Two new *Volvarina* (Marginellidae) from offshore subtidal habitats in Northern Panama

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ABSTRACT. Two new closely related species of *Volvarina*, *V. veraguasensis* n.sp. and *V. dalli* n. sp., are described from offshore subtidal habitats off the Caribbean coast of Panama, and the variability of their shells is presented. A fossil form with a similar shell morphology to Recent *V. veraguasensis* is also presented. A comparison is made between both new species and previously described Caribbean species of *Volvarina*. The diversity and distribution of the genus *Volvarina* along the Caribbean coasts of Panama in comparison with adjoining regions is also commented upon.

INTRODUCTION

Deep water discoveries of Caribbean Marginellidae have until recently been known from only a few studies and dredging campaigns performed in the Gulf of Mexico towards the end of the 20th Century, being reported on by W.H. Dall (1881 and 1927) and a later study by Bayer (1971). More recently, exploration of the molluscan fauna at depths of 100-500 metres off the Honduran, East Panamanian and Colombian Caribbean coasts has revealed that the diversity of marginellid species at upper bathyal levels (c. 500m) is low in comparison with similar depths sampled in the tropical West Pacific, whereas at shallower levels (c. 70m) there appears to be a greater than expected diversity, with several cystiscid and marginellid genera being recorded (Gracia & Boyer 2004). In Boyer (2001) two new species of deep water Volvarina (V. bessei from the circalittoral, and V. hennequini from the upper bathyal) were described from off the coast of Northern Honduras. Gracia & Boyer (2004) reporting on the marginellid recolt of trawlings from the 1998-2001 INVEMAR campaigns which took place off Northeast Panama and the Peninsula La Guajira, Colombia, described another upper bathyal species, V. bayeri and demonstrated a large geographical distribution of V. hennequini from the Gulf of Honduras to Northern Colombia.

In 2003 the second author received a large quantity of dredged marginelliform material from Marcos Alvarez, Panama City. The data on a number of lots received from him, which we subsequently assembled into a single lot of a new species of *Volvarina*, proved to be very unreliable and contradictory. This new species lot comprised approximately 700 adult and juvenile specimens in various states of preservation from fresh dead to badly eroded and it is described herein as *V*. veraguasensis n. sp. The subsequent discovery by the second author of further examples of this species from offshore subtidal levels (50-190m) during a privately organised dredging expedition (MARINA EM 2) in October/November 2003, to the Northern coast of Panama between the San Blas Archipelago in the East to Bocas del Toro in the West, established beyond any doubt that V. veraguasensis is a North Panamanian species. Furthermore the discovery of another new species (V. dalli n.sp., also described in this paper) occurring sympatrically with V. veraguasensis at one of the stations, indicates that the genus Volvarina forms a significant component of the regional marginellid fauna at these depths. An exploratory trip to the southern coast of Escudo de Veraguas Island (Bocas del Toro Basin) by members of the dredging team on MARINA EM 2 during the expedition led to the discovery of molluscan fossil deposits in the bank exposed to the sea. Several specimens of a Volvarina species with a size and morphology very similar to V. veraguasensis were obtained (Fig. 27). The genus Volvarina is one of seven marginellid genera recorded from the upper middle Miocene to the Pleistocene ages in Northern Panama by Jonathan A. Todd, systematics coordinator at the NHM of the recent and fossil molluscan collections of the Panama Palaeontology Project (PPP). The fossil deposits on the North and South coasts of Escudo de Veraguas Island are in fact sites under study by the PPP and the stratigraphic sections of the site on the south of the island indicate that the exposed strata were laid down 3.5 million years ago (mid-Pliocene), and are composed of sandy mudstone. The geological processes which formed the Central American Isthmus originated with tectonic activity during the Jurassic Period, 190 million years ago. In the Cretaceous, a volcanic insular arch was formed from Northeast Colombia to Nicaragua, which closed during the Pliocene (5.7 to

2.5 million years ago) due to sedimentation processes followed by huge volcanic activity. In the Pleistocene, 2.5 to 1 million years ago, the region was subject to enormous glaciations and changes in sea level, resulting in several sectors of Panama rising and sinking, and it is these Pleistocene sediments which form todays isthmian coastal plains (for further information on Fossil Caribbean Mollusca from the lower Caribbean see Jackson et. al. 1999).

