cerata (see Domínguez *et al*., 2008 & Carmona, Pola *et al*., 2014, and summary in Table 2). Three further species of *Berghia* have also been described: *Berghia benteva* (Marcus, 1958) (originally as *Baeolidia benteva*), *Berghia creutzbergi* Marcus & Marcus, 1970, and *Berghia stephanieae* (Valdés, 2005). *Berghia creutzbergi* and *Berghia benteva* have very different colouration from the other species so have not been included in Tables 1 and 2. The history of the generic placement and relationships of these species has recently been summarised and reviewed by Carmona, Pola *et al*. (2014) so will not be repeated here.

Berghia marcusi Domínguez, Troncoso & García, 2008
Fig. 5C–G

Berghia marcusi Domínguez, Troncoso & García, 2008: 355–362, Figs 1F, 1G, 6, 7A, 7B.

Table 1 Comparison of East Atlantic species of *Berghia* (excluding *B. norvegica* and *B. benteva*).

	B. coerulescens (Laurillard, 1832)[1, 2, 5, 6, 7]	*B. verrucicornis* (Costa, 1867)[1, 2, 4, 5, 6, 7]	*B. ghanensis* n. sp.[3, 8]	*B. columbina* (García-Gómez & Thompson, 1990)[2, 4]	*B. columbina* (García-Gómez & Thompson, 1990)[8]	*B. marinae* Carmona, Pola, Gosliner & Cervera, 2014[2]
Geographic occurrence	Mediterranean, Atlantic coast from Brittany to Canaries	Mediterranean, Atlantic coast from Brittany to Senegal & Canaries	Ghana	Mediterranean, Atlantic coast from Portugal to Senegal & Canaries	Ghana	Senegal
Body (live)	Large, up to 70mm, translucent white or bluish-white	Medium, up to 30mm, translucent white or grey	Small, 11–19mm, translucent grey, head tinged orange	Medium, up to 30mm, translucent pale grey/ white tinged orange	9mm, translucent grey, head tinged orange	6.5mm preserved, translucent white with white spots
Width % length	7.5	15	7–8	8–17	12	
Orange cheek stripe	Present but often small and faint	Present	Present	Present, bright orange	Present	Present
Dorsum colour	Often orange over heart	White line, may be broken	White line, may be broken	Bright orange over heart, may continue to tail tip	Medial white line, tinged orange over heart	Mainly white, orange over heart
Orange line on ceras insertions	Present on first 3 groups	Absent	Absent	Present	Present	Present
Anterior cerata	Rows	Arch	Arch	Arch	Arch	Arch
Jaw edge	Minutely denticulate	Minutely denticulate	Denticulate	Smooth		Smooth
Base of oral tentacle	Translucent red or white	Translucent grey or white	Translucent grey	Translucent orange	Translucent tinged orange	Brownish, pale yellow tip
Rhinophore	Dull to bright orange/ red, whiter anteriorly	Dull to bright orange, white tip	Orange-red, cream tip	Dull to bright orange, white tip	Orange basal half, creamy white distally	Brownish, pale yellow tip
Ceratal epidermis	Translucent white with iridescent blue	Translucent white or grey	Grey	Translucent orange or grey	Grey	Brown, greyish-white spots distally
Ring over cnidosac (tips clear)	Yellow or red	Orange-yellow often with gold-orange crescent	White, orange-red distally	Orange, may be absent	Dense yellow dots	Brown band, then yellow ring
Digestive gland in cerata	Grey or brown	Brown or orange	Brown	Reddish brown	Brown	

Principal references: [1] Ballesteros, 1980; [2] Carmona, Pola *et al.*, 2014; [3] Edmunds, 1968a; [4] García-Gómez & Thompson, 1990; [5] Schmekel & Portmann, 1982; [6] Sea Slug Forum, 1998–2010; [7] Tardy, 1962; [8] This paper

Berghia coerulescens – Er Marcus, 1957: 477–481, Figs 237, 240, 241, 245.
Berghia verrucicornis – Ev Marcus, 1972: 304–305.
Berghia verrucicornis – Thompson, 1980: 97–98.
Berghia specimen B – Edmunds, 1968a: 214–217, Figs 8B, E, 9D-G.
Berghia specimen C – Edmunds, 1968a: 215–217, Fig. 8C, F.

