Revision of the Cancellariidae (Mollusca, Neogastropoda, Cancellarioidea) of the eastern Atlantic (40°N-40°S) and the Mediterranean

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ABSTRACT
The Cancellariidae living off the western African coast, the mid-Atlantic Islands and in the Mediterranean Sea are reviewed. Twenty species are studied: 3 *Admetula*, 1 *Axelella*, 2 *Bivetiella*, 4 *Brocchinia*, 1 *Cancellaria* s.l., 1 *Nothoadmete*, 1 *Loxotaphrus*, 2 *Solatia*, 1 *Sveltia*, 2 *Tribia*, and 2 *Trigonostoma. Trigonostoma gofasi* n. sp. is distinguished from the western African *T. scala* (Gmelin, 1791) n. comb. by its multispiral protoconch, wider umbilicus, smooth columellar callus, axial ribs on the sutural ramp not reaching the suture, and the absence of a siphonal fasciole; and from the central western American *T. goniostoma* (Sowerby, 1832) in its wider umbilicus, more deviated columella and in being less elongate. A species of *Solatia* which has previously been recognised as new, is not named due to lack of adequate material. The species name in the combination *Voluta cancellata* Linnaeus, 1767 is declared *nomen protectum*, making the senior name *Murex scabriculus* Linnaeus, 1758 invalid as *nomen oblitum*. A neotype is designated for *Murex scala* Gmelin, 1791. A lectotype is designated for *Cancellaria minima* Reeve, 1856, *Cancellaria similis* Sowerby, 1833, *Voluta lyrata* Brocchi, 1814, *Cancellaria angasi* Crosse, 1863 and *Cancellaria rigida* Sowerby, 1832; the latter name refers to a West African and not a West American species. Distribution data are updated, and relations to fossil taxa are indicated when applicable. The protoconchs of 17 species are figured; only the protoconch type of the bathyal species *Brocchinia decapensis* and *Nothoadmete euthymei* n. comb. remain unknown. Egg capsules attributed to one of the North West African *Bivetiella* species are figured.

KEY WORDS
Mollusca,
Neogastropoda,
Cancellariidae,
central eastern Atlantic,
western Africa,
Mediterranean,
new species.

RÉSUMÉ

Révision des Cancellariidae (Mollusca, Neogastropoda, Cancellarioidea) de l'Atlantique oriental (40°N-40°S) et de la Méditerranée.

Les Cancellariidae vivant le long de la côte ouest de l'Afrique, autour des îles de l'Atlantique central et dans la Méditerranée, sont étudiés. Les vingt espèces se répartissent comme suit : 3 *Admetula*, 1 *Axelella*, 2 *Bivetiella*, 4 *Brocchinia*, 1 *Cancellaria* s.l., 1 *Nothoadmete*, 1 *Loxotaphrus*, 2 *Solatia*, 1 *Sveltia*, 2 *Tribia*, et 2 *Trigonostoma. Trigonostoma gofasi* n. sp. se distingue de *T. scala* (Gmelin, 1791) n. comb., espèce ouest-africaine, par sa protoconque multispirale, son ombilic plus évasé, un callus columellaire lisse, des côtes axiales sur la rampe suturale n'atteignant pas la suture, et l'absence d'un bourrelet siphonal ; et de *T. goniostoma* (Sowerby, 1832), espèce ouest-américaine, par son ombilic plus ouvert, sa columelle plus déviée, et sa forme moins allongée. Une espèce non-décrite de *Solatia* déjà reconnue auparavant n'est pas encore nommée faute de matériel suffisant. Le nom spécifique dans la combinaison *Bivetiella cancellata* (Linnaeus, 1767) est déclaré *nomen protectum*, invalidant le nom plus ancien *Murex scabriculus* Linnaeus, 1758 comme *nomen oblitum*. Un néotype est désigné pour *Murex scala* Gmelin, 1791 ; et un lectotype pour *Cancellaria minima* Reeve, 1856, *Cancellaria similis* Sowerby, 1833, *Voluta lyrata* Brocchi, 1814, *Cancellaria angasi* Crosse, 1863 et *Cancellaria rigida* Sowerby, 1832 ; ce dernier nom réfère à une espèce ouest-africaine et non à une espèce ouest-américaine. Les données de distribution sont mises à jour et les relations avec des espèces fossiles sont indiquées le cas échéant. Les protoconques de 17 espèces sont figurées ; la protoconque des espèces bathyales *Brocchinia decapensis* et *Nothoadmete euthymei* n. comb. reste inconnue. Des capsules ovulaires présumées appartenir à une espèce ouest-africaine de *Bivetiella* sont figurées.

MOTS CLÉS
Mollusca,
Neogastropoda,
Cancellariidae,
Atlantique central est,
Afrique de l'Ouest,
Méditerrannée,
nouvelle espèce.

INTRODUCTION

The Atlantic Cancellariidae living off the African continent are still poorly known. In 1862, Petit de La Saussaye listed four species for the west African coast, while about a century later, Marche-Marchad (1958: 31) mentioned six species-level taxa for the Northwest coast of Africa. Equatorial regions of Africa were largely ignored in the pre-1950 literature, and the few species described from off western South Africa were usually not included in the fauna studied here.

The region covered in the present paper has traditionally been divided into "marine provinces" (Woodward 1870: 72; Fischer 1950: 74; Briggs 1974). Briggs (1974) distinguishes, mainly based on the fish fauna: the Lusitania province, from the western entrance of the English Channel to Cape Verde, including the Mediterranean; the West African and St. Helena-Ascencion province, from Cape Verde to Mossamedes; and the southwestern African province, from Mossamedes to Cape of Good Hope (Fig. 1). Cape Agulhas itself belongs to the southeastern African Agulhas province (Briggs 1974: 149) and therefore is not included here.

The Cancellariidae do not fit very well into this scheme, and a more refined one may be appropriate. The area covered here comprises several different hydroclimatic regions due to cold upwellings, thermal fronts, ocean currents, and reduced salinity during the rainy season. In the tropical eastern Atlantic, Le Loeuff & Cosel (1998: 310) suggested five hydroclimatic regions (Fig. 2): the Northern Alternance Region (Cape Blanc to Cape Verga) and the Southern Alternance Region (Cape Lopez

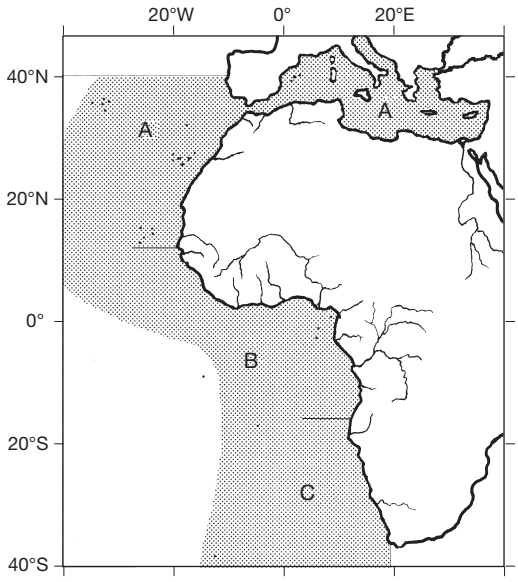

FIG. 1. — Studied area (grey; the extreme western part is omitted), and marine provinces involved (after Briggs 1974): **A**, Lusitania province (its part N of 40°N is not indicated); **B**, W African province; **C**, southwestern Africa subprovince.

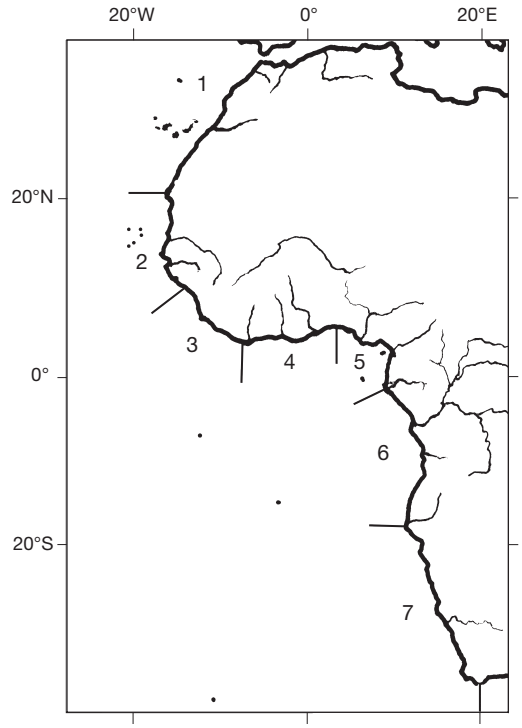

FIG. 2. — Hydroclimatic regions of western Africa (after Le Loeuff & Cosel 1998), and nearby areas: **1**, N of Cap Blanc; **2**, Northern Alternance Region; **3**, Western Typical Tropical Region; **4**, Atypical Tropical Region; **5**, Eastern Typical Tropical Region; **6**, Southern Alternance Region; **7**, S of Cape Frio.

to Cape Frio) undergo strong seasonal contrasts in water temperature, with permanent or periodical upwellings of colder water; the Atypical Tropical Region (Cape Palmas to Benin/Nigeria border), and the intercalated Western and Eastern Typical Tropical Regions with warm water and coastal salinity fluctuations. Outside cited regions, cold upwelling waters are permanently present N of Cap Blanc and S of Cap Frio. Many marine benthic species, including several cancellariids, have distribution areas in relation to these regions (see Fig. 3 and Table 1).

In the last decades, knowledge of the western African Atlantic Cancellariidae has improved considerably and therefore the present paper aims at compiling and reviewing this new information with respect to the 20 West African and Mediterranean cancellariids currently known.

ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
ATR	Atypical Tropical Region;
AV	author's colln (A. Verhecken);
BMNH	Natural History Museum, London;
CLL	Conchylia Linnaeana, Linnean Society, London;
ETTR	Eastern Typical Tropical Region;
FS	colln F. Swinnen, Lommel, Belgium;
HUJ	Hebrew University, Jerusalem;
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels;
KMMA	Koninklijk Museum voor Midden-Afrika, Tervuren;
MCNA	Museo de Ciencias naturales "Alfacs", San Carlos de la Rapita, Tarragona;
MCZ	Museum of Comparative Zoology, Harvard;
MHNG	Muséum d'Histoire naturelle, Genève;
MMF	Museu Municipal do Funchal, Madeira;
MNCN	Museo nacional de Ciencias naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris;
MOM	Musée océanographique, Monaco;

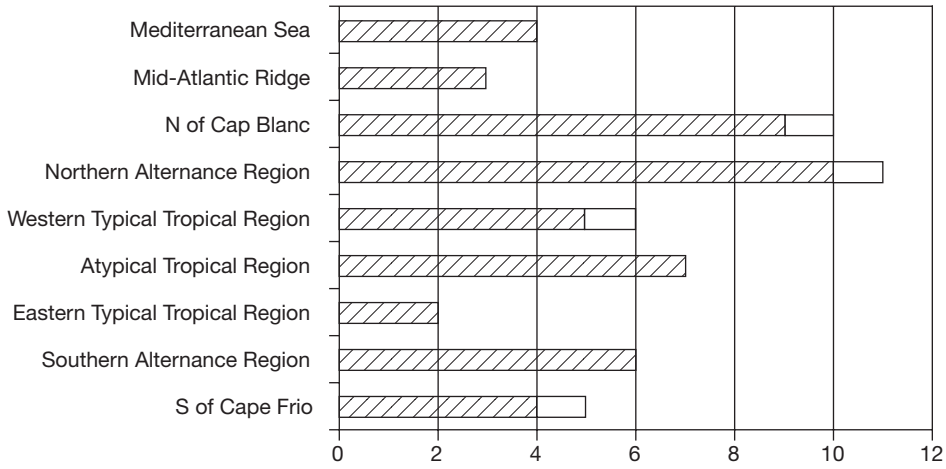

FIG. 3. — Graphic presentation of the number of cancellariid species in the hydroclimatic regions (see Fig. 2). White bars, occurrence not certain.

MPN	Museo di Paleontologia dell'Università degli Studi Federico II, Napoli;
MSNG	Museo di Storia naturale, Genova;
MSNM	Museo civico di Storia naturale, Milano;
NAR	Northern Alternance Region;
NMSZ	National Museums of Scotland, Zoology, Edinburgh;
NMW	Naturhistorisches Museum, Wien;
NMWZ	National Museum & Galleries of Wales, Department of Zoology, Cardiff;
REP	colln R. E. Petit, North Myrtle Beach, South Carolina;
RMNH	Nationaal Natuurhistorisch Museum, Leiden;
RP	colln Ron Parsons, Billingame, California;
SAM	South African Museum, Cape Town;
SAR	Southern Alternance Region;
SMF	Senckenberg Institut und Museum, Frankfurt/Main;
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC;
WTTR	Western Typical Tropical Region;
ZMA	Zoologisch Museum, Amsterdam;
ZMUC	Zoologisk Museum, Copenhagen;
ZMHU	Zoologisches Museum der Humboldt Universität, Berlin;
Code	*International Code of Zoological Nomenclature* (ICZN 1999);
colln	collection;
d	shell collected dead;
lv	specimen collected alive;
psu	practical salinity units;
stn	station.

MATERIAL AND METHODS

The limits of the area studied here are set arbitrarily as follows (Fig. 1, indicated in grey): West: mid-Atlantic ridge; North: 40°N latitude; East: African and European coastline, including the Mediterranean coast, and the 18°30'E longitude line south of Cape of Good Hope; South: 40°S latitude. In the north, this area slightly overlaps with the area covered by Bouchet & Warén (1985), but these authors concentrated on species normally living deeper than 300 m. For this overlap region (33°-40°N), the present paper includes one species more (*Brocchinia clenchi*) than the two (*Axelella minima* and *Brocchinia azorica*) studied by Bouchet & Warén (1985).

For the area off the southern part of Africa, only the species with main distribution area situated west of Cape of Good Hope are treated here. Therefore, *Cancellaria semidisjuncta* Sowerby, 1849 and *Africotriton* cf. *crebriliratus* are not included in this review.

As there are no exclusively shallow-water cancellariids in the NE Atlantic, all species presently known to live in the eastern Atlantic – excluding its Antarctic and Subantarctic regions – have been dealt with by Bouchet & Warén (1985) and the present paper.

TABLE 1. — Presence of radula, protoconch type and distribution of Cancellariidae in the West African hydroclimatic regions (terminology of Le Loeuff & Cosel 1998). Abbreviations: **NAR**, northern alternance region; **WTTR**, western typical tropical region; **ATR**, atypical tropical region; **ETTR**, eastern typical tropical region; **SAR**, southern alternance region; **m**, multispiral; **p**, paucispiral; **u**, unknown; **+**, present; **–**, absent; **×**, occurrence; *, occurring deeper than 300 m; **?**, to be confirmed.

	Page	Radula	Proto-conch	Mid-Atlant. ridge	Medit.	N of Cap Blanc	NAR	WTTR	ATR	ETTR	SAR	S of Cape Frio
Admetula cornidei	286	u	p			×	×					
Admetula gittenbergeri n. comb.	289	u	p				*					
Admetula italica	290	u	p			?	?	?				
Axelella minima	292	u	p	×	×	×						
Bivetiella cancellata	295	+	m		×	×	×	×	×	×	×	
Bivetiella similis	303	u	m		×	×	×	×	×		×	?
Brocchinia azorica	310	u	m	*								
Brocchinia clenchi	311	u	p	×		×						
Brocchinia decapensis	314	–	u								*	*
Brocchinia nodosa	316	–	m				*					
Cancellaria africana	317	+	p									*
Loxotaphrus deshayesii	319	u	p				×	×	×			
Nothoadmete euthymei n. comb.	321	+	u									*
Solatia piscatoria	322	+	m			×	×		×	×		
Solatia sp.	324	u	p						×			
Sveltia lyrata	324	+	m			*	*		×		*	*
Tribia angasi	327	u	p			×		×				
Tribia coronata	330	u	p		×							
Trigonostoma gofasi n. sp.	336	u	m			×	×	×	×		×	
Trigonostoma scala n. comb.	339	u	p				×				×	
Number of species per hydroclimatic region				3	4	9+1?	10+1?	5+1?	7	2	6	4+1?

This is based mainly on the rich western African collections of MNHN and on material in many museums and private collections, as well as on material collected by American, Belgian, British, Danish, Dutch (12 campaigns), Monacan, South-African and Spanish oceanographic expeditions. A list of the 20 species dealt with here is provided in Table 1.

As the cancellariid supraspecific classification is in urgent need of revision, subfamily names are avoided here, while the application of some generic names may be tentative. All genus level names are here used as genera. Genera are listed alphabetically, as are species.

Distribution maps are given: captures of one or a few specimens are indicated as circles, black circles, etc.; regions where many specimens were taken, or from where no precise locality is known, are indicated as grey areas. In cases where distribution areas for a species are geographically close but separated by a blank area (e.g., for *Tribia angasi* (Crosse, 1863), *Loxotaphrus deshayesii* (Duval, 1841), etc.) it cannot be decided yet whether this is due to a real separation or to a lack of data from the area in between.

When relevant, elementary statistical data on shell dimensions are provided, with the purpose of supplying additional descriptive information regarding their variability, and graphs allow a simple visual evaluation, applicable to comparison of closely related species.

The protoconchs of all studied species except *Brocchinia decapensis* and *Nothoadmete euthymei* n. comb. are known and figured here if a good shell was available. SEM photographs were made at KBIN, unless indicated otherwise. Numbers of protoconch whorls were counted according to Verduin (1982: 129, fig. 4) (see Fig. 4).

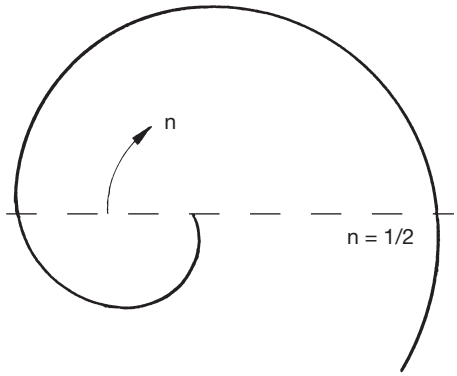

FIG. 4. — Counting the number of protoconch whorls used in this paper (after Verduin 1982: 129, fig. 4).

Bibliographic references for species names cited only once in this paper can be found in Petit & Harasewych (2005).

SYSTEMATICS

Order NEOGASTROPODA Wenz, 1938
Superfamily CANCELLARIOIDEA
Forbes & Hanley, 1851
Family CANCELLARIIDAE Forbes & Hanley, 1851

Genus *Admetula* Cossmann, 1889

Admetula Cossmann, 1889: 224.

TYPE SPECIES. — *Cancellaria evulsa* Solander *in* Brander, 1766, Eocene, England (original designation).

REMARKS

Cossmann's argument (1889: 224) for proposing the new section *Admetula* was his idea that the name *Bonellitia* Jousseaume (1887: 223) was incorrectly formed ("Bonelli" should lead to *Bonellia*), and preoccupied in the emended form. He stated that the differences between *Admetula* and *Bonellitia* are the presence of varices in *Admetula* and its shell thickness. Sacco (1894: 42) rejected these differences, stating that *B. bonellii* frequently has varices; and Cossmann (1899: 33) agreed, stating: "Il n'y a donc aucun motif pour maintenir la séparation que j'ai arbitrairement faite", thus accepting *Admetula* as a junior subjective synonym of *Bonellitia*. This usage was followed by Wrigley (1935: 364), Wenz (1943: 1369) and Marks (1949: 456), and by the present author in earlier papers (see Verhecken 1986a: 34).

However, the history of use of *Bonellitia* and *Admetula* is rather confuse: Stewart (1927: 413) and Squires (1984: 36) used *Admetula* as a section or a subgenus of *Bonellitia*. Sieber (1936: 100) used the combination *Admete* (*Bonellitia*) *evulsa* for the type species of *Admetula*. Eames (1957: 49) used *Admetula* as a subgenus of *Bonellitia*, for forms with less muricate sculpture. Hickman (1980: 67) used the genus *Bonellitia*, with as subgenera the tabulate *Bonellitia* s.s. (with flat sutural ramp and very distinct shoulder) and the non-tabulate *Admetula.* Several authors followed Cossmann in classifying *Admetula* in the subfamily Admetinae, genus *Admete*, where it can hardly belong because of its strong columellar folds.

In a series of papers, Petit *et al.* (Petit 1984: 38; Petit & Harasewych 1991, 2000; Landau *et al.* 2006: 85) used *Admetula* as a genus distinct from *Bonellitia*, based on the sharp sculpture of *Cancellaria bonellii* Bellardi, 1841 (type species of *Bonellitia*) versus the smoother sculpture of *A. evulsa*. This distinction leads to inclusion in *Admetula* of the three following species here studied.

Admetula cornidei (Altimira, 1978)
(Figs 5A-F; 64A, B)

Admete cornidei Altimira, 1978a: 170, fig. 1.

Admetula cornidei – Petit & Harasewych 1991: 181.

TYPE MATERIAL. — Holotype: 11 × 6 mm, deposited in the Instituto de Investigaciones Pesqueiras, Barcelona (Altimira 1978a: 170); but in June 1987 this specimen could not be traced. In later correspondence (J. Castellví Piulachs, 31 March 1995) the director of this Institute (now Institut de Ciències del Mar) stated that the holotype is not in its reference collection. Neither is it in MNCN (Templado *in litt.*): its actual whereabouts is unknown.