Materials and methods

The second author performed 32 dredging operations at stations in 50 to 200m depth, on mud and sand substrata in the area between the San Blas Archipelago and Bocas del Toro, Northern Panama. V. veraguasensis was dredged from ten of these stations and V. dalli from one (see table 1. for relevant station list and further details). For details of the dredging technique employed, see Wakefield & McCleery (2004). The dredge rapidly clogged with mud, resulting in 'bite-sampling' over short distances. All of the shells obtained were in a dead state, as both adult and juveniles, and therefore no living animals or radulae were available for study. Photographs of the shells were taken using a digital SLR camera and macro lens with twin flash illumination.

The lot of 700 shells of *V. veraguasensis* were obtained from Marcos Alvarez (Panama City), and although their usefulness was limited due to the unreliability of the data given for the shells, the sheer quantity provided an opportunity to study the variability of its shell morphology and chromatism.

The fossil specimens of *V. cf V. veraguasensis* were easily removed from the soft sandy mudstone sediments at the base of the exposed coastal bank.

Abbreviations

BM(NH): Natural History Museum, London.
AWC: Andrew Wakefield Collection.
TMC: Tony McCleery Collection.
INVEMAR: Instituto de Investigaciones Marinas de Punta de Betin, Santa Marta, Colombia.
PPP: Panama Palaeontology Project.
Dd: dead dredged shell.
ad. : adult.
juv.:juvenile.

SYSTEMATICS

FamilyMarginellidae Fleming, 1828GenusVolvarina Hinds, 1844

Type species : *Marginella nitida* Hinds, 1844 (subsequent designation by Redfield, 1871), junior synonym of *Volvarina mitrella* Risso, 1826.

Volvarina veraguasensis n.sp. Figs 1-12, 25.

Type material. Holotype, ad dd, 8.14 x 3.27mm, dredged off Veraguas Province, Golfo de los Mosquitos, N. Panama (Figs 1-3, 25), BM(NH) reg. no. 20040887.

Paratype 1, dd ad, 12.5 x 4.51mm, dredged in 190m, off Veraguas Province, Golfo de los Mosquitos, 9°12.1'N 081°35.4'W, stn 5 (MARINA EM 2), (Figs 4-6), BM(NH) reg. no. 20040888.

Paratype 2, dd ad, 11.7 x 4.19mm, dredged in 190m, off Veraguas Province, Golfo de los Mosquitos, 9°12.1'N 081°35.4'W, stn 5 (MARINA EM 2), (Figs 7-8), AWC.

Paratype 3, dd ad, 11.1 x 4.19mm, dredged off Veraguas Province, Golfo de los Mosquitos, N. Panama, (Figs 9-10), TMC.

Type locality. Golfo de los Mosquitos, N. Panama, offshore.

Other material examined. 23 ad dd, L= 8.50-13.0 mm, dredged from stations 1, 5, 11, 14, 16, 19, 21, 26, 31 and 32 MARINA EM 2 expedition, San Blas to Bocas del Toro, N. Panama, in 50-190metres, TMC.

Approximately 700 dd ad and juv, locality data unreliable (ex. M. Alvarez), AWC and TMC.

6 Fossil specimens plus shell fragments, adult L= 11.0 to 13.5mm (Fig 27), provisionally identified as *V. veraguasensis*, from mid-Pliocene deposits on the south coast of Escudo de Veraguas Island (09°06'N 081°33'W), Bocas Del Toro Basin.