Remarks I agree with Domínguez *et al*. (2008) and with Carmona, Pola *et al*. (2014) that my *Berghia* specimen B from Jamaica (Table 2) is *B. marcusi*. Edmunds (1968a) gives a description and drawings of this specimen, but a colour photo of the living animal is published here for the first time (Fig. 5D). It is paler, with much less orange than in Brazilian specimens, but is very similar to a specimen from Columbia found by Dominguez Tejo (2001) which was identified by Rudman (2003) as *B. rissodominguezi*. However, Rudman's identification was before the publication of *B. marcusi*, and the specimen could actually be *B. marcusi*.

A photo of a specimen of *Berghia* from Florida with much brighter orange markings and bluish distally on the cerata by Judy Townsend (2009) and another with paler orange and less blue by Sandra Edwards (2012) may also be *B. marcusi* but they both have bulbous cerata, broadest about two-thirds of their length, whereas photos of *B. marcusi* referenced here all have linear, parallel-sided cerata. Ceratal shape can vary depending on whether an animal is active or resting, relaxed or alarmed (see discussion of *Berghia ghanensis*, above). Thus while these Florida specimens appear to be *B. marcusi*, it is possible that they belong to another undescribed species of *Berghia* in the Caribbean.

Photographs of two *Berghia* from North Carolina by Dr Rick Fox are very similar to the two Florida specimens and are printed here (Figs 5C, F & G). One of these shows the characteristic boomerang-shaped orange cheek patch running from the base of the oral tentacle to the base of the rhinophore which is clearly shown in the photo by Carmona, Pola *et al*. (2014). The ratios of body width to length in two photos of the darker specimen are 11 and 13 and in three photos of the paler specimen are all 11. These characters lead me to conclude that Fox's specimens from North Carolina are *B. marcusi*. The *Berghia* from North Carolina identified by Marcus (1961) as *B. coerulescens* is therefore most probably also *B. marcusi*.

Berghia specimen C from Jamaica (in Edmunds, 1968a) is very orange in colour but falls within the range of colouration of other *B. marcusi*: it differs in the pale ring near the ceras tip which is only orange in a few cerata (Fig. 5E, Table 2). Thompson's specimens from Jamaica described under the name *B. verrucicornis* (Thompson, 1980) are similar in colouration to both *B. marcusi* and *B. rissodominguezi*. However, they were both sexually mature with spawn at 18mm long and had yellow-tipped orange rhinophores so I agree with Domínguez *et al*. (2008) that they are more likely to be the smaller species, *B. marcusi*.

Looking at the specimens attributed to *B. marcusi* in Figs 5C–G and elsewhere (as referenced above), some are so different in appearance that they may not all be the same species. It is therefore possible that there are two species confused under this name, but for the present, because there are specimens intermediate between the extreme colour forms, I maintain them all as *B. marcusi*.

Berghia rissodominguezi Muniain & Ortea, 1999
Fig. 5B

Berghia rissodominguezi Muniain & Ortea, 1999: 144–150, Figs 1, 2A, Plate 1A.
Berghia specimen A – Edmunds, 1968a: 214–217, Figs 8A, D, 9H-J.

Remarks The third *Berghia* from Jamaica described by Edmunds (1968a) as specimen A is much larger than any of the *B. marcusi* reported by Domínguez *et al*. (2008), and it differs from them in colour of the digestive gland ducts and of the apical ring of the cerata (Table 1). A photograph of the living animal is published here for the first time (Fig. 5B). A similar specimen, 25mm long, from the Gulf of Mexico has been photographed by Zurik (2004a, b) which Rudman (2004) considered is probably *B. rissodominguezi*. Dr Claudia Muniain has kindly sent me a photograph of a specimen from Argentina from where the species was first described which has brown digestive gland ducts in the cerata and bright orange-red markings on the sides of the head and at the ceratal insertions. Both Zurik's specimen and my one have black digestive gland ducts and paler orange-red markings on the head and body, but

Table 2 Comparison of West Atlantic species of *Berghia* (excluding *B. benteva* & *B. creutzbergi*)