Single paratype: MCNA, unnumbered shell (Fig. 5A, B): 10.2 × 6.1 mm, aperture height 5.0 mm (given by Altimira as respectively 10.7 × 5.8, and 5.7 mm). This shell was in the late Altimira's collection; after his death the marine gastropods were acquired by MCNA, which lent the paratype for study.

FIG. 5. — **A**-**F**, *Admetula cornidei* (Altimira, 1978); **A**, **B**, paratype, Mauritania, N of Cabo Blanco, 75 m (MCNA); **C**, **D**, off Western Sahara, trawled, muddy bottom; **C**, AV 0046/1; **D**, AV 0046/2; **E**, juvenile white shell, Mauritania, Banc d'Arguin, TYRO stn B-1, 53-64 m (ZMA); **F**, shell without periostracum, trawled off Western Sahara, sandy mud, 50-60 m (RP); **G**, **H**, *A. italica* (D'Ancona, 1872), off Northern W Africa (Torres-Alba colln). Scale bars: 1 mm.

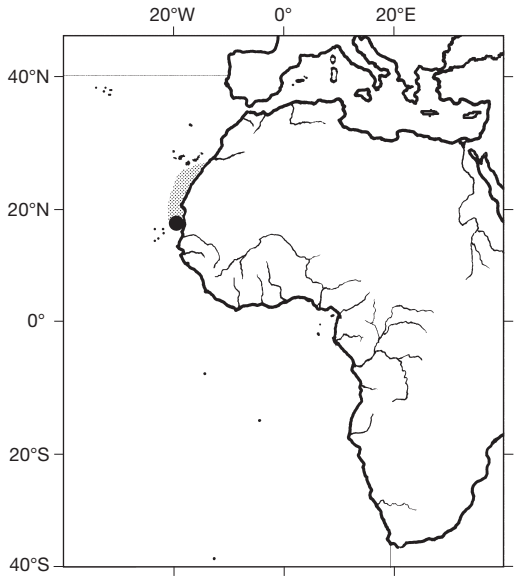

FIG. 6. — Distribution area of *Admetula cornidei* (Altimira, 1978) (grey area) and *A. gittenbergeri* (Verhecken, 2002) n. comb. (●).

TYPE LOCALITY. — Mauritania, N of Cabo Blanco, ATLOR VII stn 55, 22°00'N, 17°14'W, 75 m (Altimira 1978a: 170, 171; 1978b: 173). About 65% of the sample volume taken at that station consisted of fragments of the bivalve *Pinna* cf. *ramulosa*.

MATERIAL EXAMINED. — The paratype, and:
Off Western Sahara. 50-60 m, 12 specs: 8.5 × 5.2 mm and 6.9 × 4.8 mm (AV 0046, Fig. 5C, D); 8.4 × 6.0 mm (AV 0047); 7.4 × 5.1 mm (AV 0048); 8.6 × 5.3 mm, 8.0 × 5.5 mm (AV 0659); 8.4 × 5.5 mm, 8.3 × 5.9 mm (90-120 m) (AV 0025); 5.8 × 4.1 and 5.9 × 4.4 mm (REP); 10.0 × 5.7 mm (RP, Fig. 5F); 7.5 × 5.3 mm (FS).
Canary Islands. CANCAP stn 3123, 29°21'N, 17°40'W, 125 m, 1 spec. (RMNH).
Mauritania. Banc d'Arguin, TYRO stn B-1, 19°33.8'N, 16°54.5'W, 53-64 m, a white very juvenile shell, 4.0 × 3.0 mm (ZMA, Fig. 5E).

DISTRIBUTION (Fig. 6). — Known only from off Canary Islands, Western Sahara and Mauritania, 50-125 m.

DESCRIPTION

Shell thin, ovately oblong, brown to whitish. Protoconch paucispiral, slightly deviated from teleoconch shell axis; number of whorls: 1 1/8-1 1/2; maximum diameter 1.1-1.2 mm, exposed height 0.9-1.3 mm. Protoconch sculpture: nucleus smooth; further on some smooth growth lines and, on the last quarter of whorl, 6 smooth spiral lines. Transition to the teleoconch indistinct indicated by onset of axial sculpture.

Teleoconch with up to 3 1/4 rounded whorls. Axial sculpture on 1st to 3rd whorl: 15-20, 16-19, 16-18 ribs; 14-17 broad rounded ribs on last whorl, less conspicuous near the peristome. Spiral sculpture of flat bands (0.1-0.15 mm wide), numbering 6, 5-7, 6-8 on 1st-3rd whorl respectively; one secondary spiral line between primary spirals on third whorl; 12-15 primary spirals on last whorl, with one secondary line between. Suture slightly impressed. Aperture oblong, 4.5-5.0 mm high, 2.5-2.9 mm wide. Outer lip flared out, very slightly crenulated. Six short lirae inside outer lip; another set of such lirae is visible deep inside the aperture (RP), but no lirae in other shells. Columella inclined abaxially, forming a neat angle of about 120° with parietal side of the aperture; with three folds: posterior one the strongest, the anterior one is very small (not shown in Altimira 1978a: fig. 1). The rim of the siphonal fold (interpreted as a third columellar fold by Altimira) forms a very prominent "tooth". Transparent brownish callus on the columellar side of aperture. Columellar field concave because of siphonal fasciole; no umbilicus. A pale brown periostracum with short hairs (length 0.2 mm) remains on fresh specimens; the hairs are placed on the spiral lines.

REMARKS

Two white juvenile specimens from off Canary Islands (CANCAP stn 3123 [RMNH]) and Mauritania (TYRO stn B-1 [ZMA]) have a very squarish protoconch profile, but otherwise do not differ considerably from the other material.

The dimensions of the 13 shells studied here (not including the white juveniles just mentioned) give a linear correlation factor r^2 between shell height and width of 0.82, with $p < 0.005$ (Fig. 7). A few whitish juvenile shells, here identified as *A. cornidei*, might possibly belong to *A. italica* D'Ancona, 1872 (see below).

Admetula cornidei differs from the Eastern South-African *A. epula* Petit & Harasewych, 1991, in its more slender outline, thinner shell, and having the

"hairs" of the periostracum rather close-set on the spiral cords, and not confined to the intersections with the axial ribs. Petit & Harasewych (2000: figs 1-4) figured a more slender shell of *A. epula* (more resembling *A. cornidei* than does the *A. epula* holotype), and their newly described species *Admetula afra*, also from SE Africa. In form and sculpture both are very similar to *A. cornidei*, but the distance to NW Africa, and the direct development of these species as evidenced by their paucispiral protoconch, should exclude conspecificity. Height/width distributions for *A. cornidei* and *A. epula* partly overlap (Fig. 7). Combining the data for both species yields a correlation line (not figured) with $r^2 = 0.95$, and $p < 0.005$, indicating that they cannot be distinguished based on height/width data only.

There are several species, cited as *Bonellitia* or *Admetula*, in the European Mio-Pliocene; e.g., *A. italica* is closely related.

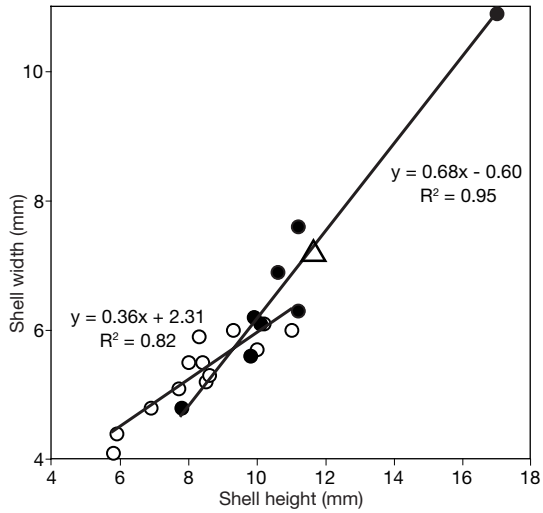

FIG. 7. — Dispersion diagram and linear correlation line of shell dimensions for *Admetula cornidei* (Altimira, 1978) (○), *A. epula* (Petit & Harasewych, 1991) (●) and *A. italica* D'Ancona, 1872) (△).

Admetula gittenbergeri
(Verhecken, 2002) n. comb.
(Figs 8; 64C, D)

Bonellitia gittenbergeri Verhecken, 2002: 508, figs 11-14.

TYPE MATERIAL. — Holotype: 12.2 × 8.4 mm (RMNH 56456); paratypes: all from type locality: (1) 13.4 × 8.8 mm, (2) 11.6 × 8.3 mm, (3) 11.9 × 8.1 mm (RMNH 56457).

TYPE LOCALITY. — Off Mauritania, TYRO Mauritania-II Exped. 1988, stn MAU 2.040,18°51'N, 16°53'W, 500 m, fossil coral debris, macrourids.

MATERIAL EXAMINED. — Only the type material is known.

DESCRIPTION

Shell solid, with rounded whorls and a relatively large body-whorl; dimensions up to 13.4 × 8.8 mm. Colour whitish.

Protoconch paucispiral, with 7/8 whorl. Maximum diameter 1.1 mm, exposed height 0.8 mm. Fine spiral striae (not visible on Fig. 64C, D) remain on otherwise eroded protoconch.

Teleoconch with up to 3.5 whorls. Spiral sculpture starts abruptly. The second and third teleoconch whorls have five main spiral bands consisting of two close-set ridges, separated by a very thin line; width of complete spiral bands about 0.1-0.15 mm, on third whorl a single secondary spiral in between main spirals. Body-whorl with 12 main spiral bands, up to 0.3 mm wide; a set of secondary and tertiary spirals also present. Axial sculpture of 12 and 13 low rounded ribs on second and third teleoconch whorl respectively; 10 axials on the body-whorl. Aperture porcelaneous white, large, almost semicircular; height 7.0 mm, width 4.6 mm. Outer lip thick, flared out, with no inner lirae in holotype; 8 short solid ridges in paratypes, posterior ridge placed somewhat apart. Columella with two sharp folds and a prominent "tooth" at the rim of the short wide siphonal canal. Columellar glaze white, very thin adapically on holotype, thicker in the umbilical region; paratypes with thicker callus. Umbilicus completely closed by callus, concave region formed by weak fasciolar ridge. Periostracum very thin, fawn, with short hairs (up to 0.3 mm length) arranged along middle line between close-set spiral cords.

REMARKS

The first teleoconch whorl of all four shells is strongly corroded, so that its sculpture has disappeared. For

the rest, the holotype is in perfect condition, but the outer lip is slightly less developed than in the paratypes. This species is most similar to *A. cornidei* living in the same area, but differs mainly in being broader and in having a much more solid shell. *A. gittenbergeri* n. comb. has broader and more rounded axial ribs, and spiral sculpture of double bands, versus a single broad band in *A. cornidei. Admetula gittenbergeri* n. comb. can have eight lirae inside the outer lip, and shell and periostracum are whitish.

In general outline, shells of *A. gittenbergeri* n. comb. somewhat resemble juvenile shells of "*Cancellaria*" *africana* Petit, 1970, from the Cape of Good Hope area, which are more slender however, have a larger protoconch, a relatively higher spire and a straight columella.

This species is very similar to *Cancellaria ringens* Sandberger, 1859, from the Tertiary (Rupelian, Lower Oligocene) of the Mainz Basin, Germany; but the fossil species has a prominent "tooth" at about half height inside the outer lip, and its late-Paleogene age can hardly suggest a direct relation between both species.

Admetula italica (D'Ancona, 1872) (Fig. 5G, H)

Cancellaria italica D'Ancona, 1872: 112, pl. 12, figs 5a, b, 6a, b.

?*Admetula* sp. – Vera-Peláez *et al.* 1995: 160, figs 4I-L, 6I, J.

Admetula malacitana Vera-Peláez & Muñiz-Solis, 1995: 297-300, pls I, II.

Admetula italica – Vera-Peláez *et al.* 1995: 160, figs 4I-L, 6I, J.

Contortia italica – Landau *et al.* 2006: 65.

TYPE MATERIAL. — Syntypes of *C. italica*: 1 adult, 26 × 16 mm, Val d'Era, was in the collection of the geologist Roberto Lawley (1818-1881); many juveniles from Colline Pisane were in the Italian Central Paleontological Collection in the Royal Museum in Firenze. The actual whereabouts of these syntypes is not documented; their possible presence in the Paleontological Department of Museo Zoologico "La Specola", Università degli Studi di Firenze, could not yet be confirmed.

TYPE LOCALITY. — Val d'Era and Orciano Pisano, Pliocene, Italy.

MATERIAL EXAMINED. — One eroded recent shell from off NW Africa (Torres-Alba, Málaga, Spain).

DISTRIBUTION. — The fossil shells are known from the Pliocene of Italy and southern Spain. Recent shells are said to have been taken off Western Sahara to Mauritania.

DESCRIPTION

Recent shell white, 11.5 × 7.2 mm, spire turriculate.

Protoconch, fossil: figured by Landau *et al.* (2006: pl. 2, figs 1, 2) and by Vera-Peláez & Muñiz-Solis (1995: pl II); recent: paucispiral with 1 3/4 whorls, maximum diameter 1.2 mm, exposed height 1.2 mm.

Teleoconch: 3 1/4 rounded whorls, separated by a narrow but distinct, almost flat sutural zone (width 0.5 mm at the start of the last whorl). Spiral sculpture: on whorls 1-3: 6, 6, 7 spiral ridges, 0.2 mm wide, running over the axial ribs. The last whorl has 14 spirals; there is one narrow spiral ridge in the sutural zone. Axial sculpture on whorls 2-3: 17, 16 rounded ribs. On the last quarter of the last whorl this sculpture becomes very confuse. On the shoulder of the whorls, the rounded ends of the axial ribs penetrate into the sutural zone up to the spiral ridge, leaving an unsculptured zone about 0.2 mm wide. Aperture: 5.8 mm high, 3.1 mm wide. Columella strongly inclined abaxially, with 2 strong folds, and the rim of the siphonal canal apparently forming a third fold. Outer lip smooth inside, without inner lirae. No trace of an umbilicus.

REMARKS

Landau *et al.* (2006: 66) consider *Contortia malacitana* "conspecific with *C. italica*, possibly a thinner-shelled deeper water form"; but reasons for including the species in *Contortia* and not in *Admetula* are not given.

The single recent shell here studied is rather heavily corroded and has several bore-holes; no sculpture remains on the heavily drilled and corroded protoconch, and a narrow strip of the outer lip is broken away near the siphonal canal: this may result in a slight change of aperture outline. It was taken by a commercial fishing boat in the area Morocco-Canary Islands-Mauritania. This region is normally

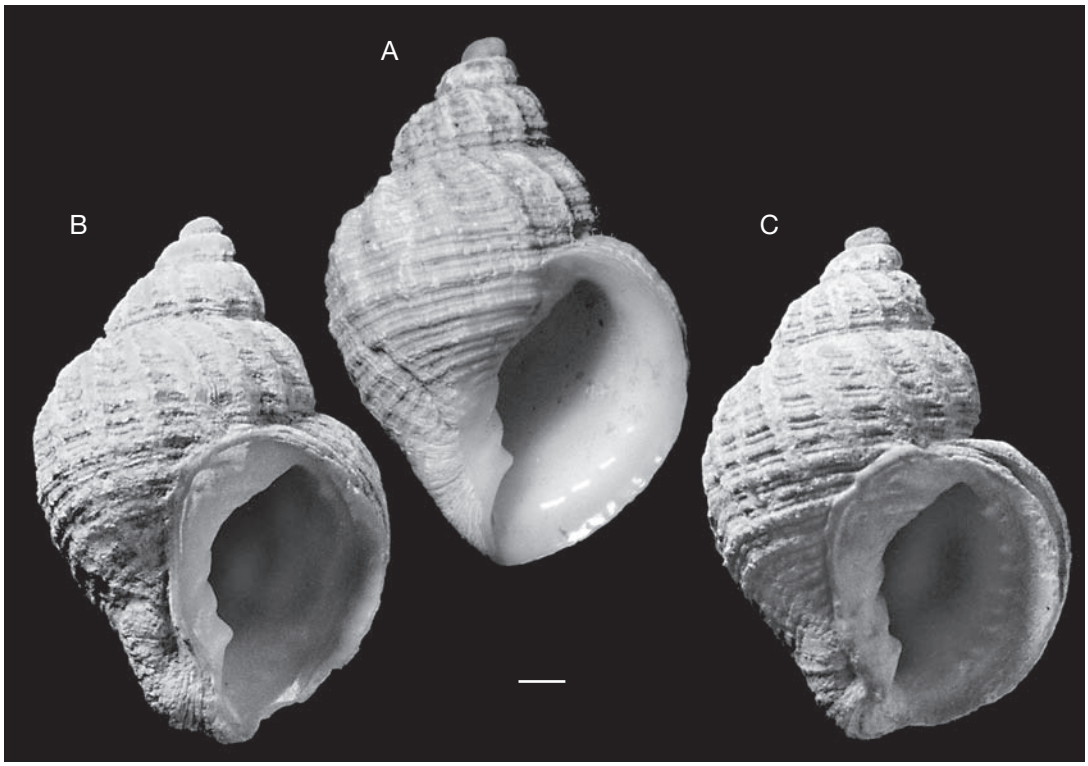

FIG. 8. — *Admetula gittenbergeri* (Verhecken, 2002) n. comb., Mauritania, MAU stn 2.040, 18°51'N, 16°53'W, 500 m: **A**, holotype (RMNH 56456); **B**, **C**, paratypes (RMNH 56457). Scale bar: 1 mm.

covered by Málaga fishermen: exceptionally they may go as far as Senegal, but never enter the Gulf of Guinea (Torres-Alba *in litt.*). The exact locality is unknown; it is only specified to be taken "in deep water". The possibility cannot be excluded that the few "recent" shells of *A. italica* actually known (only one seen by the present author) are in fact fossils dredged by fishermen at some outcrop of Pliocene deposits in the vaguely described area.

This shell is rather similar to *A. cornidei*, but it can be distinguished from equal-sized shells of the latter by its less slender outline, stronger sutural shoulder and more deviated columella. In a height/width graph (Fig. 7), this shell is located outside the 99% confidence area of the *A. cornidei* shells; it fits well on the correlation line for *A. epula* (Petit & Harasewych, 1991). But more material of these three species is needed for a better view on their relation.

The present shell is somewhat similar to *Admetula epula* from South Africa, east of 20°E; in the publication of that species, the present W African shell was mentioned as "an undescribed north-western African species of *Admetula*". As far as can be judged on this corroded shell, its protoconch seems to be of the same type as that of *A. epula.* The distance from Mauritania to the South Point of Africa is considerable, but at least *Bivetiella similis* and S*veltia lyrata* (both with a multispiral protoconch) show that cancellariid species can occur over similar distances. This shell differs slightly from *A. epula* in being less heavy, in having the whorls more shouldered, and the last whorl less rounded than in *A. epula*.

The identification of this single eroded shell can only be preliminary, but there is a fair resemblance to *A. italica* shells from the Spanish and Italian Pliocene. A few whitish juvenile shells tentatively identified as *A. cornidei* might possibly belong to this species.

Vera-Peláez & Muñiz-Soliz (1995) discussed the relationships between the fossil *A. malacitana* and the fossil species cited as *Bonellitia serrata* (Bronn, 1831), *Admetula evulsa* (Solander, 1766), *Cancellaria* (*Merica*) *contorta* Basterot, 1823 and *C.* (*M.*) *altavillae* (Libassi, 1859).

Genus *Axelella* Petit, 1988

Axelella Petit, 1988: 130, replacement name for *Olssonella* Petit, 1970 (non *Olssonella* Glibert & Van de Poel, 1967).

TYPE SPECIES. — *Cancellaria smithii* Dall, 1888, Recent, Western Atlantic (original designation for *Olssonella* Petit, 1970).

REMARKS

Several European Neogene species have been classified under *Babylonella* Conrad, 1856, proposed as a subgenus of *Cancellaria* and originally including 11 Eocene and Oligocene species from Alabama, USA. Cossmann (1889: 231) subsequently designated *Cancellaria elevata* Lea, 1833, as type species; he included in *Babylonella* species ranging from the Senonian to the Pliocene. Extending this extremely long genus lifetime to include recent times does not seem appropriate without solid evidence. This, together with the rather confuse history of the use of *Babylonella* for European fossils (not discussed here), made it preferable not to use the latter genus, awaiting a good revision of cancellariid genera (see above).

The generic position of the following species is not very clear. Bouchet & Warén (1985), on the advice of Petit, placed it in *Olssonella* (now *Axelella*).

Axelella minima (Reeve, 1856)
(Figs 9; 58A; 59A, B)

Cancellaria minima Reeve, 1856: spec. 77 (text pages unnumbered). — Verhecken 1984a: 1-9.

Sveltella minima – Nordsieck 1968: 51.

Narona minima – Gubbioli & Nofroni 1985: 20.

Olssonella minima – Bouchet & Warén 1985: 263, figs 692, 693. — Ardovini & Cossignani 1999: 66, unnumbered fig.

TYPE MATERIAL. — A lectotype is here designated: BMNH 1968410/1, 6.5 × 3.4 mm (Fig. 9A; Bouchet & Warén 1985: fig. 692), in order to provide a reference regarding the variability in shell form within this species. Two paralectotypes, BMNH 1968410/2 (Verhecken 1984a: fig. 2) and BMNH 1968410/3.

TYPE LOCALITY. — Unknown to Reeve (1856); the board that held the shells mentions in pencil: "Gibraltar. R. McAndrews collection" and "Madeira. R. McAndrew" (possibly referring to MacAndrew 1856: 132, as "?sp. ined."); there is also a reference to the Cuming collection; but all these data may have been added afterwards. Monterosato (1878: 97, note 2) first published a locality for this species: the Canary Islands.