Description. Holotype (Figs 1-3, 25); Shell small (8.14 x 3.27mm, W/L ratio 40%), elongate ovate, smooth, glossy. Spire moderately high (14% of shell length), generally straight sided, with slightly stepped sutures. Nucleus blunt, rounded. Labrum almost straight, with slight labial inflexion in the middle third. Labial shoulder weak, suture sweeping apically to insertion point on suture or slightly below it. Aperture narrow at apical end, widening from mid point to base due to concave aspect of parietal wall in region of plications. Base rounded. Anterior and posterior notches absent. Four oblique plications occupying basal 41% of aperture; first plication strongest, continuing around the base and onto the labrum as a weak external varix, continuing to weaken progressively to finally fade out before labial insertion. Second to fourth plications progressively descreasing in strength. Weak ridge on parietal wall running from posterior end of aperture to the outer end of the fourth plication, continuing as a slight groove to the level of the second plication.

Colour pale pinkish yellow background colour with three evenly narrow reddish-brown spiral lines on last adult whorl. Most posterior line lies immediately below suture, remaining visible on spire whorls up to nucleus. Most anterior line emerges at mid-apertural position. Middle line positioned mid-way between anterior and posterior lines. Lines equally spaced when viewed from dorsal. Animal and radula unknown.

Habitat. Soft mud substrate in 50-190 metres.

Distribution. Currently known to occur offshore from the San Blas Archipelago to Bocas del Toro, Northern Panama. Probably endemic to this region, since it is not represented in the INVEMAR dredged samples from Eastern Panama and Northern Colombia, nor was it found during the dredging operations in Northern Honduras by B. Besse and F. Hennequin (see Boyer 2001).

Remarks. Deep water molluses are normally found in small numbers. However, the unusual abundance of shells of this species in the material examined enabled us to clearly establish its variability limits. It is very variable in size (L= 6.7-13mm) and in the intensity (as opposed to the position) of the spiral lined pattern: the lines may be clearly marked, through indistinct to completely absent. The absence of spiral decoration may be an effect of the natural fading of dead shells, or may represent a normal occurrence in a percentage of animals of a population. The species is fairly constant in shape (W/L ratio from 36% to 40%), with occasional aberrant variations in the form of the spire such as a weak step in the suture (Figs 11,12).

The three narrow spiral lines on the last whorl encourage a comparison with V. bessei (Boyer, 2001), which occurs further North at similar depths off Northern Honduras. It too bears a very stable pattern of three spiral lines but these are much finer in proportion to the size of the shell than in V. veraguasensis. V. bessei has a larger shell and has an angular 'ramp' anteriorly whereas V. veraguasensis has a smoothly rounded anterior. The labrum of V. finely bessei is denticulated whereas V_{\cdot} veraguasensis has a perfectly smooth labrum. Boyer (2001) tentatively placed V. bessei in a 'group *canillum*' on the grounds of the anterior 'ramp' being similar to that found on the type specimen of Prunum canillum (Dall, 1927), but the assignment of V. veraguasensis to such a group would be clearly incorrect since this feature is not present.

Etymology. From the Veraguas Province of Panama, off which the species was dredged during the MARINA EM 2 expedition.

Volvarina dalli n.sp. Figs 13-24, 26

Type material. Holotype, ad dd, 7.75 x 2.62mm, dredged in 50metres, Stn 1 MARINA EM 2, West of

Colón, Panama (9° 09'N 080° 33'W), (Figs 13-15, 26), BM(NH) reg. no. 20040889.

Paratypes from same locality as holotype;

Paratype 1, dd ad, 9.18 x 2.83mm,(Figs 16-18), BM(NH) reg. no. 20040890.

Paratype 2, dd ad, 9.67 x 3.00mm, (Figs 19, 20), AWC.

Paratype 3, dd ad, 7.78 x 2.69mm, (Figs 21, 22), TMC.

Paratype 4, dd ad, 8.47 x 2.78mm, (Figs 23, 24), TMC.

Other material examined. 3 dd ad, L=8.21mm, 8.40mm & 8.50mm, same locality as type material, TMC.

Type locality. West of Colón, Panama (9° 09'N 080° 33'W).