	B.rissodominguezi Muniain & Ortea, 1999[1, 4]	*B.rissodominguezi* (*Berghia* specimen A)[5, 6]	*B. marcusi* Domínguez, Troncoso & García, 2008[2, 3, 4]	*B. marcusi* (*Berghia* specimen B)[5, 6]	*B. marcusi* (*Berghia* specimen C)[5, 6]	*B.stephanieae* Valdés, 2005[4]
Geographic occurrence	Argentina, Brazil, Caribbean	Jamaica	Brazil, Caribbean	Jamaica	Jamaica	Caribbean
Body (live)	Large, up to 52mm, translucent white or grey, tinged orange on head	40mm translucent grey, suffused orange dorsally	Medium, up to 20mm, translucent white	12mm, translucent grey	13mm translucent orange anteriorly, grey posteriorly	Medium, up to 20mm, translucent grey,
Width % length	11,12, 12, 13	13, 14	12; 13 (12mm)	10, 11, 15	10, 16	
Orange cheek stripe	Absent[4] or present[1]	Present	Present, running transversely to just in front of rhinophores	Present, running transversely to just in front of rhinophores	Present	Present but ochre
Dorsum colour	White or partly or entirely orange	Grey, suffused orange dorsally	White band from base of oral tentacles to tail, back often suffused orange	White band narrowing to a line on tail	Mainly orange fading to grey posteriorly, some white patches	Broad white band covering head & entire dorsum
Orange line on ceras insertions	Absent[4] or present[1]	Present	Present	Present	Present	Present but beige or ochre
Anterior cerata	Arch	Arch	Arch	Arch	Arch	Rows
Jaw edge	Smooth or denticulate	Denticulate	Denticulate	Denticulate		Smooth
Base of oral tentacle	Grey	Orange	Pale orange/red	Orange	Orange	Grey base, white distal half
Rhinophore	Creamy white to dull or bright orange, yellow/cream apically	Orange basally, yellow distally	Red basally, white-cream distally	Orange basally, creamy white distally	Orange	White distal half, sparse papillae
Ceratal epidermis	Translucent grey	Translucent violet-grey	Translucent grey	Translucent grey	Translucent grey	Translucent white, distal ⅓ white or grey
Ring over cnidosac	Yellow/orange	Yellow	Orange, whitish below	Broad yellow ring with orange crescent	White to pale yellow or orange	May be small yellow ring
Digestive gland in cerata	Reddish brown, bluish or blackish	Blackish brown	Brown/orange	Buff to greyish yellow	Olive-green	Greenish, brownish ochre or beige

Principal references: [1]Muniain & Ortea, 1999; [2]Domínguez *et al*., 2008; [3]Marcus, 1957; [4]Carmona, Pola *et al*., 2014; [5]Edmunds, 1968a; [6]this paper.