MATERIAL EXAMINED. — The shells mentioned by Verhecken (1984a), plus:
Azores. S of Faial, CANCAP stn 5.126, 38°30'N, 28°38'W, 300 m, 2 specs (RMNH).
Morocco. 33°59'N, 7°50'W, 155 m, 1 spec. (MNHN). — 30°17'N, 10°01'W, 145 m, 1 spec. (MNHN). — 34°08'N, 7°30'W, 170 m, 1 spec. (MNHN). — W of Cape Yubi, CANCAP stn 2.036, 28°00'N, 13°22'W, 540-580 m, 3 specs (RMNH).
Off Western Sahara. 50-60 m, 3 specs (AV). — 22-26°N, 8 m, 2 specs (FS).
S of Selvagem Pequena. CANCAP stn 3.081, 30°01'N, 16°01'W, 91 m, 2 specs (RMNH). — CANCAP stn 3.083, 2 specs (RMNH). — CANCAP stn 4.103, 425 m, 3 specs (RMNH).
Canary Islands. 1 spec. (BMNH [R. MacAndrew]); 12 specs (FS). — S of Fuerteventura, 28°02'N, 14°28'W, 170 m, 2 specs (FS). — Punta de Jandia, CANCAP stn 2.003, 2.010, 2.011, 2.022, 2.023, 2.034, 2.073, 2.075, 28°03'N, 14°30'W, 83-550 m, a total of 17 specs (RMNH). — Lanzarote, Punto del Carmen, 40-45 m, 2 specs (FS). — S and E of Lanzarote, CANCAP stn 4.038, 4.041, 4.086, 4.088, 4.090-4.092, 55-785 m, 20 specs (RMNH).
Madeira. 18-200 m, *c.* 200 specs (FS). — 35-40 m, 20 specs (ZMA). — 410-580 m, 1 spec. (MNHN); *c.* 200 specs (NMWZ 1985.158); 8 specs (SMF [Watson]); 3 specs (HUJ 12116 [Watson]); 1 spec. (ZMHU). — SE Madeira, 74-145 m, 15 specs (FS); 1 spec. (USNM 64403, ex Dall colln); 11 specs (BMNH 1911.10.26.9590-9 [Watson]); 3 specs (BMNH 1966184 [J. M. Moniz colln]); 2 specs (BMNH 1853.4.11.161-162 [R. MacAndrew] with old label "*Cancellaria* new?"); 43 specs (BMNH 1911.10.26.9605-9624 [Watson 1897]). — CANCAP stn 3059, 108 m, 1 spec. (RMNH). — W of Deserta Grande, 100 m, CANCAP stn 2.048, 1 spec. (RMNH).

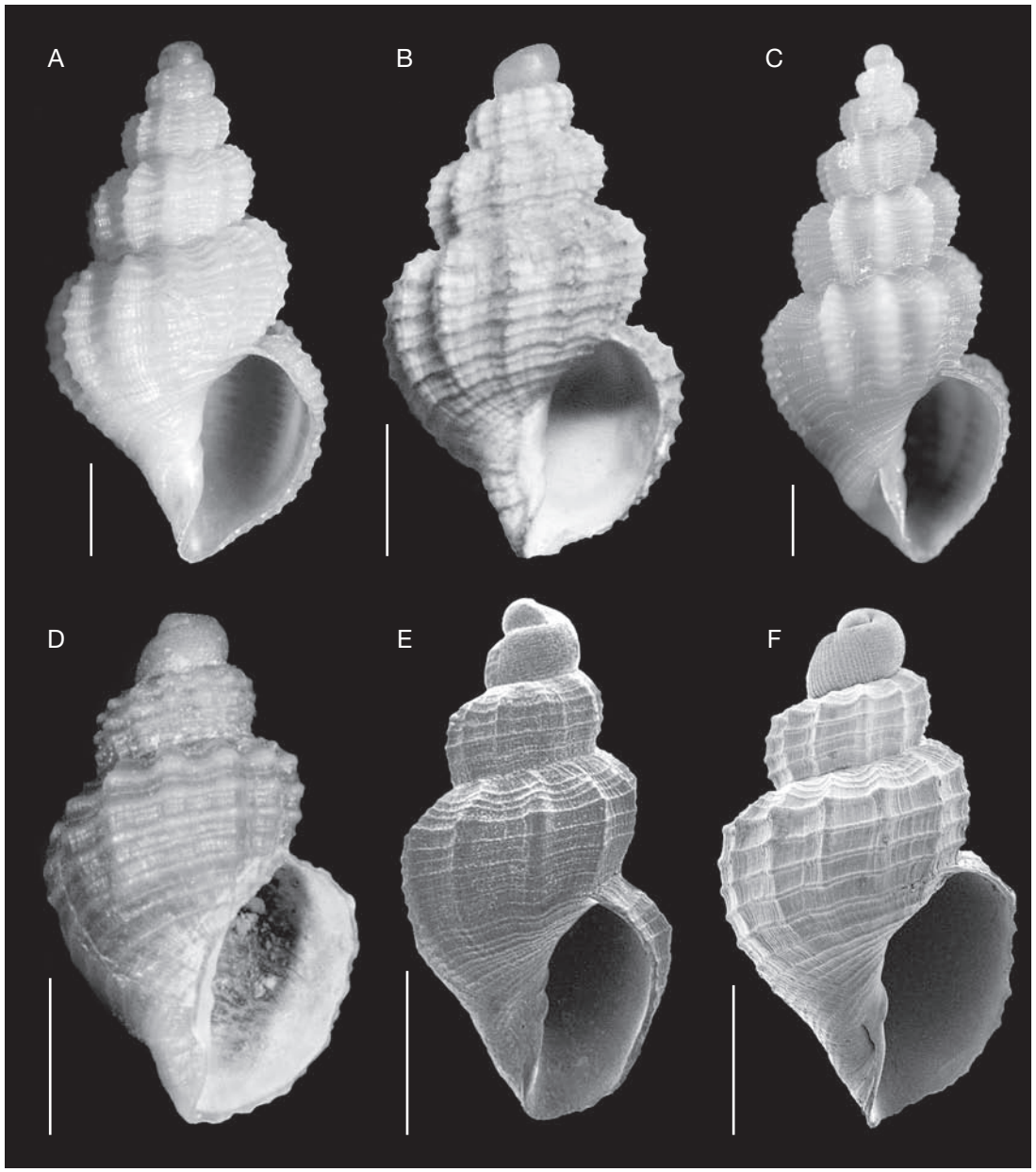

FIG. 9. — *Axelella minima* (Reeve, 1856): **A**, lectotype (BMNH 1968410/1); **B**, paralectotype (BMNH 1968410/3); **C**, Western Sahara, off Cape Bojador (AV 0044); **D**, **E**, Madeira, W of Deserta Grande, CANCAP stn 1.021, 32°29'N, 16°32'W, 228-240 m; **D**, AV 0040; **E**, RMNH (photo: M. Düggelin, SEM laboratory, University of Basel); **F**, Madeira, *J. Charcot* stn 58 (MNHN). Scale bars: 1 mm.

"Off SW Spain, Canary Islands, Madeira and Gibraltar", 5 lots, up to 8.1 × 3.7 mm, (USNM [Jeffreys, McAndrew]).

Mediterranean. "Fide Horsfall, from Ponsonbys collection", 1 spec., 9.4 × 4.3 mm (BMNH): maximum size for known shells, but the literature mentions a height

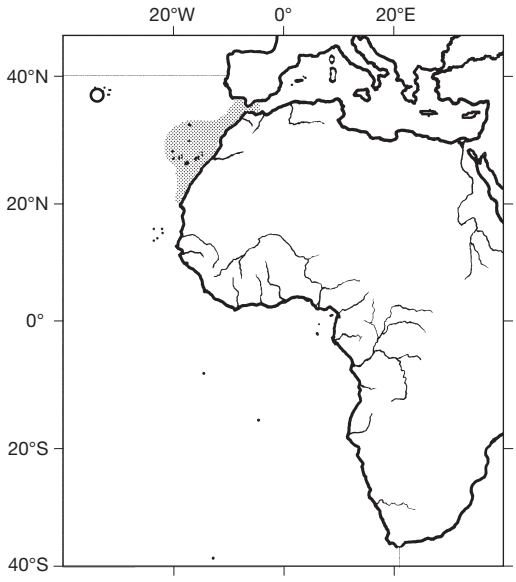

FIG. 10. — Distribution area of *Axelella minima* (Reeve, 1856).

up to 13 mm (see Verhecken 1984a: 8).

DISTRIBUTION (Fig. 10). — Roughly between 22-38°N and 3-29°W (adapted from Verhecken 1984a): Azores (2 specs), off Morocco (3 specs), Western Sahara (5 specs), the Canary Islands (55 specs), Madeira (some 500 specs), Selvagem islands (9 specs), and the westernmost Mediterranean: off Alboran Island (1 spec., 90-100 m, Luque *et al*. 1985: 12); off Marbella (numerous shells, 50-200 m, Gubbioli & Nofroni 1985: 20). These last two citations support the Mediterranean locality "Gibraltar" given by MacAndrew (1856: 132); they mention shells up to 7 mm high.

Bathymetry: material has been collected between 8 and 680 m; a single dead shell taken at 1085 m (Verhecken 1984a: 2) may not be representative for the bathymetry of this species. The shells collected off Madeira by Swinnen were dead and/or damaged, so that their depth data (between 14 m and dredge limit 200 m) do not necessarily reflect the bathymetric distribution of this species. See also Verhecken (1984a: 6, 7). Bouchet & Warén (1985: 263) conclude "this will probably prove to be a shallow water species".

DESCRIPTION

Shell small, fusiform, white to pale brownish. Dimensions: normally up to about 6 mm height, exceptionally to 9.4 mm. Protoconch slightly deviated from teleoconch shell axis, paucispiral (mean: 1.25-1.50, but max. up to two whorls), maximum diameter 0.62 mm; elaborate sculpture (Fig. 59A, B). Transition to teleoconch clearly visible. Teleoconch with up to five whorls. Axial sculpture of 8-14 rounded ribs (faint to strong) on all whorls; microsculpture of growth-lines. Spiral sculpture: broad rounded ridges, 2-7 on first, 3-11 on second whorl. Secondary spirals, very faint to strong, may occur between the primaries. Sutures impressed to deeply impressed. Aperture widely elongate, with faintly indicated siphonal canal. Outer lip thin, without inner lirae. Traces of a very thin callus may be present. Umbilicus closed or sometimes showing only a very narrow slit.

REMARKS

Jeffreys (1885: 49) mentioned that MacAndrew dredged "the typical form" and "a variety" off Madeira and the Canaries, and stated that the variety "has the whorls angulated below the suture as in the fossil species" *Cancellaria subangulosa* Wood, 1848. A similar difference can be seen in Figure 9A-C versus 9D-F. The phenomenon of weakly and strongly sculptured shells within one species is also seen in some other cancellariid species, e.g., *Brocchinia clenchi*, *Tribia angasi*. It has become clear that a figure published earlier (Verhecken 1984a: fig. 3) as "slender form" was due to an error in the imaging system; this is now corrected in Figure 9E. The shell of Figure 9F has a microsculpture of small nodules between the spiral bands of the teleoconch (Fig. 58A).

The two lots of about 200 shells (NMWZ; FS) may support the statements by Watson (1897: 277) and by Nobre (1937: 23) that the species is "very common everywhere" off Madeira. However, unpublished work by Swinnen (MMF) showed that the distribution of shells in mud dredged off Madeira in depths to 200 m can differ strongly between localities.

Biometric data have already been published (Verhecken 1984a).

Axelella minima is probably the species referred to by Nobre (1884: 52) when citing *Cancellaria subangulosa* Wood from off Southern Portugal (see also Nobre 1938-1940: 153, citing "*C. subangulosa* Weink.").

Robert MacAndrew (1856: 132, 154) listed a "?sp. ined." from Gibraltar, Canary Islands and Madeira, sand, 8-24 fathoms; and also a "sp. ined." from Canary and Madeira Islands, sand, 22-44 m. It is not clear what he may have referred to. Based on the localities, the former may well be *A. minima*; or he may have distinguished slender and more ventricose forms of that species.

A single shell labelled "*Cancellaria minima* Reeve, Madeira, V. W. MacAndrew col., old label Preston 19/6/11" (BMNH) is here tentatively identified as a strongly sculptured *Admete viridula* (Fabricius, 1780). This is an Arctic or deep water species with as recorded southern distribution limit the deep waters off the British Isles (Bouchet & Warén 1985: 258). This single shell is judged insufficient evidence for establishing the occurrence of this species off Madeira. However, also Nobre (1884: 51) cited *A. viridula* from "West of Portugal"; about half of the western coastline of Portugal is south of 40°N and is included within the limits set for the present study. The whereabouts of Nobre's material is unknown: I did not find it, nor any other cancellariid, in the Nobre collection at Porto in 1982.

Cancellaria subangulosa and *C. fusiformis* Cantraine, 1835 from the European Neogene are rather similar to *A. minima*, but have a multispiral protoconch.

Genus *Bivetiella* Wenz, 1943

Bivetiella Wenz, 1943: 1356, *nomen novum* for *Bivetia* Jousseaume, 1887: 193 *non* 163. *Bivetiella* was proposed as a subgenus of *Cancellaria*.

TYPE SPECIES. — Jousseaume designated the type species of his preoccupied genus *Bivetia* in these words: "Bivetia Bivet Adans. (Similis Sow.) type". Obviously, this refers to "Le Bivet" of Adanson (1757: 123), an unavailable pre-Linnean name. However, *Bivetia bivet* can be considered an available name for a new taxon proposed by Jousseaume (ICZN 1999: art. 12.2.1); it is a junior synonym of *Cancellaria similis* Sowerby, 1833. Consequently, the type species of *Bivetiella* Wenz, 1943 is *Bivetia bivet* Jousseaume, 1887 (ICZN 1999: arts 67.2.1, 67.7, 67.8) and not *C. similis* as given by Wenz, but the distinction is only formal. Also Marks (1949: 456) proposed for a new subgenus of *Cancellaria* s.s. the name *Bivetiella*, with *C. similis* as type species; it is a homonym and (subjective) synonym of Wenz' name. For more details on *Bivetiella*: see Jung & Petit (1990: 103).

REMARKS

The *Bivetiella* species here studied tolerate important changes in salinity: from about 39 psu in the eastern Mediterranean (*B. cancellata*), to less than 10 psu off Guinea (Le Loeuff & von Cosel 1998: 318) for *B. cancellata* and *B. similis*. Both species generally occur from intertidal to about 100 m, but a few specimens of both have been taken at depths to 280-300 m; the latter depths may not represent their normal bathymetry.

Bivetiella species very similar to those studied here occur in European and N African Miocene and Pliocene strata. Several specific names have been given to these taxa: e.g., for *cancellata*: *dertonensis* Bellardi, 1841, *pluricosticillata* Sacco, 1894 and *praecedens* Beyrich, 1856 (discussed by Davoli [1982: 22]); *stromboides* Grateloup, 1832 and *subcancellata* d'Orbigny, 1852 (discussed by Cahuzac *et al.* [2004]).

Bivetiella cancellata (Linnaeus, 1767)
(Figs 11; 13-18; 21A; 22; 23A; 24A; 25)

Murex scabriculus Linnaeus, 1758: 751, no. 473.

Voluta cancellata Linnaeus, 1767: 1191, no. 413. — Born 1780: figs 7, 8.

Murex scabriusculus Linnaeus, 1767: 1191, no. 413.

Buccinum pyrozonias Gmelin, 1791: 3488 (see Petit 1984: 58).

Cantharus triplicatus Röding, 1798: 133 (*ibid.*).

?*Buccinella rotundata* Perry, 1811: pl. 27, fig. 2.

Cancellaria cancellata – Lamarck 1822: 113.

Cancellaria costata Sowerby, 1822: pl. 218, fig. 2.

Cancellaria (*Bivetia*) *scabriuscula* – Pallary 1900: 259 with varieties *major* and *minor* (both *nomen nudum*).

Bivetiella cancellata – Glibert 1960: 66.

TYPE MATERIAL. — Three shells that could be part of Linnaeus' type series are in CLL; photographs were made available by K. Way. Two of them are definitely *B. cancellata*; the smallest, third shell is strongly eroded and might be a *B. similis*. The CLL label (by Dance 1963) mentions: "Hanley has isolated three unmarked specimens not said to be from a marked box". Therefore, and since material has been added to the Linnean collection by Linnaeus' son and by J. E. Smith (Dance

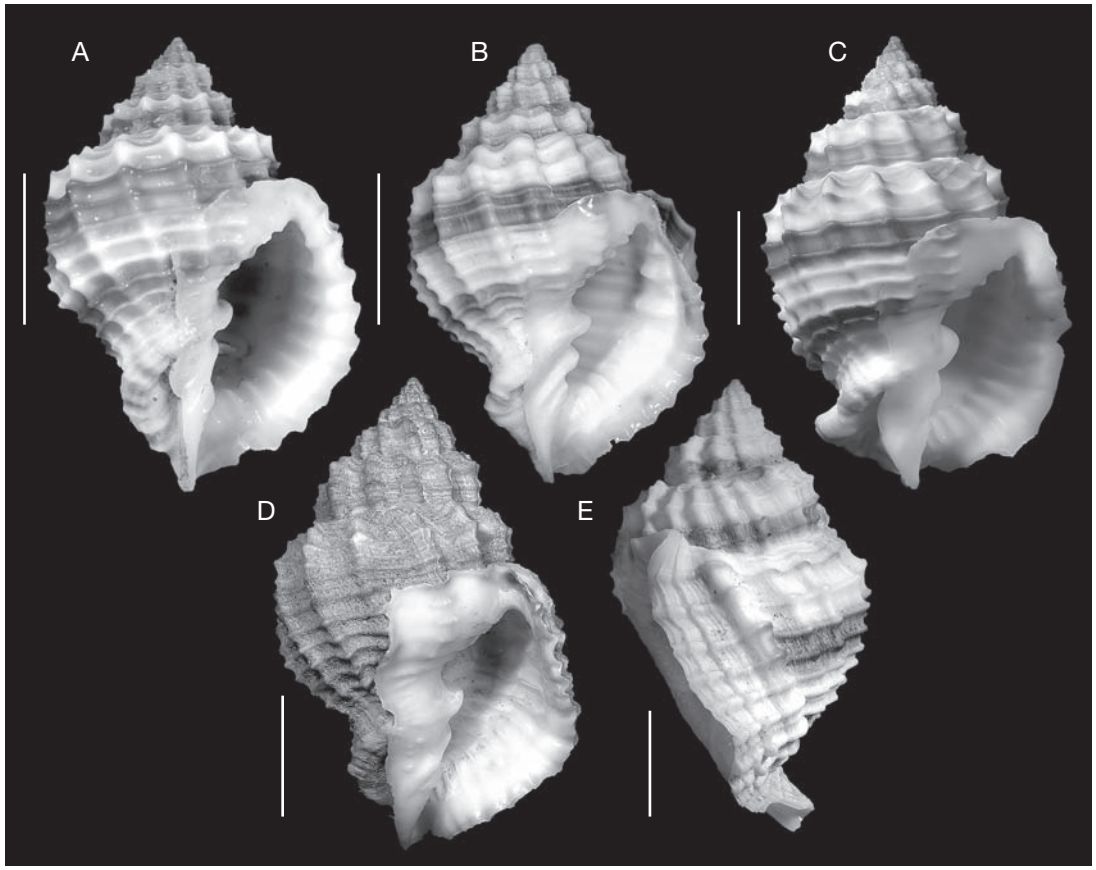

FIG. 11. — *Bivetiella cancellata* (Linnaeus, 1767): **A**, Spain, Malaga, Playa de la Misericordia (AV 0763); **B**, Angola, Luanda province, Pointe de Mussulo, shell deposits on beach (MNHN); **C**, Italy, Sicily, Trapani (AV 0778); **D**, shell with periostracum, Eastern Spain, off San Carlos de la Rapita (AV 1152); **E**, shell in side view, showing posterior channel, "stromboid notch" and curled siphonal canal, same locality data as Figure 11B (MNHN). Scale bars: 10 mm.

1967: 3, 4), there is no evidence that one of these shells now in CLL was known to Linnaeus and recognised as *V. cancellata* when the nominal species was established. Hanley mentioned (1855: 223) "the presence of that shell […] in the Linnaean cabinet (as declared in the list), where, of the objects therein contained, it alone answers to the description". Dance (1967: 10) discussed the value of "the list" and did not accept it as a basis for decision regarding type status. Moreover, Hanley mentioned "that shell" and "it alone", but there are now three shells in CLL. It cannot be established now if one of them, and if so, which one, was in the collection at the time of the description; therefore this lot cannot be used for lectotype designation. No specimen of this species is found in the Maria Ulricae collection at Uppsala (Dodge 1955: 101).