Description. Holotype (Figs 13-15, 26); Shell small (7.75 x 2.62mm, W/L ratio 34%), smooth, glossy, elongate-ovate, spire high (24% of total shell length), straight sided, suture slightly stepped. Nucleus wide, blunt, rounded. Labrum almost straight, with slight labial inflexion in the middle third. Labial shoulder very weak, sweeping slightly posteriorly to insert well below suture line of previous whorl. Aperture narrow posteriorly, gradually widening to rounded base anteriorly. Anterior and posterior notches absent. Parietal wall almost straight. Four oblique columellar plications occupying lower 43% of apertural length; first plication strongest, continuing around the base and onto the labrum as a weak external varix, continuing to weaken progressively to finally fade out before labial insertion. Second to fourth plications progressively descreasing in strength. Weak ridge on parietal wall running from posterior end of aperture to the outer end of the fourth plication, continuing as a slight groove to the level of the second plication.

Colour pale pinkish yellow background, with three evenly narrow reddish brown lines. Most posterior line lies immediately below suture, remaining visible on spire whorls up to nucleus. Most anterior line emerges at mid-apertural position. Middle line positioned between the other two, but always slightly closer to the most anterior line.

Animal and radula unknown.

Habitat. Soft mud substrate at 50 metres.

Distribution. Only found at one dredging station (MARINA EM 2, stn 1) West of Colón, Panama (9° 09'N 080° 33'W). Further distribution unknown, but probably endemic to the type locality, since it was absent from the Alvarez lots, from the remainder of the stations dredged in MARINA EM 2, and from the INVEMAR dredged samples from Eastern Panama and Northern Colombia. It was also not found during the dredging operations in Northern Honduras by B. Besse and F. Hennequin (see Boyer 2001).

Remarks. This is a very fusiform species, only slightly variable in profile (W/L ratio from 31% to 35° ₀). Major differences between *V. dalli* and *V. veragnasettsis* are the high spired and narrow shell (no apparent intergrading morphologies in the material studied) and the slightly different placement of the central spiral line (closer to the anterior in *V. dalli*). *V. veragnasettsis* is also generally larger than *V. dalli*. As both species bear the same non-variable spiral system of decoration, we consider them to be closely related yet distinct species.

Fusiform deep water members of the Prunuuv Volvarina complex are found elsewhere in the Caribbean e.g. V. styria (Dall, 1881), P. torticulum (Dall, 1881), P. redfieldi (Tryon, 1882), all from the Gulf of Mexico off the West coast of Florida, but all differ in morphology from V. dalli. The closest species both geographically and morphologically appears to be the Northern Caribbean V. gracilis (C.B. Adams, 1851), with a type locality of Jamaica. At about 6.5 mm in length, this narrow and elongate species is smaller than V. dalli. A photograph of the Lectotype (MCZ 186119) in Clench & Turner (1950) shows that V. gracilis has a proportionally shorter spire with a more rounded nucleus, and three wide orange-brown bands which do not lie in the same position as those of V. dalli. We therefore conclude that V. dalli is distinct from and not closely related to V. gracilis, and that it is therefore not part of the 'group V. gracilis' as proposed by Boyer (2000).

Etymology. Named in honour of W.H. Dall, who described several fusiform deep water Marginellidae from the Gulf of Mexico.

DISCUSSION

Although *V. veraguaseusis* appears morphologically similar to *V. avena* (Kiener, 1834), the latter is wider anteriorly, does not express the spiral line pattern, and in common with the vast majority of decorated *Volvarina* species has a pattern of spiral bands of variable width. In fact the one unifying feature of *V*. *veraguaseusis*, *V. dalli* and *V. bessei* is the stable nature of the pattern. The spiral pattern on the fossil specimens is only very weakly evident subsuturally, but the columella and apertural morphology arc otherwise very similar to those of recent specimens of *V. veraguaseusis*. So far no species of *Volvarina* resembling our two new species has been discovered on the Pacific side of the isthmus. This is to be expected for such deep water species since they would have effectively experienced separation of Atlantic and Pacific populations much earlier than those species which inhabited shallow water.