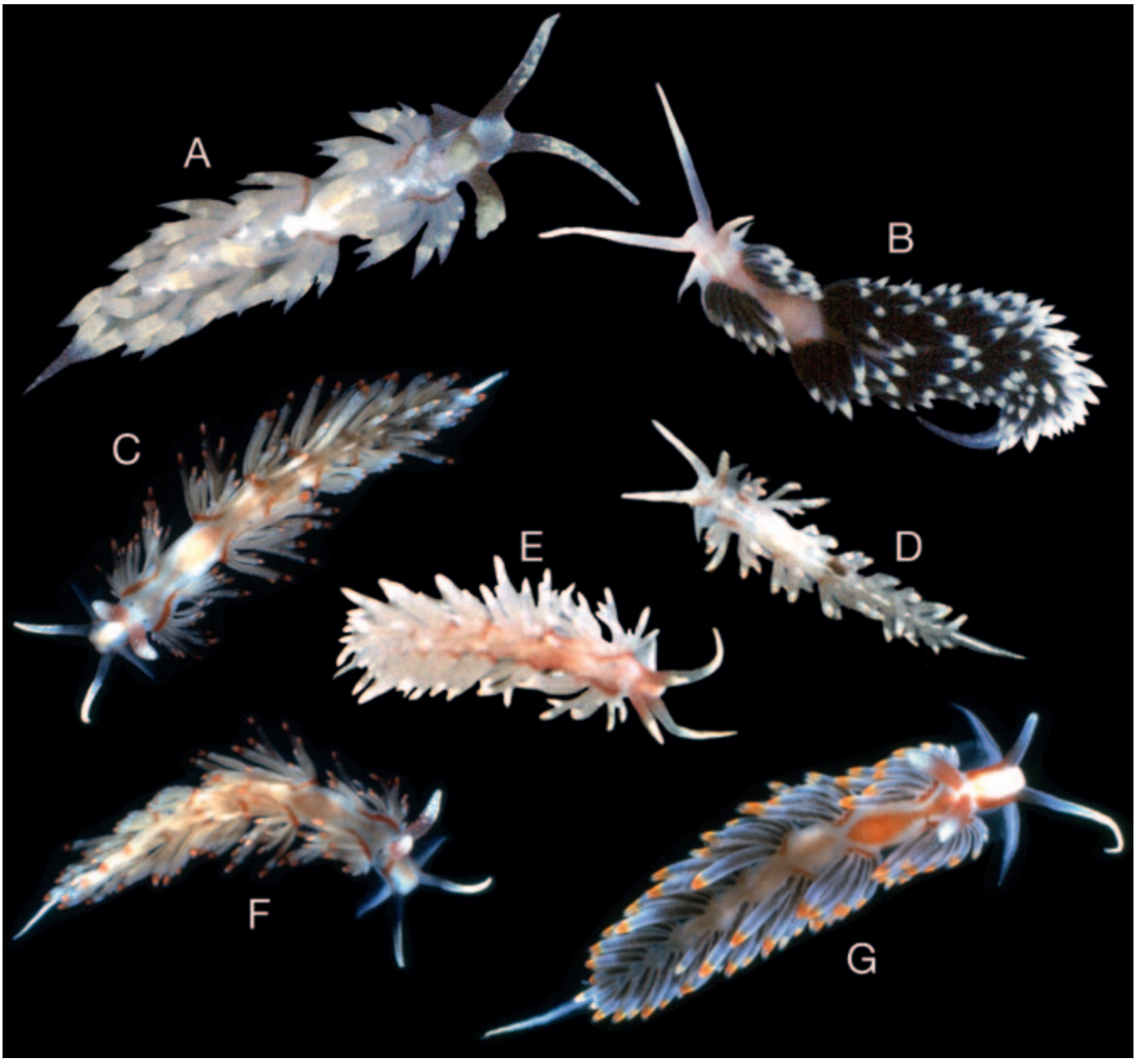


Figure 5A *Berghia columbina* (García-Gómez & Thompson, 1990), Ghana, 1969. **Fig. 5B** *Berghia rissodominguezi* Muniain & Ortea, 1999, 40mm long, November 1961, Jamaica (specimen A of Edmunds, 1968a). **Figs 5C–G** *Berghia marcusi* Domínguez, Troncoso & García, 2008: **C** & **F** two views of same specimen, **G** a more colourful specimen, both from North Carolina, photos by Dr Rick Fox; **D** 12mm long, February 1962, **E** 13mm long, March 1962, both from Jamaica (specimens B & C respectively of Edmunds, 1968a).

all specimens have pale rhinophores and a yellow ring in the cnidosac region of each ceras (Fig. 5B). A specimen from St. Lucia photographed in Valdés *et al.* (2006) also has black digestive gland ducts and the characteristic yellow rings near the ceras tips, but it has very faint markings to the ceratal insertions and bright orange rhinophores and oral tentacles. A photo of a similar specimen from Brazil has been published by Padula, Bahia, Vargas & Lindner (2011). (Other specimens identified by Rudman (2003) as *Berghia rissodominguezi* are probably *Berghia marcusi*, a species that had not been described at the time of Rudman's identification.)

Discussion

This paper describes five species of the family Aeolidiidae from Ghana one of which is named as a new species, a second appears to

be an undescribed species but further material is required before it can be described fully and named, while a third is amphiatlantic in occurrence. Re-examination of three specimens of *Berghia* collected in Jamaica confirms that these differ from East Atlantic species but belong to two recently described species of the genus from the West Atlantic, *Berghia marcusi* and *Berghia rissodominguezi*. Photos of specimens of *Berghia* from North Carolina and Florida are also considered to be *B. marcusi*.