Consequently, the type must be looked for in the references given by Linnaeus, which were already discussed by Brocchi (1814: 307, 308), Hanley (1855: 223) and Pallary (1900: 259): 1) Adanson 1757: pl. 8, fig. 16 is almost certainly a *B. similis* (see Pallary 1900: 259; Fischer-Piette 1942: 219); 2) Seba 1758: pl. 49, figs 45, 46, 48 are not cancellariids; fig. 54 is almost certainly a dorsal view of a *B. cancellata* (although cited as a reference for the fossil *Cancellaria hirta* by Brocchi, 1814), but that figure is not mentioned by Linnaeus; and 3) Gualtieri 1742: pl. 48, figs B-E (this is the only reference given by Linnaeus already for *Murex scabriculus*): D and E are not cancellariids; B is difficult to identify since not even the columellar folds are shown, but C might represent a *B. cancellata*. So, if the current meaning of this commonly used name is to be maintained, only the specimen

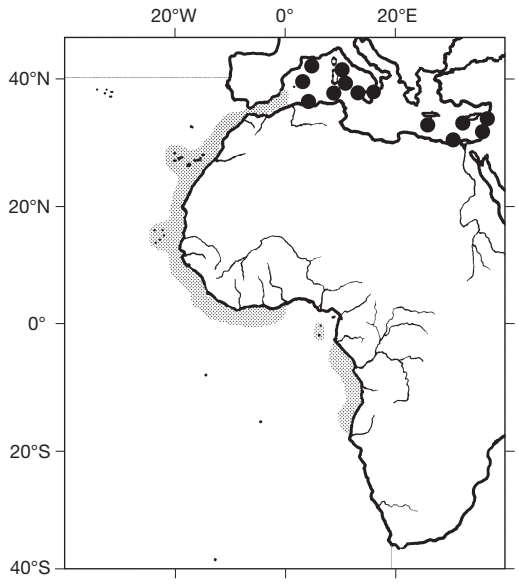

FIG. 12. — Distribution area of *Bivetiella cancellata* (Linnaeus, 1767).

figured on Gualtieri's figure C is a candidate for lectotype designation. However, the figure is rather crude and is not sufficiently detailed for lectotype designation, in view of the rather subtle distinction between *B. cancellata* and *B. similis*. Gualtieri's material is kept in the Certosa di Calci at Pisa, but there is no cancellariid among the marked specimens of that author (Curini-Galletti *in litt.*). This means that no specimen for lectotype designation based on one of these figures is available.

In spite of this complex nomenclatural situation, there is a general consensus about the identity of this species. Good figures are given in Born (1780: pl. 9, figs 7, 8), Lamarck (1798: pl. 374, fig. 5a, b); in the classical 19th century monographs: Kiener (1841: fig. 2), Sowerby (1849b: fig. 51), Reeve (1856: pl. 3, fig. 13a, b), Tryon (1885: fig. 34), Löbbecke (1886: pl. 11, figs 1-9); and in rather recent publications, e.g., Abbot & Dance (1982: 226).

Since there is no doubt about the general usage of the name *Voluta cancellata*, and the species is not involved in a zoological problem (the relation with *B. similis* is cleared by a lectotype designation for the latter in the present paper), a neotype cannot be validly designated (ICZN 1999: art. 75.2).

TYPE LOCALITY. — "O. africano" (Linnaeus, 1767), the "African ocean".

MATERIAL EXAMINED. — Out of the abundant material in nearly every collection seen, a geographically representative selection is given here.

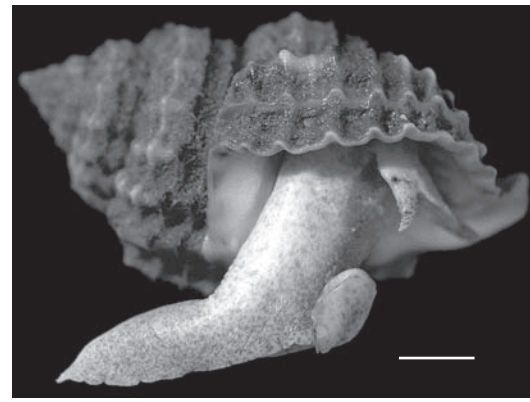

FIG. 13. — *Bivetiella cancellata* (Linnaeus, 1767), shell with fresh-dead animal, Spain, off San Carlos de la Rapita (AV 1152). Scale bar: 7 mm.

Spain. Malaga, Playa de la Misericordia, 6 specs (AV 0763). — Torrox, beach, 42 specs (AV 0774). — Almeria, 1 spec. (AV 0775). — Torrevieja, 7 specs (AV 0768, AV 0769). — Benidorm, 30 m, 1 spec. (AV 0775). — San Carlos de la Rapita, 35 specs (AV 0769).
Baleares Islands. Ibiza, 1 spec. (AV 0608). — Minorca, 1 spec. (AV 0759). — Formentera, 1 spec. (AV 0761).
France. Gulf of Marseille, 3 specs (KBIN). — Marseille, 6 specs (MNHN). — Cannes, 1 spec. (KBIN IG1738).
Italy. Naples, 2 specs (SMF), 1 spec. (MSNG).
Sicily. Trapani, 1 spec. (KBIN, Buyle colln), 1 spec. (AV 0778). — Palermo, 1 spec. (MNHN). — Messina, 1 spec. (MNHN).
Greece. Crete, 3 specs (AMNH 157631).
Tunisia. Bizerte, 3 specs (MHNG), 2 specs (ZMUC).
Algeria. Alger, 1 spec. (RMNH); 10 specs (KBIN). — Oran, many specs (MNHN); 8 specs (KBIN, Dautzenberg colln); 12 specs (SMF, Kobelt).
Morocco. Melilla, 3 specs (RMNH); 1 spec. (AMNH); 1 spec. (AV 0766). — Ceuta, Anse Almadrabo, 20-36 m, mud, 6 specs (MNHN).
Mauritania. *Calypso*, many stns, 16-99 m, 40+ juvenile specs (MNHN). — Banc d'Arguin, many CANCAP-II, III stns, mostly in muddy sand, 15-280 m, many specs often together with *B. similis* (RMNH).
Senegal. Dakar region, Cap Manuel, 18 m, 6 specs (MNHN, Marche-Marchad). — Off Gorée, 50 m, 10 specs (MNHN). — St. Louis, 2 specs (MNHN).
Cape Verde Islands. CANCAP VII stn 7072, 3 specs (RMNH). — Stn 7073, 1 spec. (RMNH). — Stn 7076, 2 specs (RMNH). — Sao Vincente, 1 spec. (AV 0758).
Guinea. NO *André Nizéry*, SEDIGUI II stn B9CH, B11CH, B14CH, 518CH, 1 spec. (MNHN, von Cosel). — SIDEGUI I, stn 1443CH, 1 spec. (MNHN, von Cosel). — Off Conakry, Tamara island, *Calypso* stn 8, 1 spec. (MNHN).

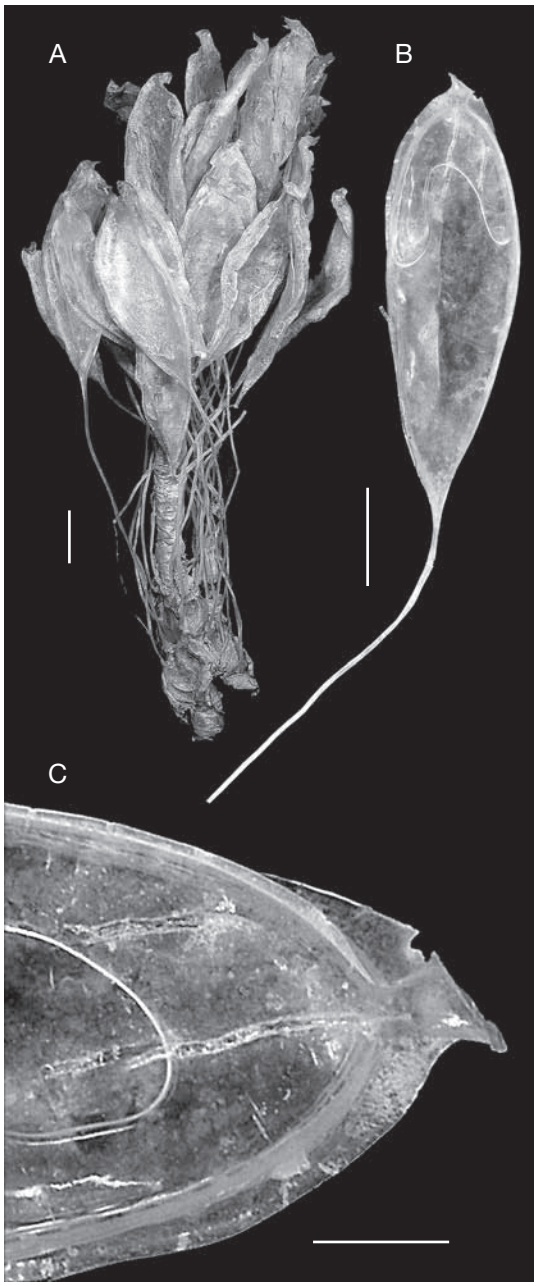

FIG. 14. — Empty egg capsules attributed to *Bivetiella cancellata* (Linnaeus, 1767), Spain, Malaga province, Rincon de la Victoria, in fishermen's net, leg. S. Gofas (MNHN): **A**, dried bundle of capsules; **B**, wetted single capsule (the curved line inside is a liquid meniscus); **C**, detail of B, showing escape opening. Scale bars: 5 mm.

Liberia. Off Garraway, *Calypso* stn 15, 4°34'30"N, 8°31'W, 1 spec. (MNHN).
Ivory Coast. Abidjan, 3 specs (MNHN, Marche-Marchad). — Grand Bassam, NO *Anthea Bencachi* I, stn 3, 5°8.9'N, 3°48.6'W, 35 m, 1 spec. (MNHN).
Ghana. Off Tema Bay, 37 m, juvenile (ZMUC). — Off Volta river mouth, GALATHEA stn 44, 40 m, 2 specs (ZMUC). — ATLANTIDE stn 85, 5°37'N, 0°38'E, 50 m, grey mud, 7 specs (ZMUC). — Mia Mia (near Takoradi), 10 m, sand, 2 specs (AMNH).
Benin. Ouidah, 6°10'N, 2°05'E, 100 m, 1 spec. (MNHN, Marche-Marchad).
Sao Tomé Island. Guadelupe, Praia das Conchas, beach, 2 specs (MNHN, Gofas). — *Calypso* stn 123, 5 m, 1 spec. (MNHN).
Principe Island. *Calypso* stn P7, 4 m, 1 spec. (MNHN).
Gabon. Port Gentil, Cap Lopez, 0°39'S, 8°43.5'E, 60 specs (MNHN, Bernard).
Congo. Congo river mouth, Banana, 7 specs (AMNH 80060); 1 spec. (ZMHU, *Valdivia*); 3 specs (MNHN). — Moanda, 3 specs (KMMA). — Île des Pêcheurs, Mission Gruvel stn 359, 3 specs (MNHN). — Pointe Noire, 1 spec. (MNHN, von Cosel); 1 spec. (KBIN); 1 spec. (AV 0745).
Angola. Ambriz, 80 m, 1 spec. (AV 0607). — Luanda, 1 spec. (AMNH), 3 specs (KMMA), 3 specs (AV 0762, AV 0770). — Palmeirinhos, 20-30 m, 1 spec. (MNHN, Gofas). — Lobito, 3 specs (KMMA). — Novo Rodendo, 1 spec. (AMNH). — Porto Alexandre, Mossamedes, 5 juv. specs (MNHN, *ex pisce* Lophiidae, S. Gofas leg.). — Baia do Baba, 2 specs (MNHN, Gofas).

DISTRIBUTION (Fig. 12). — Widely distributed and locally common along the West-African coast (including the Cape Verde [RMNH], Canary, São Tomé and Principe islands [MNHN]; but not Madeira [Swinnen pers. comm.]); from Morocco south to Angola (MNHN, Gofas); rather common in the Alboran Sea.

Mediterranean: off eastern Spain, French coast (Locard 1886: 157), Baleares, Corsica (Locard 1897: 302), Sardinia (Doneddu & Manunza 1989); becoming rarer eastward (because of the positive salinity gradient of about 3 psu?), Sicily (1 spec. [AV 0778]; Grasso 1985: rare), Crete, Cyprus (Tornaritis 1987: 104), Egypt (Pallary 1912: 86), Israel (Van Aartsen *et al.* 1984: 39; Barash & Danin 1992: 147) and Syria (Gruvel & Moazzo 1929: 420).

Bathymetry: from intertidal to 280 m.

Unconfirmed references: Fosse du Cap Breton, Bay of Biscay (Jeffreys 1885: 50; Locard 1886: 157; 1897: 302, referring to De Folin but apparently based on unpublished communications) but this might possibly be based on misidentifications of shells of *Brocchinia nodosa* (Verrill, 1885) thought to be eroded juveniles of *B. cancellata*; Adriatic Sea (Olivi 1792: 141; repeated by several authors, but the species is not mentioned by Cossignani [1992]); Red Sea (see Verhecken 1986b: 150).

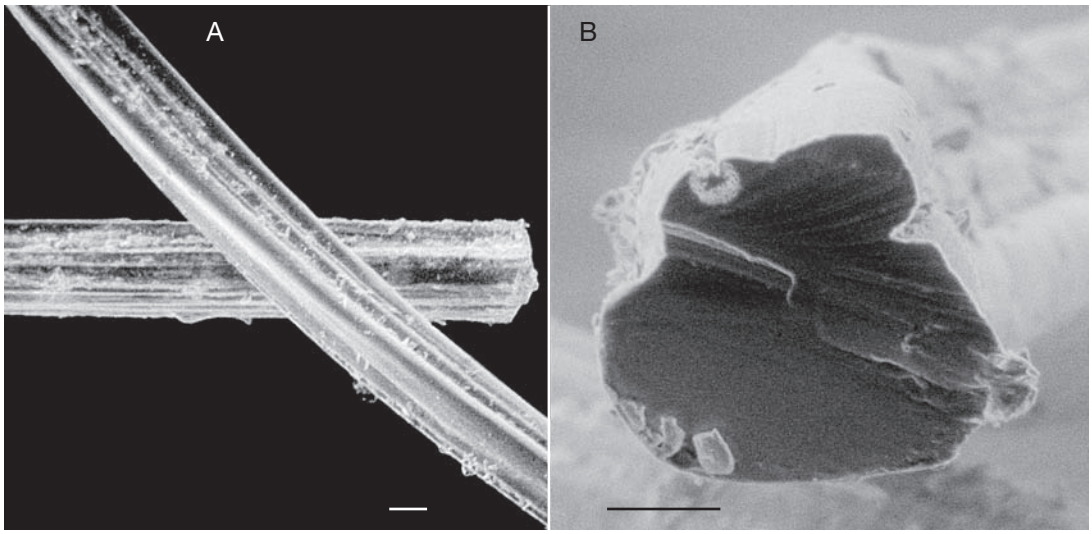

FIG. 15. — *Bivetiella cancellata* (Linnaeus, 1767), stalk of egg capsule of Figure 14: **A**, longitudinal view; **B**, cross section. Scale bars: 100 µm.

DESCRIPTION

Shell with rounded but slightly shouldered whorls, with a coarse cancellated sculpture, spire prominent; dimensions up to 46.4 × 30.0 mm. Shell white with brown bands: one near the periphery of the whorls; on the last whorl: another on the anterior part, and sometimes a third near the suture.

Protoconch (Figs 16-18) brown, transparent, multispiral with 3-3 1/4 rounded naticoid whorls. Measurements: maximum diameter: $\bar{x}$ = 1.58 mm (σ = 0.08, n = 10), exposed height: $\bar{x}$ = 1.12 mm (σ = 0.11, n = 10). Nucleus small, max. diameter: $\bar{x}$ = 0.26 mm (σ = 0.02, n = 10), transparent pale brown. Sculpture: on the nucleus (3/4 whorl): microscopic nodules (Figs 16; 17B); then about two whorls with two sets of non-collabral ribs crossing each other, forming a neat cancellated sculpture oblique to the shell axis; followed by about 1/2 whorl with little sculpture: a few zigzag lines from the cancellated sculpture may continue into this area (Fig. 18); and sometimes 4-6 rather strong spiral bands may gradually increase in strength, as predecessors of the teleoconch spiral sculpture. Transition to teleoconch sculpture is very clear (Figs 17A; 23A).

Teleoconch with up to seven whorls, with a prominent cancellated sculpture of broad rounded axial ribs and narrow, well defined spiral cords crossing over the axial ribs. This cancellated sculpture is already clearly present on the first half whorl of teleoconch (Figs 23A; 24A; difference with *B. similis*). The horizontal rectangular areas delimited by these cancellations only have a fine microsculpture of growth-lines, crossing over the spiral cords (Fig. 21A). An intritacalx of short thin white lamellae, consisting of a soft material wearing off very easily, is formed along these growth-lines.

Axial ribs: 9-13, 10-13, 10-11, 10-12, 11-12 and 12-13 on whorls 1-6 respectively. Spiral cords: 4, 4-5, 4-6, 4-6 and 5 on 1st to 5th whorl respectively. Width of spirals gradually increasing from 0.2 to 0.5 mm. A secondary spiral may occur on anterior part of the last whorl. Thickened varices may be present on the younger whorls.

Sutures well impressed, whorls rounded, sometimes slightly shouldered. Aperture white, oval, pointed towards both ends. Outer lip crenulated, with a "stromboid notch" on the basal lip between the two brown bands (Fig. 11E); 8-12 strong lirae, 13 in very large shells; and a narrow posterior canal.

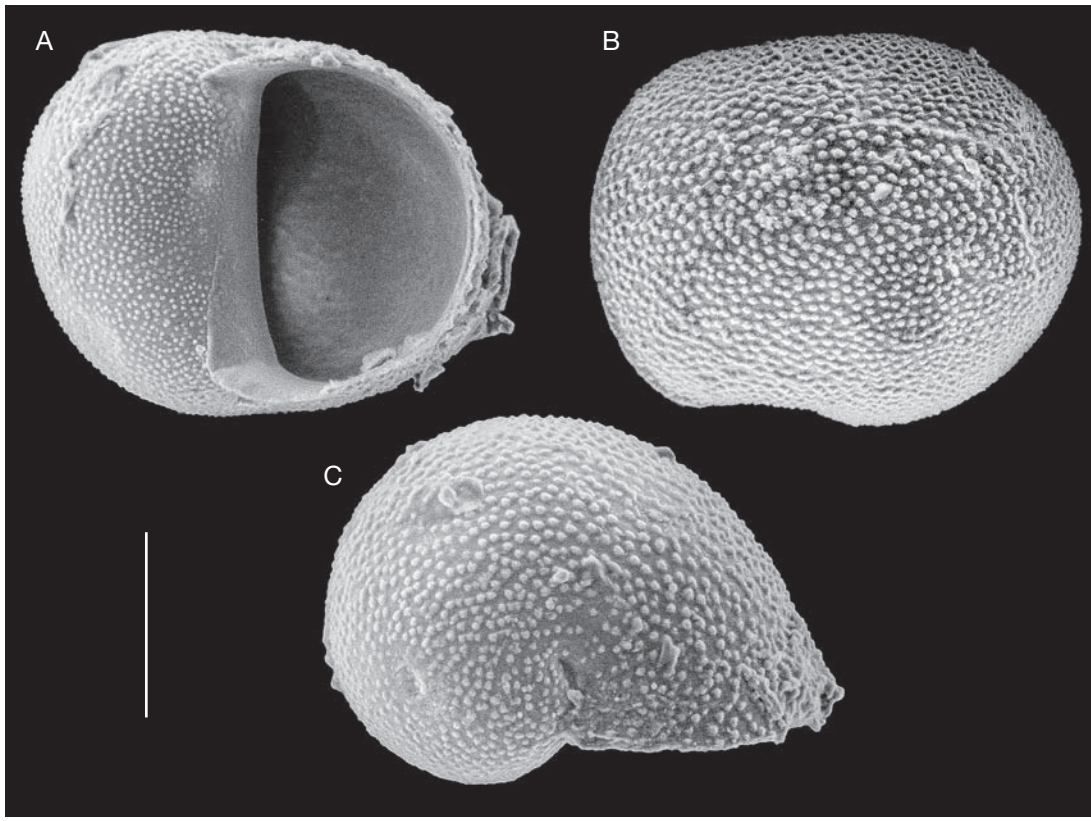

FIG. 16. — *Bivetiella cancellata* (Linnaeus, 1767), embryonic shell taken from egg capsule of Figure 14B: **A**-**C**, front, back and top views. Scale bar: 100 µm.

White translucent callus covering columellar side, and partly reflected over the umbilical slit. Columella with three folds: anterior one small, central fold with square-cut profile, and posterior one strongest and rather sharp. Siphonal fasciole well developed, often incorporating the earlier siphonal canal pointing away from the aperture. Siphonal canal present, often relatively long, and slightly reflected abaxially. Umbilicus: a narrow slit, half covered by reflected callus.

Fresh shells have a thin pale-brown periostracum (Fig. 11D), anchored between the thin intritacalx lamellae.

The anatomy and radula have been described by Graham (1966: 140). The animal is pale fawn dotted with brownish red (Fig. 13).

REMARKS

This is the most common of eastern Atlantic Cancellariidae. Its habitat seems to vary from the "biocenosis coralinas de plataforme" (Vera-Peláez *et al.* 1995: 140) to muddy bottoms (Spada pers. comm.). Dutch expeditions (CANCAP, MAU) collected many specimens, mostly on combinations of sand and mud, between 12 and 280 m (RMNH). Grasso found a living specimen at 90 m off Cape Passero, Sicily.

Observations of living animals (taken by fishermen of San Carlos de la Rapita, Eastern Spain) in an aquarium, indicate that this species burrows in sand, and when retracting into the shell, a mass of sandy soil adheres to the sole, thus closing off the aperture. Sand also remains attached to the

periostracum (see also Weinkauff 1867: 172). The animals only survived for a few days.