Whilst records of bathyal species of marginellidae and cystiscidae from the Caribbean basin remain scarce, the same does not seem to apply to shallower subtidal levels in 50 to 200 or so metres. Boyer (2004) reports that the INVEMAR samplings off Colombia and Northeastern Panama in 70 metres yielded several species of marginelliform gastropods, naming examples from the genera Gibberula and Volvarina. Dredging in depths of 50 to 200m, the recolt of MARINA EM 2 was also very productive, with about eight species of Marginellidae in four genera, and about ten species of Cystiscidae in four genera being collected, and this despite the dredge only taking bites out of the substrate rather than performing a prolonged drag. It can be concluded that the marginellid fauna at subtidal depths on the continental slopes is significant and the diversity high. Boyer (2004) also makes the observation that the generic composition of bathyal marginellid diversity is closely linked to the diversity observed at shallower levels. If such vertical bathymetric relationships are operational, and as Volvarina appears to be dominant in the marginellid fauna at depths of 50-200m in the Panama region, then one would expect the diversity of this genus to be even greater in shallower coastal tidal levels. From the field observations of the second author, this indeed appears to be the situation since numerous undescribed species of Volvarina, both new and previously described, are present in very shallow water in this region.

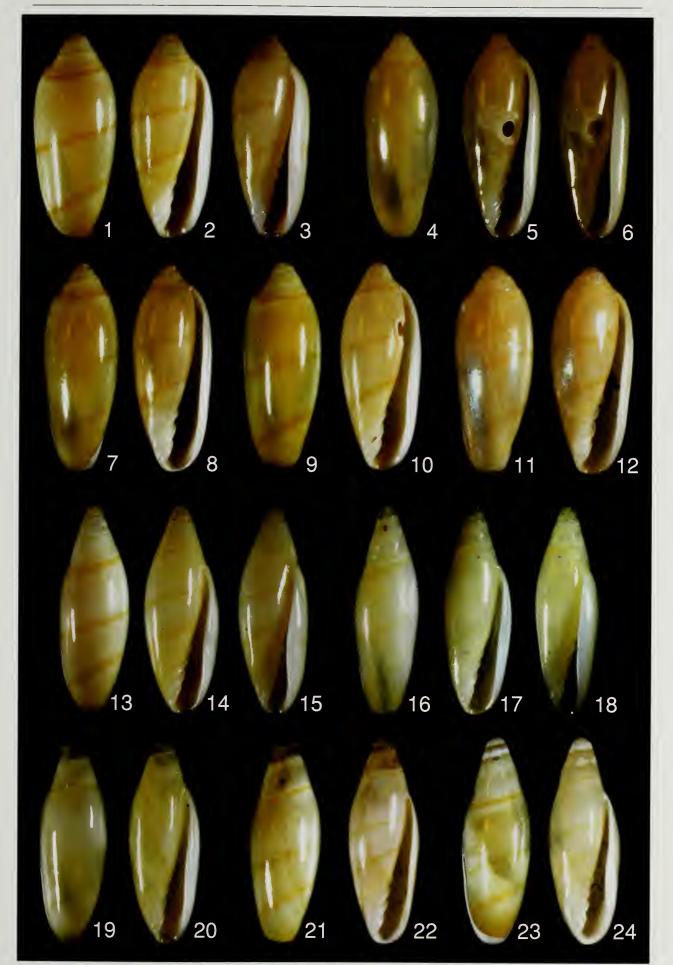
Figures 1-24

1-12. Volvarina veraguasensis n.sp., Veraguas Province, Golfo de Los Mosquitos, Panama.
1-3. Holotype, 8.14 x 3.27mm, BM(NH) reg. no. 20040887; 4-6. Paratype 1, 12.5 x 4.51mm, MARINA EM 2, stn. 5, BM(NH) reg. no. 20040888; 7-8. Paratype 2, 11.7 x 4.19mm, MARINA EM 2, stn. 5, AWC; 9-10. Paratype 3, 11.1 x 4.19mm, TMC; 11-12. 6.78 x 2.60mm, MARINA EM 2, stn. 11, TMC.
13-24. Volvarina dalli n.sp., West of Colón, N. Panama.

13-15. Holotype, 7.75 x 2.62mm, BM(NH) reg. no. 20040889; 16-18. Paratype 1, 9.18 x 2.83mm BM(NH) reg. no. 20040890; 19-20. Paratype 2, 9.67 x 3.00mm, AWC; 21-22. Paratype 3, 7.78 x 2.69mm, TMC; 23-24. Paratype 4, 8.47 x 2.78mm, TMC.