Ceratal glands of *Spurilla* and *Berghia*

Edmunds (1966) described the ceratal glands and behaviour of species of Aeolidiidae from Jamaica under the names *Spurilla neapolitana* and *Berghia coerulescens*, however it is clear from the work of Carmona and colleagues summarised above that these names are incorrect. The specimens identified as *Spurilla neapolitana* were actually *Spurilla braziliana* while those identified as *Berghia coerulescens* comprised both *Berghia marcusi* and *Berghia rissodominguezi*. Specimens of both of these species were serial sectioned and have similar ceratal glands, but the diagram in Edmunds (1966) Fig. 17 is from *Berghia rissodominguezi* (my *Berghia* specimen A) while the data on nematocysts exploded in Table 7 Column E is from *Berghia marcusi* (my *Berghia* specimen B).

Crossing the Atlantic Ocean

How did aeolid nudibranchs cross the Atlantic? And how did *Spurilla braziliana* reach the Indian and Pacific Oceans? Species could cross the Atlantic Ocean in one of the following ways:

(a) by planktotrophic (teleplanic) larvae
(b) on floating vegetation
(c) on boat hulls
(d) in bilge water discharged from boats
(e) deliberate translocation by humans

I know of no evidence that any species of aeolid has been deliberately translocated so we can rule out (e). Transport by means of (c) or (d) is relatively recent, the last few hundred years for (c) and the last few decades for (d). Several species of dorid nudibranch from Ghana occur on both sides of the Atlantic and a few extend into the Indo-Pacific region (Edmunds, 2013 and earlier papers). Some of these dorids feed on encrusting Bryozoa which live on boat hulls and so have probably only colonised such a wide area over the last few hundred years. This is unlikely to have given sufficient time for substantial genetic change and speciation but it could explain the records of *Spurilla braziliana* from the Indo-Pacific: Carmona, Lei *et al*. (2014) point out that these records are all relatively recent and that the DNA profiles from a very wide geographical area are virtually identical. This colonisation is unlikely to have occurred via boats because the animals would have had to survive either in the cold waters round Cape Horn, or in the slightly warmer waters round the Cape of Good Hope in which case they should also occur on the Atlantic coast of southern Africa. The most likely route for *Spurilla braziliana* to reach the Indo-Pacific is probably in bilge water via the Panama Canal.

Berghia benteva may have crossed the Atlantic relatively recently either on boat hulls or in bilge water. This hypothesis could be confirmed if DNA profiling of populations from the East and West Atlantic shows that they are very similar.

For the remaining species of *Spurilla* and *Berghia* the process of speciation is probably the result of occasional transatlantic crossing by (a) or (b) (Edmunds, 1977). The crossing must have been rare because if it were frequent there is likely to have been sufficient gene flow between the populations in east and west to swamp local adaptation and so prevent speciation. *Spurilla sargassicola* lives on floating *Sargassum* which can drift enormous distances, so it seems reasonable to hypothesise that at least some of the five species of *Spurilla* survived a transatlantic crossing feeding on anemones attached to *Sargassum*, and then their veligers metamorphosed in shallow waters near the new shore. These and their descendents would then adapt to local conditions and eventually evolve into distinct species. A similar process by (a) or (b) could explain how speciation occurred in the 11 species of *Berghia*: Carmona, Pola *et al*. (2014) using DNA profiling to show the relationships of nine species found that *B. rissodominguezi* and *B. stephaniae* are sister species in the West Atlantic while *B. columbina* and *B. marinae* are sister species in the East Atlantic. These four species are more similar to each other than to any of the remaining species so their common ancestor must have crossed the Atlantic and then undergone further adaptation and speciation both in the east and in the west. It

is perhaps surprising that no aeolidiids have been described from Ascension Island (Padula, Wirtz & Schrödl, 2014) as one might expect veligers to reach an island midway between America and Africa more frequently than crossing the entire ocean which is what ancestral *Berghia* and *Spurilla* must have done. However, the amount of shallow water suitable for sea anemones to inhabit round Ascension may be insufficient to sustain a population of aeolidiids whose sole food is just one or a few species of sea anemone.

Occasional transatlantic crossing implies that sibling populations on both sides of the ocean gradually diverge and it is an arbitrary decision as to whether they should be regarded as separate species or subspecies or varieties. DNA differences of 0–5% may be trivial whereas differences of >10% can be considered sufficient for specific separation (Carmona *et al*., 2013). If the two forms are very similar morphologically they are unlikely to be given different names whereas if they have only a relatively small genetic difference but with marked morphological divergence they are likely to be considered distinct species.

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