The shell of this species is fairly constant over its wide distribution area: see Figure 11A, B, representing shells from Eastern Spain and Angola. Its variability, including extreme forms, was illustrated by Löbbecke (1886: pl. 11) and Kobelt (1904: pl. 78, figs 1-5, pl. 79, figs 1-6).

Egg capsules attributed to this species (leg. S. Gofas, from fishing nets, Rincón de la Victoria, Málaga, Spain, IX.1994, MNHN) are very much like the egg capsule of *Cancellaria cooperi* described and figured by Pawlik *et al.* (1988: 48). They consist of a flattened elliptical capsule (about 20 × 6 mm), pointed at both ends, with roughly rectangular cross-section, a thickened rim of about 2 mm and pre-formed hatching aperture (Fig. 14); on a long flexible stalk of about 26 mm length, 0.3 mm diameter and with an irregular cross-section (Fig. 15). An empty capsule (Fig. 14B) still contained a few empty embryonic shells (Fig. 16), in size, form and sculpture very similar to those of *C. cooperi* figured by Pawlik *et al.* (1988: 50, fig. 19), and with a sculpture like that of the nuclear whorl of *B. cancellata* and *B. similis.* The size of the nuclear shells suggests a large number of eggs in the capsule, and a pelagic larval development. Comparison with data on protoconch and distribution of all W African cancellariids (Table 1) suggests that these capsules were produced by *B. cancellata* or *B. similis*. The presence of an operculum in *C. cooperi* larvae 30 days after hatching (Pawlik *et al.* 1988: 50, fig. 21) is interesting since all known postlarval Cancellariidae are inoperculate; but no larvae were found in the few remaining embryonal whorls in these *Bivetiella* capsules.

Two columellar folds are already present in juveniles with only 3/4 teleoconch whorl, but are absent in the nuclear shells in the capsule.

The sculpture of the postnuclear protoconch (Fig. 18) superficially resembles the non-orthogonal cancellate pattern on a daphnelline turrid protoconch figured by Hickman (2004: fig. 1c). The "ragged" ending of the zigzag lines in Figure 18 suggests that this pattern on the *Bivetiella cancellata* protoconch is formed by synchronised deposition of precisely spaced zigzag lines, like the single lines on an atlantid species figured by Hickman (2004: fig. 3a), rather than by diagonal lines crossing over the whole protoconch whorl.

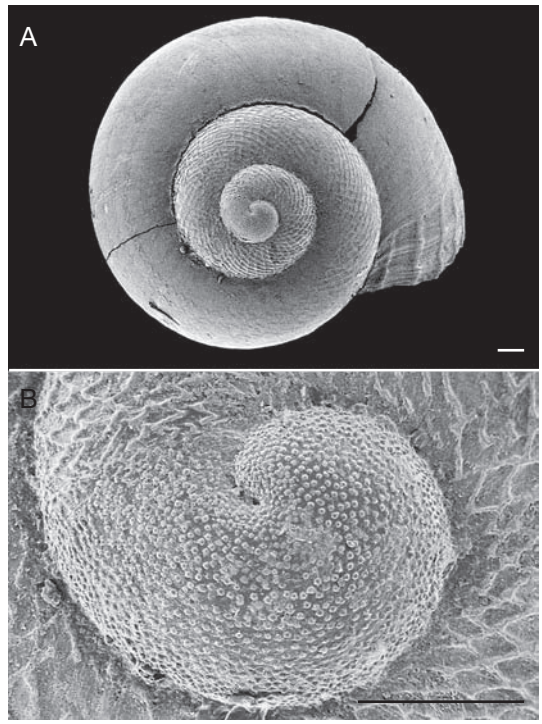

FIG. 17. — *Bivetiella cancellata* (Linnaeus, 1767), sculpture of top whorls, Mauritania, Banc d'Arguin (ZMA): **A**, protoconch plus start of teleoconch, showing the different sculptured sections; **B**, detail of embryonal whorl sculpture. Scale bars: 100 µm.

Nomenclature

The species name change by Linnaeus (*scabriculus* to *cancellata*) was discussed by Petit (1976: 34): "In the 12th edition of the *Systema Naturae* [Linnaeus] changed the placement of the species from *Murex* to *Voluta*. As he was also moving his *Buccinum scabriculum* from the 10th edition to *Voluta* in the 12th edition, he changed the name of *Murex scabriculus* to *Voluta cancellata* to avoid homonymy [...] Fortunately, the specific name in *B. cancellata* can be retained under the new [= 1973] ICZN rule (Article 59 i) [ICZN 1999: art. 59.3, remark of present author], which states that a junior secondary homonym rejected before

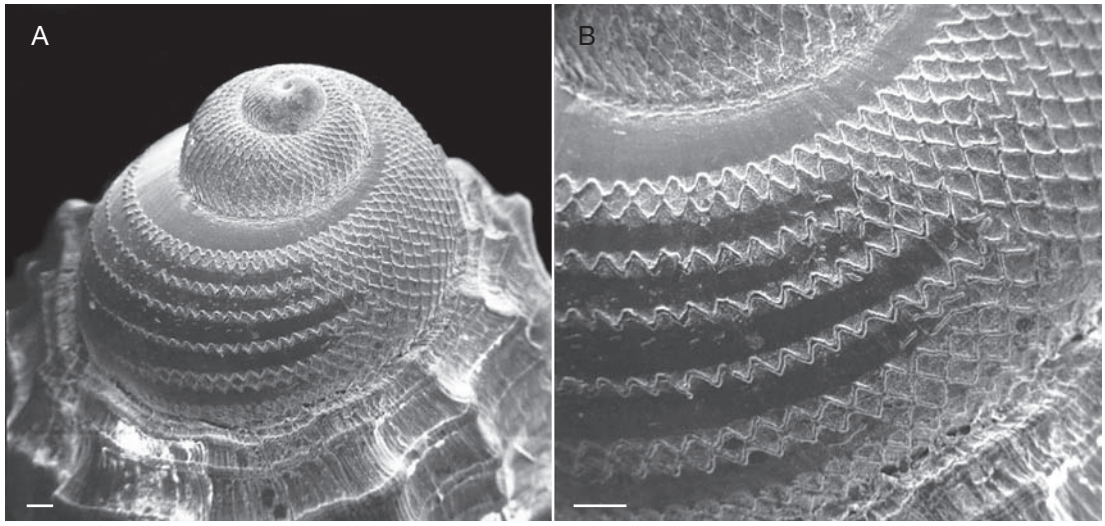

FIG. 18. — *Bivetiella cancellata* (Linnaeus, 1767), cancellated post-nuclear protoconch sculpture, disappearing towards teleoconch rim, Congo Estuary (MNHN): **A** protoconch view; **B**, detail of last protoconch whorl of A. Photos: SEM Laboratory, University of Basel; M. Düggelin, operator. Scale bars: 100 µm.

1961 is permanently rejected". Thus, Petit suggested that Linnaeus rejected *Voluta scabricula* (ex-*Murex*), a binomen he never used, as a junior secondary homonym of his newly placed *Voluta scabricula* (ex-*Buccinum*). This interpretation may be correct but has no nomenclatural value since the alleged homonymy never existed.

When introducing *Voluta cancellata*, Linnaeus (1767: 1191) gave the correct reference to his *Murex scabriculus*, but cited it as *Murex scabriusculus*: this has been interpreted as an error (Dodge 1955: 99). However, similarly *Buccinum scabriculum* Linnaeus, 1758 (p. 740, no. 412) was written *Buccinum scabriusculum* in the 1767 edition (p. 1192, no. 417). Since two names in the same work were treated in a similar way, the specific name in the combination *Murex scabriusculus* Linnaeus, 1767 is an unjustified emendation and an available name (ICZN 1999: arts 33.2.1, 33.2.3); it is a junior objective synonym of *M. scabriculus* Linnaeus, 1758. Consequently, two synonyms were created on the same date by Linnaeus (1767): *Voluta cancellata* and *Murex scabriusculus.* The only use of the specific name *scabriuscula* was by Pallary (1900: 259), but this is here not interpreted as First Reviser action since he no longer used that name in his later publications (1912: 86; 1920: 12; 1938: 18), and his choice was against stability and universality of nomenclature. Kobelt (1904: 210) deliberately chose not to reintroduce the use of *scabriusculus*; he is here considered First Reviser. Consequently, *Murex scabriusculus* is also a junior objective synonym of *Voluta cancellata.*

Apart from that, Linnaeus introduced on different dates two names for the same taxon: *Murex scabriculus* in 1758 and *Voluta cancellata* in 1767. By applying article 23.9 (reversal of precedence) of the Principle of Priority (ICZN 1999), *B. cancellata* should be recognized as the valid name. The last use of *B. scabriculus* was by Adams H. & Adams A. (1854: 276). Thus, the long-accepted junior specific name in the combination *Bivetiella cancellata* (Linnaeus, 1767) is here declared *nomen protectum* and the senior name *Murex scabriculus* Linnaeus, 1758 is invalid as *nomen oblitum*.

Here follow 26 references given in the bibliography of the present study, demonstrating the use by 17 authors since 1956 of the species name *cancellata* (combined with *Cancellaria*, *Bivetiella* or *Bivetopsis*), thus allowing application of art. 23.9.1.2 of the

Code (ICZN 1999): Marche-Marchad 1958: 31; Malatesta 1960: 185; Graham 1966: 140; Nordsieck 1968: 151; Settepassi 1972: *Cancellaria*, I-II and the eight post-1956 references given there; Malatesta 1974: 368; Petit 1976: 34; D'Angelo & Gargiullo 1978: 148; Nordsieck & Garcia-Talavera 1979: 152; Abbott & Dance 1982: 226; Petit 1984: 58; Bernard 1984: 90; Van Aartsen *et al.* 1984: 39; Grasso 1985: 12; Tornaritis 1987: 104; Doneddu & Manzuna 1989: 263; Barash & Danin 1992: 147; Vera-Peláez *et al.* 1995; and there are many more not listed in the present bibliography.

Concerning *Buccinum pyrozonias* Gmelin, 1791, based on Martini's figure (1777: pl. CIX, fig. 1017), the reader is referred to Petit (1984: 58), who concluded that it is preferable to accept this name as a junior synonym of *B. cancellata* rather than as a senior synonym of *B. similis*.

The figure of *Buccinella rotundata* Perry, 1811 looks more like an eroded shell of *B. similis* than of *B. cancellata*, but distinctive features are only schematically drawn. Since the distinction is not clear, it is better to accept the identity of *Buccinella rotundata* with *Bivetiella cancellata*, as suggested by Petit (2003: 48) rather than upsetting the nomenclature by accepting it as the valid name for *B. similis*.

Cantharus triplicatus Röding, 1798 was described with reference to *Buccinum pyrozonias* and to its Martini figure (1777: fig. 1017), but Röding also mentioned four shells in the Bolten collection. One of these might be the original for the figure given by Martini, who used numerous Bolten specimens (Dance 1986: 65). However, none of these four shells is now in Gotha museum (M. Joost *in litt.*), where the material acquired by F. C. Schmidt at the Bolten sale is deposited (Joost 1990: 39). So, we will probably never know if Röding had in hand shells of *B. cancellata* or *B. similis* when describing *Cantharus triplicatus*. Therefore, Petit's (1984: 58) conclusion is accepted that *C. triplicatus* is a junior synonym of *B. cancellata*.

Several closely related fossil taxa sometimes referred to as *Bivetiella cancellata*, such as *B. subcancellata* d'Orbigny, 1852 and *B. praecedens* Beyrich, 1856, are known from Miocene and Pliocene deposits in Europe and circum-Mediterranean countries.

Bivetiella similis (Sowerby, 1833)
(Figs 19; 21B; 23B; 24B; 25)

Cancellaria similis Sowerby, 1833: no. 41, fig. 38; 1849b: 450, pl. 94, fig. 42.

Cancellaria assimilis "Sow." – MacAndrew 1856: 154. — Weinkauff 1867: 171.

Cancellaria similaris "Sow." – Reeve 1856: species 10, pl. 3, fig. 10a, b.

Bivetia bivet Jousseaume, 1887: 193.

Bivetiella similis – Wenz 1943: 1356.

TYPE MATERIAL. — Lectotype, here designated, BMNH 1968422/1, 31.3 × 23.2 mm (Fig. 19B). Paralectotypes: 3 specs (BMNH 1968422/2-4).

Sowerby's description states (1833: no. 41) "columella with three plaits, of which the lowest is the smallest and double"; shell BMNH 1968422/2 (28.2 × 19.9 mm) indeed has the anterior double fold. This abnormality is not indicated on Sowerby's figure 38 (but it is shown on Reeve's figure 10b); it is absent in all other specimens studied. Therefore, another syntype is here designated lectotype, its dimensions approach those given by Sowerby (1.2 × 0.9 inch = 30.5 × 22.9 mm). This designation is judged necessary to clarify the correct application of the name *B. similis* which has often been poorly understood, as evidenced by many incorrect identifications (as *B. cancellata*) in museum collections (see also under Distribution, below).

TYPE LOCALITY. — Unknown to Sowerby (1833); restricted to "Senegal" by Sowerby (1849b).

MATERIAL EXAMINED. — The following list is merely a geographically representative selection from material seen in museum collections.

Spain. Marbella, 4 specs (AV 0754). — Malaga, Rincon de la Victoria, 1-5 m, 20-40 m, many specs (MNHN). — Torrox, beach, 3 specs (AV 1100). — Almeria (KBIN, Buyle colln). — Peñiscola, 1 spec. (AV 0750). — Torrevieja, 1 spec. (AV 0751). — San Carlos de la Rapita, 3 specs (AV 0773).
Baleares Islands. Minorca, 1 spec (SMF).
France. Marseille, 3 specs (MNHN).
Corsica. Ajaccio, 4 specs (KBIN).
Italy. Sicily, 2 specs (KBIN).
Algeria. Gulf of Oran, 6 specs (SMF), 1 spec. (NMW). — Oran, 3 specs (MNHN, Locard).
Morocco. 1 spec. (AMNH). — M'diq, several specs (MNHN). — Ceuta, 2 specs (AV 0764). — Off Agadir, 30°25'N, 9°53'W, 115 m, 1 spec. (MNHN).
Western Sahara. In sand, 30-50 m, 2 specs (AV 0748).
Mauritania. MAU 039, 18°48'N, 16°43'W, muddy

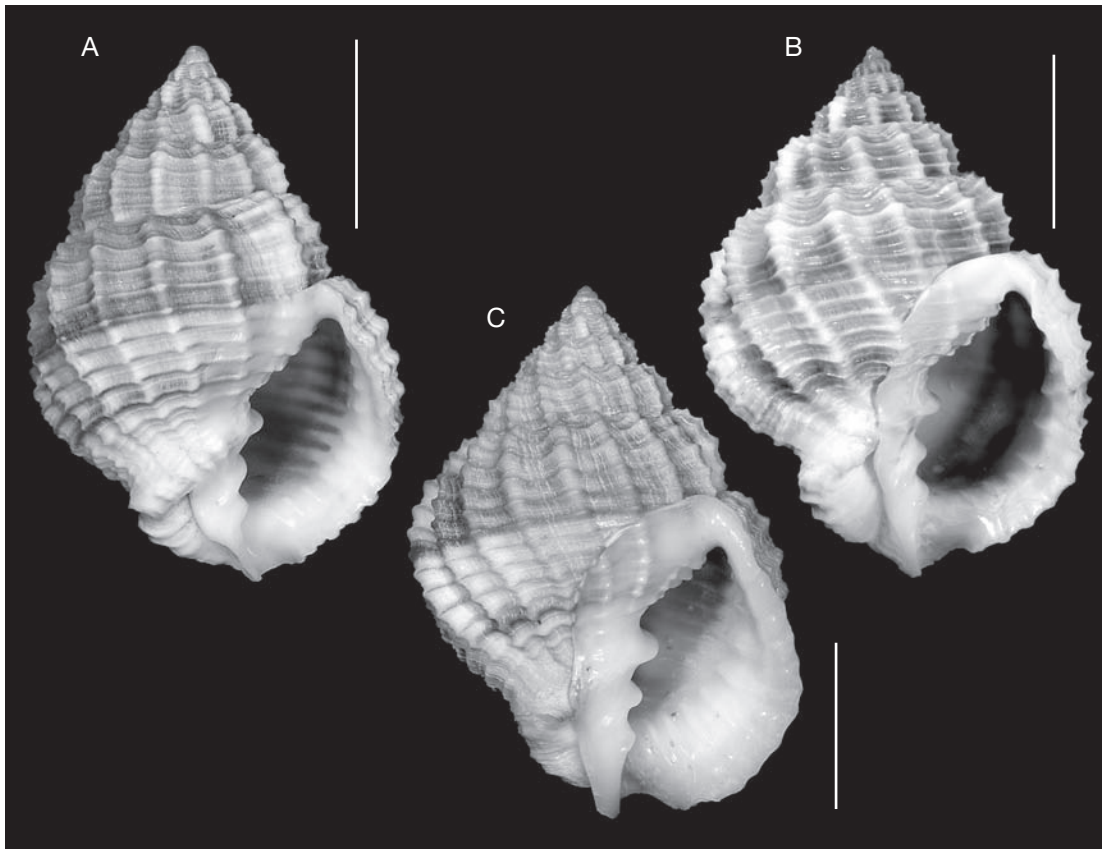

FIG. 19. — *Bivetiella similis* (Sowerby, 1833): **A**, Spain, Malaga, Torrox Beach (AV 1100); **B**, lectotype (BMNH 1968422); **C**, Angola, Luanda province, Mussulo Bay, Futungo, Ilha do Destierro (MNHN). Scale bars: 10 mm.

bottom 260-280 m, 2 specs; 65 lots MAU + CANCAP (RMNH) (often together with *B. cancellata*).
Canary Islands. Fuerteventura, 1 spec. (AV 0880).
Senegal. 3 specs (HUJ 12081); 4 specs (RMNH). — Near Carabane, mouth of Casamance, 15-20 m, 1 spec. (AV 0753). — N Casamance, von Cosel, several specs (MNHN).
Cape Verde Islands. CANCAP VI stn 6060, 6064, 6103, 1 spec. each (RMNH). — Maio Island, 1 spec. (KMMA). — Boa Vista, 1 spec. (AV 0875).
Guinea. SIDEGUI II, NO *André Nizéry*, stn B11CH, 1 spec. — Stn B12-13 DW, 9°42'N, 15°33'W, 3 specs (MNHN). — Stn B17CH, 9°14.5'N, 15°19.3'W, 2 specs (MNHN). — Stn B21CH, 9°06'N,14°35'W, 2 specs (MNHN).
Sierra Leone. ATLANTIDE stn 49, 7°29'N, 13°38'W, 74-78 m, muddy sand, 3 specs (ZMUC).
Liberia. 2 specs (KBIN).
Ivory Coast. Radiale Grand Bassam, NO *Antea Bencachi* I, stn 3, 5°08.9'N, 3°48.6'W, 1 spec. (MNHN).
Ghana. Off Volta river mouth, *Galathea* stn 44, 40 m, 1 spec. (ZMUC). — *Calypso* stn 25, 4°36'30"N, 1°31'W, 2 specs (MNHN).
Gabon. Cap Lopez, 0°39'S, 8°43.5'E, intertidal, P. Bernard, 7 specs (MNHN).
Off Congo estuary. Pointe Noire (ZMA). — Banana, 1 spec. (KMMA), 1 spec. (KBIN).
Angola. Off Ambriz, 125-155 m, 1 spec. (AV 0755). — Off Luanda, 2 specs (MNHN). — Mussulo, 3 m, sand, 1 spec. (AV 0747). — Moita Seca, 70 m, sand, 1 spec. (AV 0746). — Lobito, 1 spec. (KMMA).
Namibia. 1 spec. (AV 0749).
South Africa. Kleinzee (S of Port Nolloth), 1 spec., subfossil (SAM).

DISTRIBUTION (Fig. 20). — Because of frequent confusion with *B. cancellata*, literature data without figures are not reliable for establishing the distribution area. Specimens

in collections range from the southwestern Mediterranean (Alboran Sea; Oran; eastern Spain: off San Carlos de la Rapita) to Namibia (AV 0749) and South Africa (off Kleinzee, 120-150 m, subfossil [see below] in sediment taken in commercial offshore diamond prospection, SAM), including Canary (AV 0752) and Cape Verde Islands (AV 0758, KMMA), but not Madeira (Swinnen pers. comm.).

Bathymetry: from intertidal to 280 m.

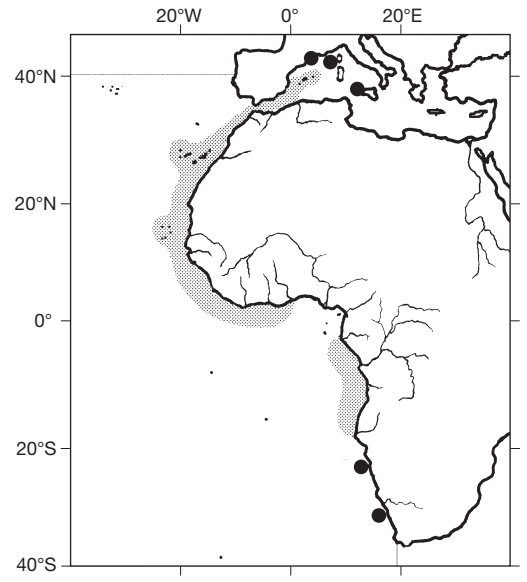

FIG. 20. — Distribution area of *Bivetiella similis* (Sowerby, 1833).