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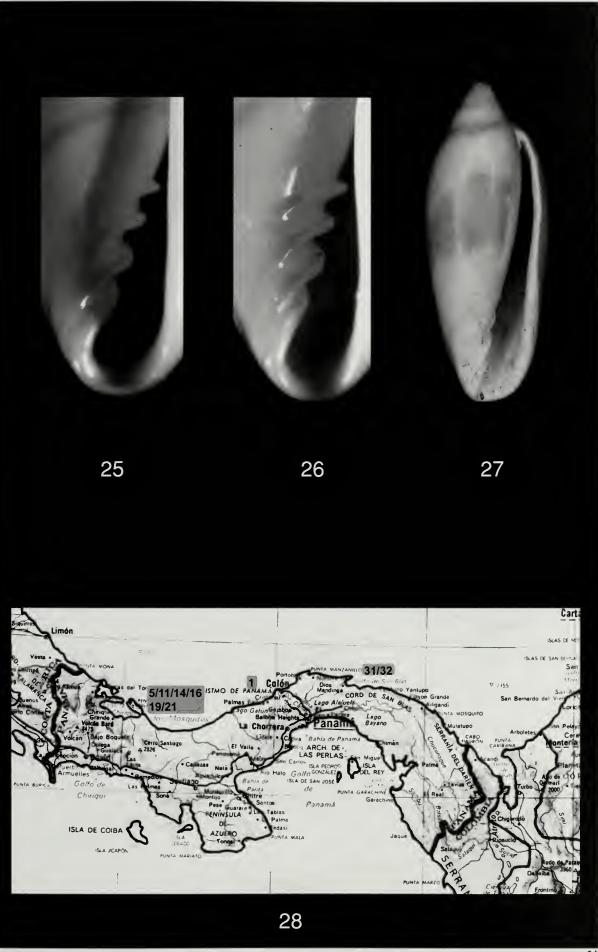
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Figures 25-28

25 V. veraguasensis n.sp., detail of columellar plications; 26 V. dalli n.sp., detail of columellar plications.
27 V. cf. V. veraguasensis n.sp., 12.6 x 5.0mm, mid-Pliocene of Escudo de Veraguas Is, N. Panama.
28 Regional map indicating dredging stations of MARINA EM 2 (see table 1).



Station	Species (Volvarina)	Quantity	Substrate	Locality	Coordinates	Depth (m)
1	veraguasensis dalli	1 8	Mud	Golfo de los Mosquitos, West of Colón	9° 09'N 080° 33'W	50
5	veragnasensis	2	Mud	Golfo de los Mosquitos, off Veraguas	9° 12.1'N 081° 34.7'W	190
11	veraguasensis	6	Mud	Golfo de los Mosquitos, off Veraguas	9° 10.9'N 081° 34.9'W	70
14	veraguasensis	1	Mud	Golfo de los Mosquitos, off Veraguas	9° 15.0'N 081° 54.9'W	40
16	veraguasensis	1	Mud	Golfo de los Mosquitos, off Veraguas	9° 15.0'N 081° 54.8'W	60
19	veraguasensis	3	Mud	Golfo de los Mosquitos, off Veraguas	9° 15.7'N 081° 53.9'W	55
21	veraguasensis	5	Mud	Golfo de los Mosquitos, off Veraguas	9° 10.5'N 081° 36.5'W	67
26	veraguasensis	5	Mud	Golfo de los Mosquitos, off Veraguas	9° 11.1'N 081° 34.5'W	80
31	veraguasensis	1	Mud	Off San Blas Archipelago	9° 38.6'N 79° 25.1'W	50
32	veraguasensis	ljuv.	Mud	Off San Blas Archipelago	9° 38.6'N 79° 07.0'W	50

 Table 1. Coordinates, substrates and depths of those stations in the MARINA EM 2 campaign which produced shells of V. veraguasensis n.sp. and V. dalli n.sp.