DESCRIPTION

Shell globose, up to 32 × 24 mm. Colour brown to almost white: spire coloured; last whorl with a broad coloured band covering the posterior half, and a narrow band near the siphonal fasciole but separated from it by a well marked depression.

Protoconch (Fig. 23B) naticoid, multispiral with 3-3 1/4 whorls, dimensions and sculpture as in *B. cancellata*. Transition to teleoconch clearly marked. On the first half of teleoconch whorl, there are 5-8 narrow, close-set spiral ridges; axials are only very slightly indicated (difference from *B. cancellata*). Teleoconch with up to 5 3/8 rounded whorls. Sculpture consists of rounded axial ribs crossed by narrow spiral cords. Number of axials: on the first teleoconch whorl this is very difficult to count because they are very vague; 9-12, 10-11, 10-14, 11-16 on second to fifth teleconch whorls respectively; number of spirals: 5-8, 5-7, 5-6, 5-6 and 4-6 on first to 5th whorl. Width of spiral: increasing with age from 0.1 to 0.3 mm. From the 4th whorl on, one spiral of second order can occur between the main spirals, and often third order spirals can be seen. Between these macro-spirals, a set of very fine close-set micro-spiral lines can be seen on uneroded shells. An additional axial sculpture of growth-lines is present between the main rounded axials: fine growth-lines, often coarser than in *B. cancellata*, and crossing over also the secondary and ternary spiral cords, thus giving them a slightly rugose look. Aperture grossly semicircular, white. Outer lip slightly crenulate, 9-11 lirae within. "Stromboid notch" only slightly indicated. Columellar callus and folds as in *B. cancellata*, but sometimes a minor fourth fold occurs at the rim of the siphonal canal. Siphonal canal shorter than in *B. cancellata*; siphonal fasciole well developed but normally without showing the former siphonal canal. Umbilical chink generally slightly wider than in *B. cancellata*.

A very thin fawn periostracum remains on well preserved shells.

REMARKS

Difference from *B. cancellata*: several authors have considered *B. similis* as a form variety (Nobre 1909: 11), or a geographic form (Bucquoy *et al.* 1882: 33) of *B. cancellata*, or living on a different substrate (Weinkauff 1867: 172), or as a different subspecies (Marche-Marchad 1958: 31) or species (Pallary 1900: 259).

The shell of *B. similis* is rather similar to that of *B. cancellata*; it is distinguished from the latter by its less-shouldered whorls, and its smoother and less coarse macrosculpture: axial ribs less pronounced, a finer and more elaborate spiral sculpture: between the main spiral cords, second order (as in the lectotype) and third order spirals can be seen on shells in pristine condition (Fig. 21B); these are lacking on *B. cancellata*. The spiral bands in *B. cancellata* are more pronounced than in *B. similis*. Both species cannot be distinguished on size and shape data only: their height/width correlation lines (with $r^2 = 0.98$, $p < 0.005$) overlap almost perfectly, but *B. cancellata* appears to grow larger than *B. similis* (Fig. 25).

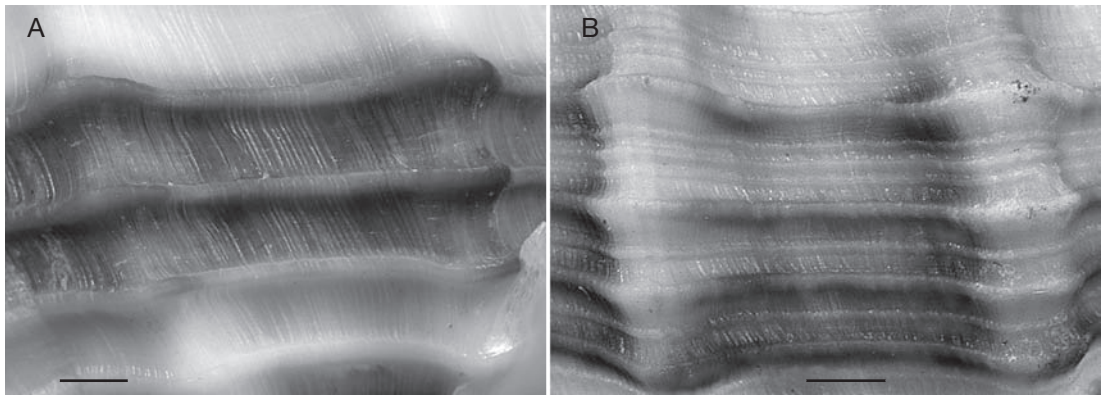

FIG. 21. — Details of teleoconch macrosculpture: **A**, *Bivetiella cancellata* (Linnaeus, 1767), eastern Spain, off Torrevieja (AV 0768); **B**, *B. similis* (Sowerby, 1833), Cape Verde, Boa Vista Island (AV 0875). Scale bars: 1 mm.

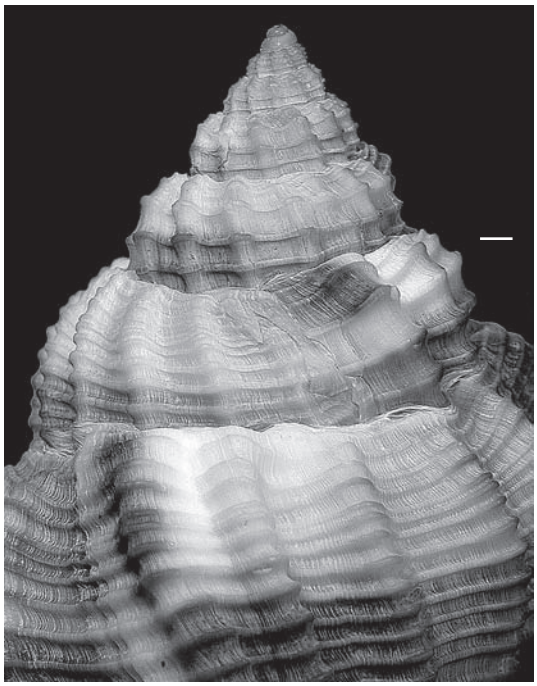

FIG. 22. — *Bivetiella cancellata* (Linnaeus, 1767), change in shell spiral macrosculpture from *cancellata*-type into *similis*-like sculpture after trauma, eastern Spain, off San Carlos de la Rapita (AV 1145). Scale bar: 1 mm.

However, a few shells have been found with sculptural characters of both "species" on different parts of the shell: on different parts of each whorl (Pallary 1900: 260, fig. 1), or abruptly changing (after a trauma?) over the whole whorl width from *B. cancellata* sculpture into a *B. similis*-like sculpture (Fig. 22) with more and slightly narrower spiral bands, but still without the microscopic spiral lines often seen in *B. similis*. The inverse change, from *similis*-type into *cancellata*-type sculpture, has not been encountered.

No difference was noticed between the protoconchs of both species, but the distinction can already be made on the first half teleoconch whorl, where *B. similis* has 5-7 close-set rugose spirals with no or only very faint axials; while *B. cancellata* has 4 or 5 distant spirals forming a coarse cancellated pattern with the clearly present axials (Figs 23; 24). This is a good differentiating character, applicable to very juvenile shells and to uneroded adult shells.

It has sometimes been suggested that *B. cancellata* and *B. similis* are conspecific (e.g., Jeffreys 1885: 50; Dautzenberg 1910b, 1912). *Bivetiella similis* seems to occur in almost the same area and often together with *B. cancellata*, but always in smaller numbers, e.g., off the Spanish south coast (P. Bouchet pers. comm.; G. Spada *in litt.*); there seems to be a tendency for *B. similis* to be more common in deeper water.

Spada (pers. comm.) found off Fuengirola, Southern Spain, on mainly muddy bottom: *B. cancellata* between 17-37 m (88 lv) and 7-37 m (25 d); *B. similis* deeper than 18 m (10 d) and 1 lv, 37 m (depth limit of sampling). Also off Mauritania, *B. similis* and *B. cancellata* were found (often together) mostly on

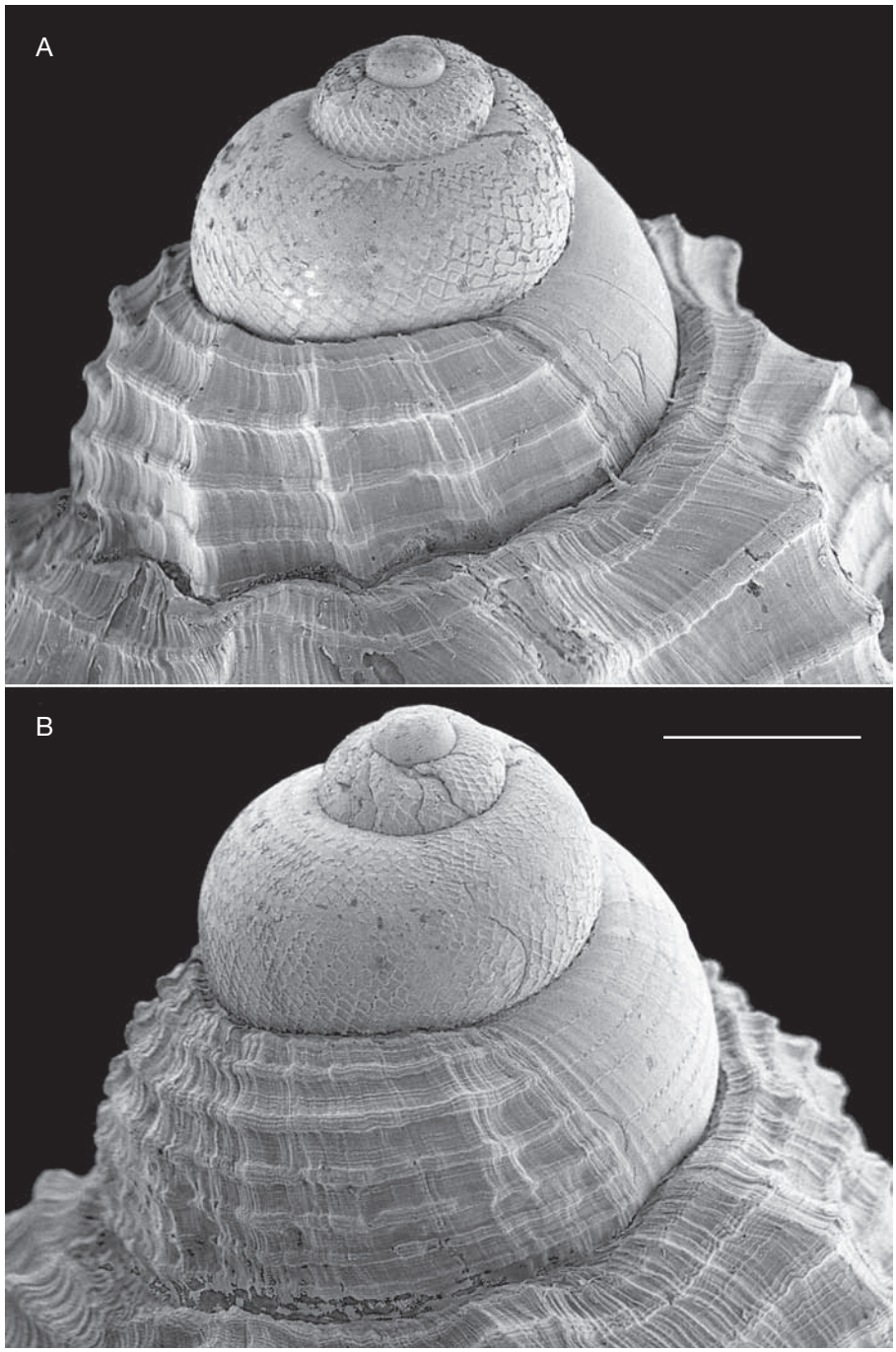

FIG. 23. — Sculpture on protoconch and first teleoconch whorl of eastern Atlantic *Bivetiella* species from Mauritania, MAU stn 2.020, 18°50'N, 16°24'W, 37 m (RMNH): **A**, *B. cancellata* (Linnaeus, 1767); **B**, *B. similis* (Sowerby, 1833). Photos: J. Goud (RMNH). Scale bar: 500 µm.

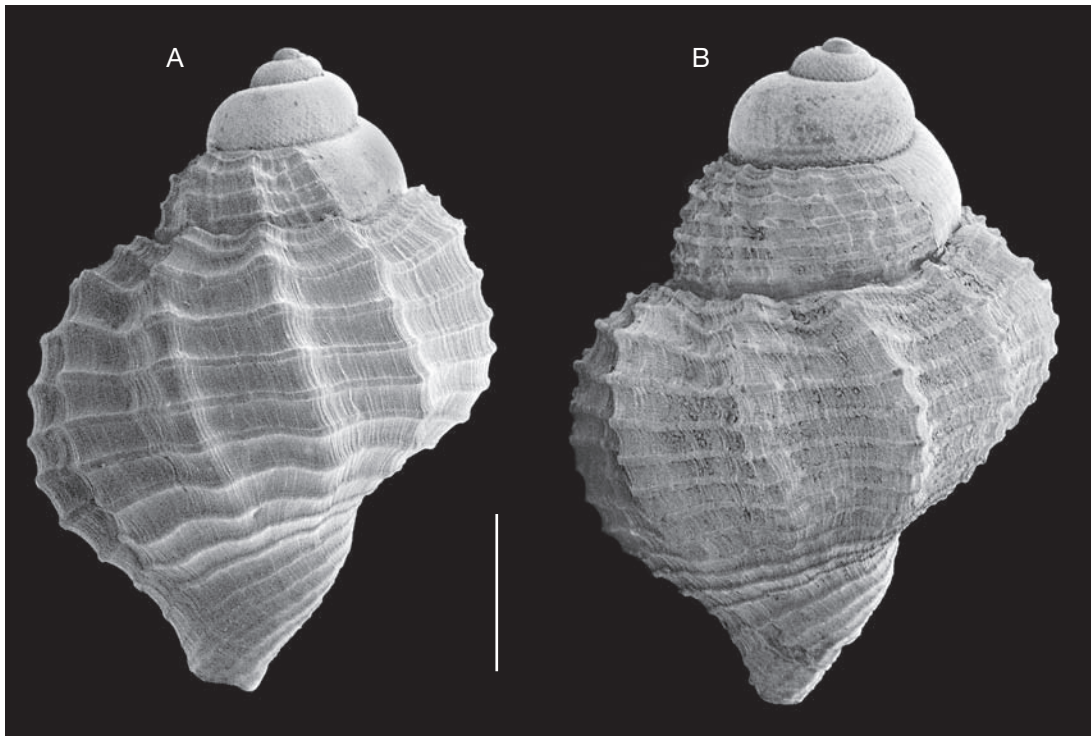

FIG. 24. — *Bivetiella* juvenile shells: **A**, *B. cancellata* (Linnaeus, 1767), Senegal, Dakar region, Thiaroye, M'Bour coast, 9-10 m (MNHN, Marche-Marchad); **B**, *B. similis* (Sowerby, 1833), Mauritania, NW of N'Diago, stn 215, 17°36'N, 16°17'W, 54 m, Richer de Forges 1981 (MNHN). Scale bar: 1 mm.

muddy and/or sandy bottoms (RMNH).

Distribution areas of *B. cancellata* and *B. similis* do not completely overlap, e.g., fishermen from San Carlos de la Rapita, Spain, bring in *B. cancellata* in fair numbers, but very few *B. similis*; but this might be a seasonal effect. Records of *B. similis* from the eastern Mediterranean are completely lacking.

Sexual dimorphism within the same species (*B. cancellata*) is conceivable. This can be checked when a number of alcohol specimens of both "forms" are available for study, although the mere presence or absence of a penis might not constitute an absolute sex character: the cancellariid *Iphinopsis alba* can have penis and pallial oviduct at the same time (Bouchet & Warén 1985: 261).

Conclusion

Although there is still no solid evidence showing that *B. similis* differs from *B. cancellata* at species level, both forms are here treated as separate species, since the shells can be distinguished rather easily.

The behaviour of the living animals was described by Weinkauff (1867: 172). Since he regarded *B. similis* as only a variety of *B. cancellata*, it is not clear if all his observations pertain to both species. His statement that *B. cancellata* lives on fine sand, and the "variety" *B. similis* on mud, cannot be accepted, since both species have repeatedly been found together on the same spot. Does this sympatric occurrence mean that they have a different feeding niche?

White shells of *B. similis* are not very rare, and seem to be more frequent than white *B. cancellata* shells.

The shells from off Namibia are very likely to be subfossil: they were recovered by dredging intended to penetrate the surficial sediment, and none look fresh or have attached organic material. They are

probably younger than the Last Glacial (J. Pether, SAM, pers. comm.).

The figures given for this species in the classical 19th century monographs are correct; Löbbecke (1886: pls 11, 12, figs 1-6) and Kobelt (1904: pls 78, 79) gave excellent illustrations of the variability in shell form of both *B. cancellata* and *B. similis.*

Cancellaria similaris, as used by Reeve with reference to Sowerby's original description and figure, is an incorrect subsequent spelling and an unavailable name (ICZN 1999: art. 33.3).

The name *Buccinum pyrozonias*, which might also be applicable to this species, has been mentioned under *B. cancellata*. The specific name in *C. assimilis* used by MacAndrew (1856) and by Weinkauff (1867) is an unavailable subsequent spelling.

References to fossil forms of *B. similis* are very scarce: Malatesta (1960: 186) mentions that, according to some authors, the species could be a surviving form of "Mediterranean Pliocene types"; but he thinks that it rather agrees with Miocene forms like *Cancellaria neuvillei* Peyrot, 1928. This view is not mentioned by Cahuzac *et al.* (2004). *Bivetiella similis* is mentioned from the Plaisancian of Altavilla, Italy, by Glibert (1960: 66), but this identification may need confirmation.

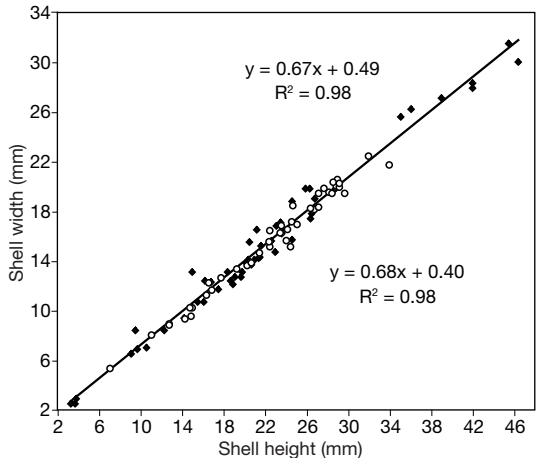

FIG. 25. — Dispersion diagram and linear correlation line of shell dimensions for *Bivetiella cancellata* (Linnaeus, 1767) (◆) and *B. similis* (Sowerby, 1833) (○).

Genus *Brocchinia* Jousseaume, 1887

Brocchinia Jousseaume, 1887: 221.

TYPE SPECIES. — *Voluta mitraeformis* Brocchi, 1814 (non *Voluta mitraeformis* Lamarck, 1811: 173), syn. *Brocchinia tauroparva* (Sacco, 1894) (cf. Petit 1986: 24), Pliocene, Italy (subsequent designation by Sacco 1894: 68).

REMARKS

Several European authors have included this taxon as a subgenus in *Narona*; this apparently goes back to Adams H. & Adams A. citation (1854: 277) of "*C. mitraeformis* Sow." in the subgenus *Narona*, together with *C. clavatula*, *C. elata* (both W Panamic) and *C. taeniata* (locality unknown, but cf. *Tribia coronata*). Obviously, the Adams made an error and meant here *C. mitriformis* Sowerby, 1832, a recent W Panamic species, now type species of *Hertleinia* Marks, 1949.

Subsequent to Hoernes & Auinger (1890: 280), *Narona* has been used as the genus name for some European fossil and recent species; however, these authors referred to Crosse (1861: 242) who mentioned only the recent species *C. mitriformis* Sowerby, 1832. Consequently, *Narona* has been used improperly for these species. Petit (1986: 24) has clearly pointed out the differences between *Narona* and *Brocchinia.*

The etymology of *Brocchinia* evidently refers to *Brocchi*, whose name has been used for other molluscan genus-level names as well. *Brocchia* Bronn, 1827, a genus of Capulidae, does not cause confusion, but the following names are likely to do so: 1) *Brochina* Gray, 1857 (p. 101), which must be considered a "correct original spelling" (ICZN 1999: art. 32.2) is a section of *Caecum*; 2) *Brocchina*, used by Pallary (1912: 116), is an incorrect subsequent spellings for *Brochina* Gray, 1857; 3) according to Rovereto (1904: 29), *Brochinia*, used by Montfort in the combination *B. glabra*, belongs in the Annelidae; 4) *Brocchina*, as used by Fulton (1922: 19, 27) and by Strong (1945: 3), is an incorrect subsequent spelling for *Brocchinia* Jousseaume, 1887. These incorrect subsequent spellings are not available names (ICZN 1999: art. 33.3) and must be disregarded.

Typical *Brocchinia* species are elongated and rather small. However, Atlantic deep water species

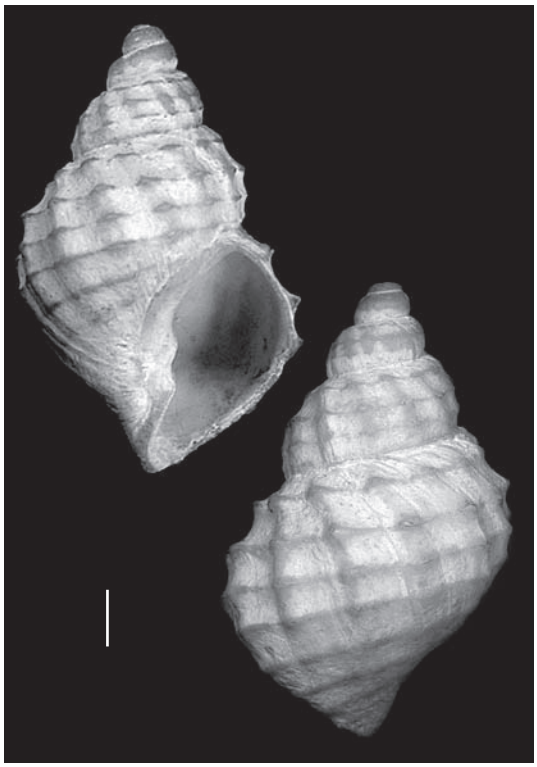

FIG. 26. — *Brocchinia azorica* (Bouchet & Warén, 1985), Azores, *Talisman* dr. 129, 38°00'N, 27°03'W, 2200 m (MNHN). Scale bar: 1 mm.

as "*Admete*" *nodosa* Verrill, 1885, "*Admete*" *decapensis* Barnard, 1960, "*Admete*" *azorica* Bouchet & Warén, 1985, and *Brocchinia pustulosa* Verhecken, 1991, have the same general features of spire form (more or less elongated), sculpture (more or less pronounced) and, especially, form of the aperture, and therefore have been included in this genus (see also Verhecken 1991a: 549; 2002: 510). Bouchet & Warén (1985: 257) already stated that "*A. nodosa* and *A. azorica* […] probably do not belong to *Admete*".

Radula absent in *B. nodosa* and *B. decapensis*; no data for the other species.

Some fossil and recent species occurring in the Pacific from Japan to New Zealand are very similar to Atlantic *Brocchinia* species, but they have been classified under several other generic names (see Verhecken 1991b: 74; 1997: 303).

Brocchinia azorica (Bouchet & Warén, 1985) (Figs 26; 65C, D)

Cancellaria sp. – Dautzenberg 1889: 30; 1927: 376.

Admete azorica Bouchet & Warén, 1985: 260, fig. 690.

Brocchinia azorica – Verhecken 1991a: 549; 2002: 510, figs 4, 5.

TYPE MATERIAL. — Holotype: 7.6 × 4.9 mm (MNHN) (Bouchet & Warén 1985: fig. 690).

TYPE LOCALITY. — SE of Pico, Azores, 38°07'N, 28°18'W, 1820 m, BIAÇORES stn 53.

MATERIAL EXAMINED. — **Azores.** The holotype. — *Talisman* dr. 129, 38°00'N, 27°03'W, 2220 m, 1 spec. (MNHN).
NW of Ireland. 2900 m, 4 specs (NMSZ), outside area studied here.

DISTRIBUTION (Fig. 28). — Off the Azores, 1250-2220 m (4 specs, Bouchet & Warén 1985: 260); off NW Ireland, 2900 m (Verhecken 2002: 510).

DESCRIPTION

"Shell short, conical, rather broad, very solid, white. The larval shell consists of 2.25 whorls, sculptured by fine spiral lines and its height is about 0.85 mm. The holotype has 2.8 postlarval whorls which are rather flat and sculptured by strong axial ribs; 11 ribs occur on the body whorl. There are also numerous irregular growth lines. The spiral sculpture consists of three often interrupted spiral lines on the upper whorls and two additional ones on the body whorl. The aperture is rather small with two large columellar folds and a strongly oblique outer lip.

Dimensions: height of the shell 7.6 mm, diameter 4.6 mm, height of the aperture 4.0 mm, breadth 2.1 mm." (Bouchet & Warén 1985: 260).

The largest shells from off Ireland measure 15.4 × 9.4 and 19.6 × 11.6 mm.

REMARKS

The protoconch of most known *B. azorica* shells is eroded, but the *Talisman* dr. 129 shell from the Azores (MNHN) has a multispiral protoconch with 2 3/4 whorls, max. diameter 1.4 mm, exposed height 1.3 mm (Fig. 65C, D).

The two unidentified single shells (MOM) from near Pico, Azores, recorded by Dautzenberg (1889:

FIG. 27. — *Brocchinia azorica* (Bouchet & Warén, 1985) from a locality outside the area studied here; off W Ireland, *Challenger* II 71/90 stn 401, 54°40'N, 12°16'W, 2900 m (NMSZ). Compare *B. decapensis*, Figure 31A. Scale bar: 5 mm.

30, 1 spec., 1287 m; 1927: 376, 1 spec., 1250 m) belong to this species. In shell form, *B. azorica* resembles *B. nodosa* (see below); dimensions of both species have been compared graphically (Verhecken 2002: 513). The conical form of larger *B. azorica* shells resembles well that of *B. decapensis* (see below, and Figs 27; 31; 32).

In form and sculpture, this species (and probably also *B. decapensis* when uneroded) rather well resembles a shell (dimensions not indicated) from Mozambique (Lussi *in litt.*) figured by Lussi *et al.* (2004: 7) under the incorrect name "*Cancellaria*" *okutanii* Petit, 1974.

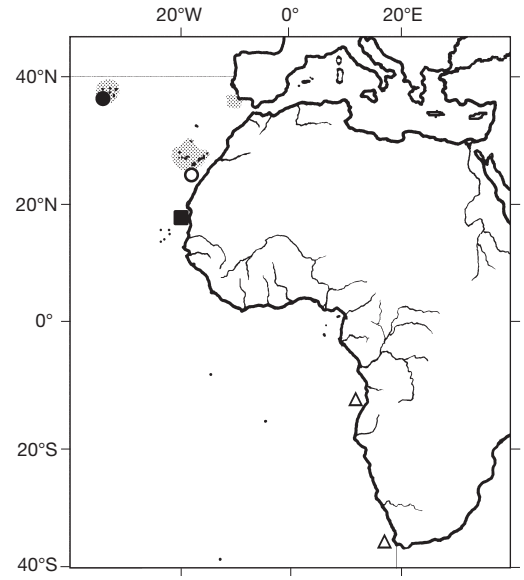

FIG. 28. — Distribution of the *Brocchinia* species in studied area: *B. azorica* (Bouchet & Warén, 1985) (●); *B. clenchi* Petit, 1986 (grey areas and ○); *B. nodosa* (Verrill & Smith *in* Verrill, 1885) (■); *B. decapensis* (Barnard, 1960) (△).

Brocchinia clenchi Petit, 1986
(Figs 29; 59C, D)

Brocchinia clenchi Petit, 1986: 24.

Cancellaria mitraeformis – Jeffreys 1885: 49 (non *C. mitraeformis* (Brocchi, 1814)).

Cancellaria pusilla H. Adams, 1869: 274, pl. 19, fig. 12 (non *C. pusilla* Sowerby, 1832).

Cancellaria (*Brocchinia*) *pusilla* – Dautzenberg 1927: 73, 377.

Narona (*Brocchinia*) *pusilla* – Nordsieck 1968: 151.

Narona (*Sveltia*) *pusilla* – Nordsieck & Garcia-Talavera 1979: 152.

Narona pusilla – Rolan Mosquera 1983: 236.

Brocchinia clenchi – Verhecken 2002: 510.

TYPE MATERIAL. — Holotype: 4.5 × 2.3 mm (USNM 849002, ex Jeffreys colln); paratypes: 5.2 × 2.6 mm (USNM 189694, ex Jeffreys colln); 6.0 × 2.5 mm (BMNH 1855.4.4.202, ex MacAndrew colln, possibly a type of *Cancellaria pusilla* H. Adams, 1869; Fig. 29A).

TYPE LOCALITY. — Portugal, Josephine Bank, west of Cape St. Vincent (about 37°N, 14°W), 610-770 m.

MATERIAL EXAMINED. — **Off S and W Portugal.** Josephine Bank, 6 specs (BMNH); 2 specs (USNM, see Jeffreys 1885: 49). — SEAMOUNT 1 stn DE48, 36°47.8'N, 14°31.7'W, 1350-1360 m, 2 specs (MNHN).
Canary Islands. 7 specs (FS). — Orotava, 1 spec. (BMNH, paratype). — Gran Canaria, SEAMOUNT 2 stn DW130, 28°08'N, 15°53.1'W, 660 m, 6 specs (MNHN). — S of Hierro, CANCAP stn 2.155, 27°35'N, 17°59'W, 700 m, 2 specs (RMNH). — SE of Fuerteventura, CANCAP stn 2062, 28°07'N, 13°45'W, 1520 m, 4 specs (RMNH). — 28°08'61.3"N, 15°43'40.1"W, 277 m, leg. A. Benites, 1 spec. (FS). — S of Fuerteventura, Punta de Jandia, CANCAP stns 2.003, 2.010, 2.013, 2.065, 2.074, 2.075, 2.078, 2.084, 2.085, 100-1520 m, 64 specs (RMNH). — Off Lanzarote, CANCAP stn 4041, 120 m, 1 spec. (RMNH). — CANCAP stn 4048, 215-325 m, 7 specs (RMNH). — CANCAP stn 4090, 65 m, 6 specs. (RMNH). — S of Palmas, CANCAP stn 4.117, 28°26'N, 17°51'W, 503 m, 1 spec. (RMNH).
Madeira archipelago. S of Selvagem Grande, CANCAP stn 3.072, 830 m, 1 spec. (RMNH).
Azores. BIAÇORES 1971, stn P28, *Jean Charcot*, 15 m, 8 specs, lv (MNHN). — Stn 14, S of Pereira, 27-38 m, 2 specs (MNHN). — São Miguel Island, 50 m, 16 specs, lv (MNHN). — CANCAP stns 5.006, 5058, 5.066, 35-180 m, 4 specs (RMNH). — N of São Jorge, CANCAP stn 5.121, 250 m, 1 spec. (RMNH). — Between Pico and São Jorge, 1250 m, 2 specs (MOM). — S of Pico, CANCAP stn 5.132, 168 m, 6 specs (RMNH). — N of Faial, CANCAP stn 5.135, 180 m, 6 specs (RMNH).
Off Western Sahara. CANCAP stn 3.107, 24°17'N, 16°49'W, 1000-1100 m, 1 spec., lv (RMNH).

DISTRIBUTION (Fig. 28). — Off S and W Portugal, Selvagem Grande, Canary Islands, Azores, off Western Sahara. Bathymetry: 15-1520 m, both extremes of this range are based on several specimens, some alive.

The locality "Bay of Biscay" given by Jeffreys (1885: 49) with reference "'Trav.' Exp. 1882, 219 fms" needs confirmation: the species is mentioned by Locard (1886: 157) with reference to Jeffreys, but is not in Locard's "Travailleur & Talisman" report (1897). The locality "Palermo", 110 m, is mentioned by Monterosato (1875: 37) for a fragment of *Cancellaria mitraeformis* (= *B. clenchi*) (repeated by Aradas & Benoit 1870: 317), but later Monterosato (1878: 97) excluded this taxon from his list of Mediterranean species, because "not yet well verified". Also the locality "Med." (Nordsieck & Garcia-Talavera 1979: 152) needs confirmation; "off Vigo, NW Spain" (Hidalgo 1917: 189) is questioned by Rolan-Mosquera (1983: 236).

DESCRIPTION

"Paucispiral nucleus smooth, heliciform, consisting of about 1 1/2 whorls; transition from protoconch to teleoconch almost imperceptible. Faint peripheral spiral cords arise midway of the first postnuclear whorl. The spiral sculpture consists of 3 to 5 extremely weak cords, with 3 usually visible on the spire whorls, and 5 or so on the body-whorl. Axial sculpture, when present, consists only of weak nodes on the periphery that are crossed by the spiral cords. Suture distinct, slightly impressed. Teleoconch of about 4 whorls; nonumbilicate. Aperture ovate with a weak but noticeable columellar callus. Columella with two distinct, rounded folds of approximately equal size, the posterior one being slightly larger and more pronounced. Siphonal canal indicated by the angled base of the columella and a minute depression in the base of the aperture. Outer lip prosocline, usually denticulate within. The denticles, which do not extend to the edge of the lip, vary in strength and number. Shell white or horn colored. Animal unknown." (Petit 1986: 24).

The paucispiral protoconch of the holotype has been figured by Petit (1986: 25, fig. 4).

Dimensions for the 26 Azores shells (MNHN): height, 3.3-5.8 mm ($\bar{x}$ = 4.8 mm, σ = 0.6); width, 2.1-2.8 mm ($\bar{x}$ = 2.5 mm, σ = 0.2).

Specimens taken off São Miguel Island, Azores, 50 m (MNHN), have a white foot.

REMARKS

This species was not treated by Bouchet & Warén (1985). Sometimes it has been referred to as *Cancellaria mitraeformis* (Brocchi, 1814), now known as *Brocchinia tauroparva* (Sacco, 1894). But it differs from the fossil forms which are very variable but in general are larger (up to 13 mm), often more heavily sculptured and, especially, have a multispiral protoconch (Janssen 1984: pl. 5, fig. 3).

The material described and figured by Petit (1986), and most of the shells studied here are rather small (up to 6 mm height) and only faintly sculptured. However, the six shells of lot PORCUPINE Atlantic stn 28, 548 m (BMNH 1885.11.5.2607-12) (see Fig. 29C, D), and also the single RMNH live collected specimen from off Western Sahara, 1000-1100 m, can be distinguished at a glance from the Azores and Canaries shells, even when they have the same dimensions.

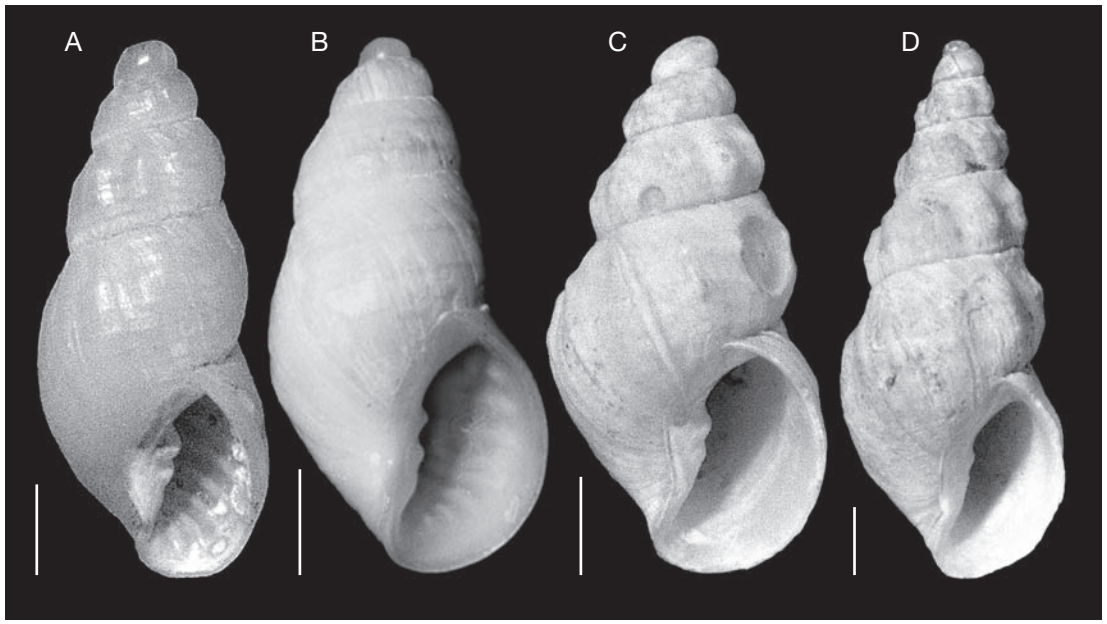

FIG. 29. — *Brocchinia clenchi* Petit, 1986: **A**, **B**, smooth shells; **A**, paratype, Canary Islands, Orotava (BMNH 1855.4.4.202, possibly a type specimen of *Cancellaria pusilla* Adams, 1869); **B**, Azores, off Terceira, 38-27 m, 38°39'N, 27°14.5'W, *J. Charcot*, BIAÇORES 1971 stn 14, sand, in *Ditrupa*; **C**, **D**, sculptured shells, PORCUPINE Atlantic stn 28, 548 m (BMNH 1885.11.5.2607-12); **C**, smaller shell; **D**, larger shell. Scale bars: 1 mm.

These seven shells have the suture more impressed, a much stronger axial sculpture, no inner lirae in the outer lip, and are up to 8.5 mm high. In this respect they are rather like the Tertiary forms (very variable themselves), except for their paucispiral protoconch which excludes them from the fossil species. The Josephine Bank and Canaries shells taken in deep water are also fairly sculptured; the Azores and Canaries shallow-water shells are often smaller and almost smooth, the spiral sculpture is very soft.

Petit (1986: 26) mentioned specimens of this species from fish traps at 43 m off Tenerife South, and some of the Azores specimens lived at 15 and 50 m. These depths are in strong contrast to the 1000-1100 m for the live collected Western Sahara specimen (RMNH). More material from different localities and depths will be needed for establishing whether or not the smaller and smoother (shallow water?) form passes gradually into the larger, heavily sculptured (deep water?) form. Until then, they are here considered one species.

The dimensions of a single somewhat aberrant shell (NMWZ 1955.1580.2258), taken in 1873 by the *Challenger* off Pernambuco, Brazil, fit reasonably well those of the eastern Atlantic shells (Fig. 30). That shell was tentatively identified as *B. clenchi* (NMWZ, see Verhecken 2002: 510, fig. 6). Subsequent to the submission of the present paper, *Brocchinia verheckeni* de Barros & de Lima, 2007 has been published. Cited *Challenger* shell is very similar. "The shape of this single Brazilian specimen, referred to as *B. clenchi* by Verhecken (2002: 510) dredged by the *Challenger* expedition (station 122) and mentioned by Watson (1886: 698) more strongly resembles *B. verheckeni* than *B. clenchi*, especially with regard to the depth of the suture, its 2 columellar folds, and the strongly nodulose ornamentation. However, they differ considerably by having just 2 and 3 spiral cords on the penultimate whorl and final whorl, respectively, and the latter a protoconch with more than one whorl" (de Barros & de Lima 2007: 66). But, the stability of the number of spiral cords and of

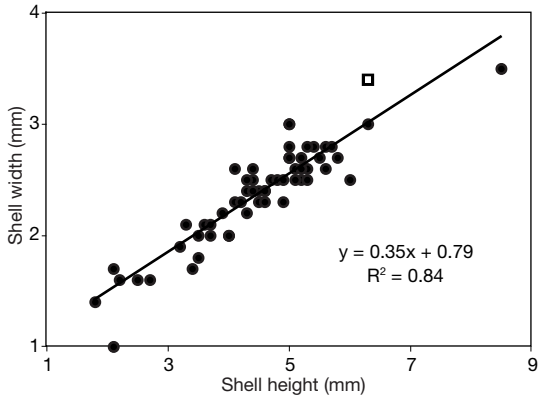

FIG. 30. — Dispersion diagram and linear correlation line of shell dimensions for West African *Brocchinia clenchi* Petit, 1986 (●) and the shell from off Brazil (□).

protoconch whorls within species of *Brocchinia* still has to be studied.

Although already pointed out by Jeffreys (1885: 49) and by Sykes (1911: 332), almost all authors overlooked the homonymy of *Cancellaria pusilla* Adams, 1869, with *Cancellaria pusilla* Sowerby, 1832. Also *Voluta mitraeformis* Brocchi, 1814 is invalid as a homonym of *Voluta mitraeformis* Lamarck, 1811; therefore the species was without a valid name. The MacAndrew shell (BMNH 1855.4.4.202), although with locality and dimensions agreeing with those given by Adams for his *C. pusilla*, is quite different from his figure, so this shell might very well not be Adams' type of *C. pusilla*. Therefore, instead of introducing a *nomen novum*, Petit (1986) described a new species so that a holotype could be designated.

This species is very similar to some other minute cancellariids living in areas far remote from the Atlantic, e.g., *Cancellaria fischeri* A. Adams, 1860, from the Strait of Korea and Indonesia (see Verhecken 1997: 300), and *Cancellaria exigua* E. Smith, 1891 (see Verhecken 1991a) from off Southeastern Australia. Shells of *B. clenchi* do not have the perforated intritacalx present on these Indo-Pacific shells.

Brocchinia clenchi is very similar to European Neogene species like *Brocchinia tauroparva* (Sacco, 1894) (= *B. mitraeformis* (Brocchi, 1814)) and *Cancellaria parvula* Beyrich, 1856.

Brocchinia decapensis (Barnard, 1960) (Fig. 31)

Admete decapensis Barnard, 1960: 439, fig. 1a. — Kensley 1973: 194.

Brocchinia decapensis – Verhecken 1991a: 549; 2002: 510.

TYPE MATERIAL. — Holotype: 27.3 × 15.0 mm (SAM A9177).

TYPE LOCALITY. — Off Cape Point, 34°37'S, 17°03'E, 2890-2960 m.

MATERIAL EXAMINED. — **South Africa**. Holotype, and 1 shell without locality data (SAM A30706).
Angola. Ambrizete, NO *Thalassa*, ZAIANGO BIOL 2, stn CP04, 7°24.92'S, 11°30.74'E, 1335 m, VIII.2000, 1 spec. lv, 21.2 × 13.4 mm (MNHN). — Stn CP07, 7°30.16'S, 11°33.38'E, 1359-1367 m, 1 spec. lv, 19.6 × 12.7 mm (MNHN).

DISTRIBUTION (Fig. 28). — Off Cape Point, 2890-2960 m, and off Ambrizete, N Angola, 1335-1367 m.

DESCRIPTION

Shell solid, off-white, with relatively high spire.

Protoconch is missing on eroded holotype and other shells seen. Teleoconch: spire high, with about four whorls. Last whorl with sculpture of axial ribs (about 18?) and about 8 or 9 spiral threads, forming nodules when crossing. Aperture semi-circular; outer lip thin, slightly flared outward; no internal lirae. Columella straight, with two folds (including rim of siphonal canal) that are solid but not very high. Strong columellar callus field. Umbilicus closed.

Animal pinkish, eyes present, no radula (Barnard 1960).

REMARKS

This is the largest species of the genus as here interpreted. All known shells have only the last whorl and aperture in reasonable condition, the rest of the shell surface is heavily corroded with loss of at least 0.5 mm layer of shell material, and loss of possibly 1-2 mm in the protoconch area. The second S African shell, even more corroded than the holotype, has the posterior fold divided into three close-set minor folds; the anterior fold appears bifid; and in between these primary folds

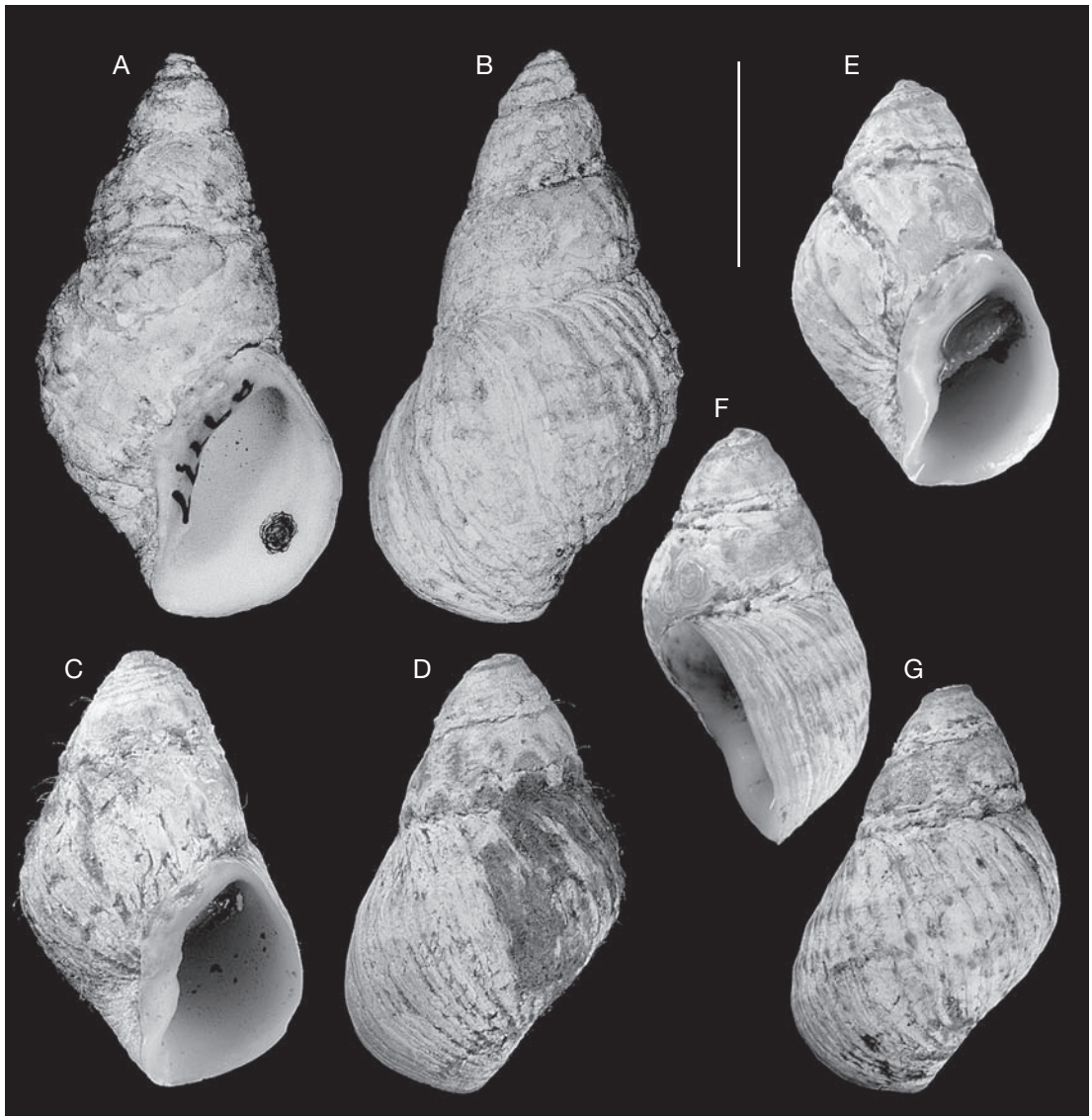

FIG. 31. — *Brocchinia decapensis* (Barnard, 1960): **A**, **B**, holotype, off Cape Point, South Africa (SAM A9177); **C**-**G**, Angola, off Ambrizete, NO *Thalassa* Zaiango Biol 2, leg. R. von Cosel, 26-28.VIII.2000 (MNHN); **C**, **D**, stn CP04, 7°24.95'S, 11°30.74'E, 1335 m; **E**-**G**, stn CP07, 7°30.16'S, 11°33.38'E, 1359-1367 m. Scale bar: 10 mm.

a third sharp fold is placed. Barnard (1960: 439, fig. 1a) figured a shell with a grooved suture, but in 1989 this was hardly visible on these two shells (see holotype: Fig. 31A, B). The Angola shells are in the same corroded condition; one of them has very faint spiral lines on the last whorl.

The possible relation with *B. azorica* (which has a multispiral protoconch indicating a pelagic development) has been mentioned above: in spite of the distance between the Cape Point to Angola and the Azores to Ireland areas, it is possible that they are conspecific (compare Figures 27 and 31A). The

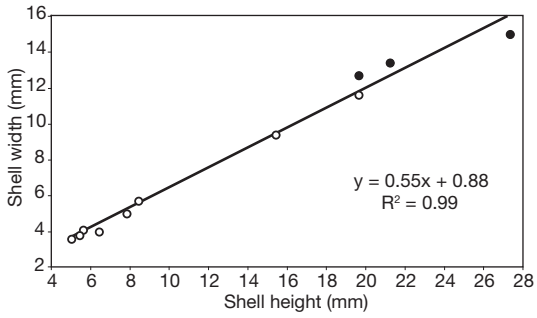

FIG. 32. — Dispersion diagram and linear correlation line for shell dimensions of *Brocchinia azorica* (Bouchet & Warén, 1985) (○) including shells from outside area studied here, and *B. decapensis* (Barnard, 1960) (●).

height/width data of *B. decapensis* and *B. azorica* together (Fig. 32) give a high linear correlation (r^2 = 0.99, $p < 0.005$), but more material of both species, and less corroded shells of *B. decapensis* are needed for a better evaluation of a possible synonymy.

Barnard (1960: 439) considered *B. decapensis* "closely comparable with *B. nodosa* from the New England coast", in spite of the higher spire or the former.

Brocchinia nodosa
(Verrill & Smith *in* Verrill, 1885)
(Fig. 33)

Admete nodosa Verrill & Smith *in* Verrill, 1885: 419, pl. 44, fig. 9.

Admete nodosa – Dall 1927: 43. — Abbott 1974: 248. — Kaicher 1978: card 1884. — Bouchet & Warén 1985: 258.

Brocchinia nodosa – Verhecken 1991a: 549; 2002: 511, figs 7, 8.

TYPE MATERIAL. — Holotype: off New Jersey, USFC *Albatross* stn 2234, 39°9'N, 72°3'W, 1475 m, 11.8 × 8.4 mm (USNM 44646). Paratype: USFC stn 2217, 39°47'20"N,69°34'15"W, 1670 m, 1 shell, actual whereabouts unknown (not MCZ, nor in Peabody Museum, Yale).

TYPE LOCALITY. — Off New Jersey, USFC *Albatross* stn 2234, 39°9'N, 72°3'W, 1475 m. The shell catalogued USNM 44646 has dimensions reasonably close to those given in the original description (12 × 8 mm), and is clearly the holotype. However, a label with it stated: "off Cape Hatteras, N. C."; obviously, that label was not correct. "The station number was correctly indicated, and the detailed data had been published both in the cruise report and in the original description of the species. The locality label accompanying the type has now been clarified" (Harasewych *in litt.* 10.V.2000).

MATERIAL EXAMINED. — **Eastern Atlantic.** Bay of Biscay, BIOGAS 1972-1980, stn CP07, 44°10'N, 4°16'W, 2170 m, 5 specs, up to 14.3 × 9.6 mm (MNHN). — *Challenger* II, AT219, 57°25'N, 10°28'W, 1991 m, 3.VIII.1982, 1 spec., 11.1 × 8.6 mm (NMSZ 1994128.13001).
Mauritania. Off Banc d'Arguin, MAU, stn 105, 19°43'N, 17°44'W, 1600-1900 m, 1 spec. lv., 14.8 × 11.9 mm (RMNH).
Apart from the two types, and the nine specimens mentioned by Bouchet & Warén (1985), more material is known from the western Atlantic.
Western Atlantic. SE of Cape Henlopen, Delaware, RV *Eastward*, Cr E-6-78, stn 43, 38°45.8'N, 72°41.6'W, 2 specs, 1850-1950 m (USNM 757000). — *Albatross*, stn 2739, Delaware Bay, 1460 m (USNM 76786). — NE of Norfolk, RV *Gillian*, Cr. 75-089 stn 29, 1630-1760 m, 1 spec. (USNM 757272). — Off Fernandina, Florida, *Albatross*, stn 2668, 30°58'N, 79°38'W, 678 m, 3 juveniles (see Dall 1927: 1, 43, who also mentioned unspecified material from off Nantucket, 1470 m, and S of Long Island, New York, 1765 m).

MEASUREMENTS. — Up to 16 × 10 mm.

DISTRIBUTION (Fig. 28). — Western Atlantic: from about 42°N, off Nantucket, Massachusetts, to 31°N, 1460-1950 m; off Fernandina, Florida, 678 m (Dall 1927); Eastern Atlantic: off NW Ireland (57°N), 1991 m; Bay of Biscay, 2170 m; off Mauritania (19°N), 1600-1900 m.

DESCRIPTION
Shell white with dull surface; globose, with large aperture.

Protoconch (corroded on most shells) multispiral (Bouchet & Warén 1985: 260). Spire short, with up to three whorls. Axial sculpture of 12 rounded ribs; spiral sculpture of three weak spiral lines, with strong to pointed nodules when crossing the axials. Last whorl 86% of total shell height. No umbilicus. Aperture ovate; outer lip smooth within; columellar callus white. Columellar fold broad; one blunt fold at rim of siphonal canal.

The animal has no radula (Bouchet & Warén 1985: 260).

REMARKS

The occurrence of this species off NW Ireland, originally based on one very juvenile shell (2.2 × 1.7 mm, Bouchet & Warén 1985), is now confirmed by a specimen of 11.1 × 8.6 mm (NMSZ 1994128-13001) (Verhecken 2002: 512, fig. 7), but with eroded protoconch. Also in material from the Bay of Biscay the protoconchs are completely eroded. The protoconch type was identified as multispiral (2 3/4 whorls, max. diameter 1.4 mm), based on the juvenile shell (Rockall Trough, INCAL 1976 stn DS5, 56°28'N, 11°12'W, 2503 m, MNHN), identified in 1985 by a process of elimination (AV). More recent data (Verhecken 2002: 510-512) now show that also *B. azorica* has a protoconch of the same type and dimensions, thus casting some doubt on that identification.

Only one live-taken specimen (RMNH) testifies the occurrence of this species in the area studied here.

The only fossil species from the European or African Neogene, closely related to *B. nodosa*, seems to be *B. gerdae* Janssen & Petit, 2003 from the Late Langhian (Miocene) of Nordlohne, Lower Saxony, Germany, which reaches only a height of 4.7 mm.

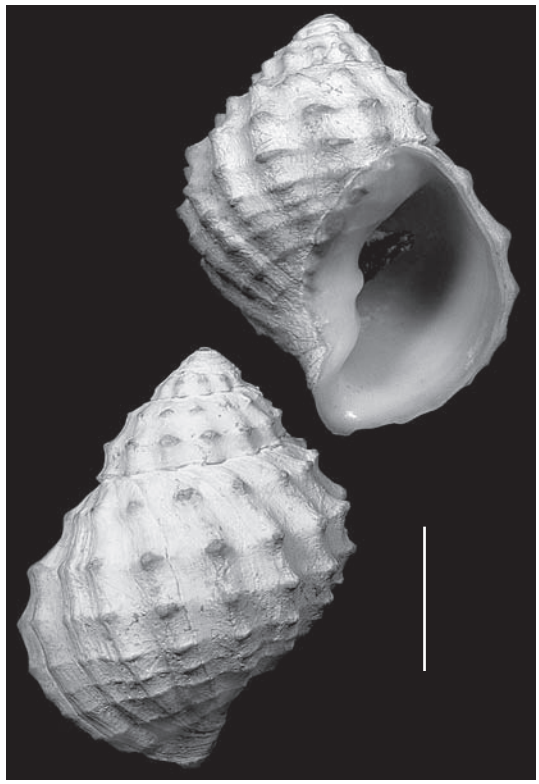

FIG. 33. — *Brocchinia nodosa* (Verrill & Smith *in* Verrill, 1885), Mauritania, off Banc d'Arguin, stn MAU 105, 19°43'N, 17°44'W, 1600-1900 m (RMNH). Scale bar: 5 mm.

Genus *Cancellaria* Lamarck, 1799

Cancellaria Lamarck, 1799: 71.

TYPE SPECIES. — *Voluta reticulata* Linnaeus, 1767, Recent, Caribbean (by monotypy).

Cancellaria africana Petit, 1970
(Figs 34; 64E, F)

Cancellaria imbricata Watson, 1882a: 325; 1886: 274, pl. 18, figs 10a-c. — Sowerby 1903: 230. — Barnard 1959: 12.

Cancellaria africana Petit, 1970: 86 (*nomen novum* for *C. imbricata* Watson, 1882, *non* Hoernes, 1856). — Lussi *et al.* 2004: 7.

TYPE MATERIAL. — Holotype (of *C. imbricata* Watson): BMNH 1887.2.9.940, 20.5 × 12.3 mm.

TYPE LOCALITY. — Off Cape of Good Hope, *Challenger*, stn 142, 35°04'S, 18°37'E, 275 m.

MATERIAL EXAMINED. — **South Africa.** Off Cape Town, the holotype; 3 specs, up to 23.2 × 13.6 mm (AV 0216). — Off Agulhas Bank, 2 specs, ex pisces (AV 0930).

DISTRIBUTION (Fig. 35). — Type locality, and off Agulhas Bank; 240-350 m (Lussi *et al.* 2004: 7). Moreover (not seen): off Cape Point, Pieter Faure, 247-298 m, 14 specs (SAM); Agulhas Bank, 4 specs, up to 26 mm high (RP).

DESCRIPTION

Shell solid (SAM) to thin (AV); relatively sharp spire measuring 36% (SAM) to 55% (AV) of total shell height; and a rather inflated body-whorl. Colour yellowish to greyish white (SAM shells studied) to white (AV). Shell dimensions up to 29 × 17 mm (Kensley 1973: 194); 27.3 × 18.1 mm for shells studied. Protoconch (Fig. 64E, F) paucispiral, axis slightly deviated, with one rounded whorl; relatively

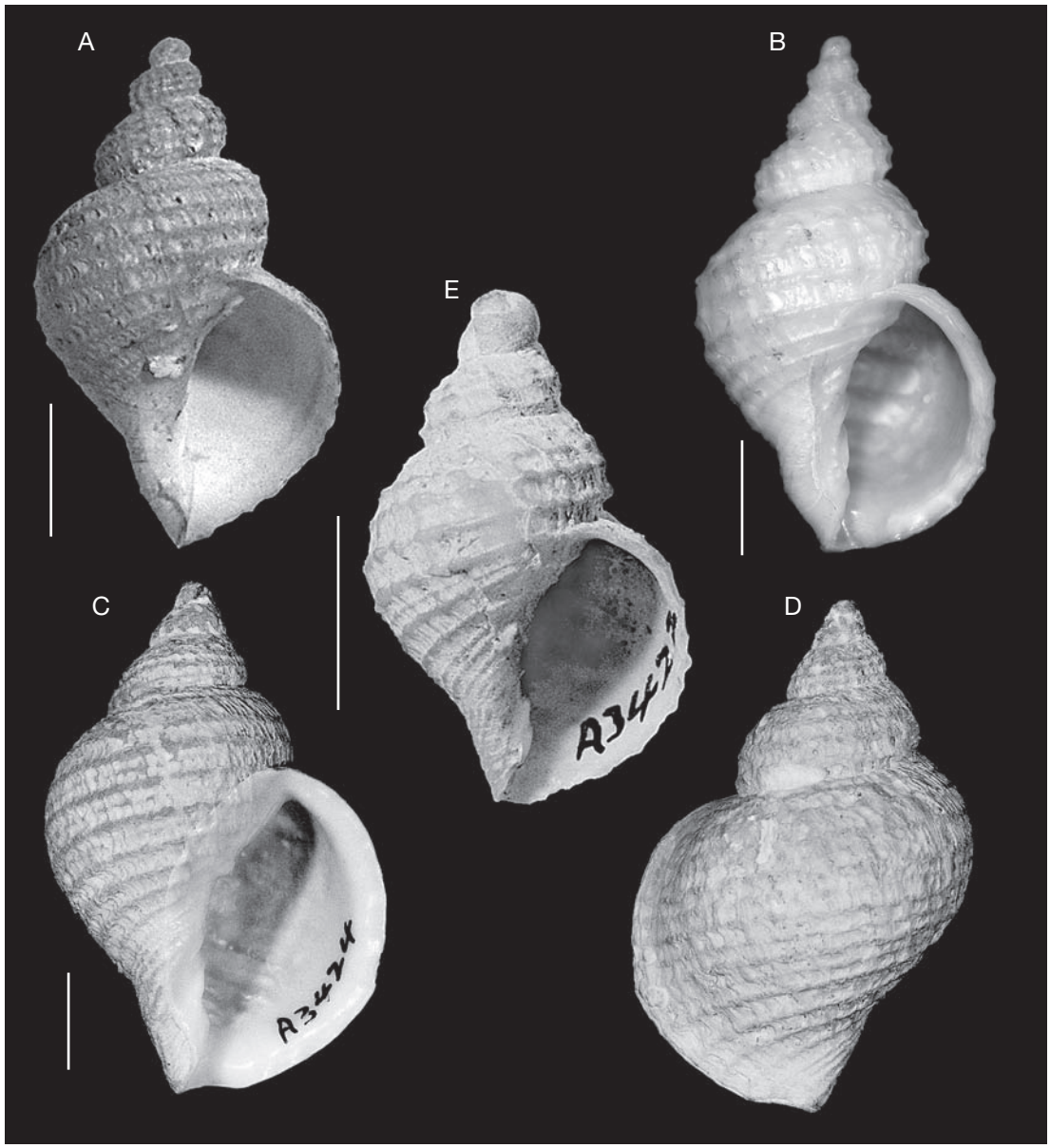

FIG. 34. — *Cancellaria africana* Petit, 1970: **A**, holotype of *Cancellaria imbricata* Watson, 1882, South Africa, off Cape of Good Hope, *Challenger* stn 142, 270 m (BMNH 1887-2-9-90); **B**, off Cape Town (AV 0216); **C**-**E**, off Cape Point, 342 m; **C**, **D**, off Table Mountain, 58 miles, *Pieter Faure* stn PF15085, 342 m (SAM A3424); **E**, Cape Point, 18 miles, *Pieter Faure* stn PF14516, 243 m (SAM A3422). Scale bars: 5 mm.

large, max. diameter (measured perpendicularly to teleoconch shell axis) 1.6-1.7 mm (AV) to 2.0 mm (SAM), exposed height 1.5 mm. No sculpture visible on the four protoconchs studied. Sharp delimitation between proto- and teleoconch. Teleoconch: up to 4.5 rounded whorls with depressed sutures.

Prominent sculpture of rounded spiral bands, up to 0.4 mm wide: 4, 5 and 11-19 on teleoconch whorls 1-4 respectively. Axial ribs broad, rounded, numbering 10, 11-13, and 14 on 1st to 3rd whorl respectively, very vague on fourth whorl. Axial sculpture of fine lamellae placed almost tangentially to the whorl surface; the imbricate aspect of these shells may be due to their rather corroded surface. Aperture white, almost semicircular. Outer lip slightly flared out, no inner lirae. Columella vertical, with two strong folds (apart from the sharp rim of the siphonal canal) delimiting a well defined groove in between. Columellar callus well defined but rather thin, covering the umbilical chink.

Preserved animal greenish; radula typically cancellariid (Barnard 1959: 13, fig. 12).

REMARKS

This species is here placed in *Cancellaria* (s.s.) only because no other genus seems to be available (see Petit 1970). Its spiral sculpture looks like that of *Cancellaria rosewateri* Petit, 1983 from the Gulf of Mexico, but the Caribbean species lacks the imbrications between the spiral bands, has the spire less slender and the body-whorl less inflated. Within the area studied, *C. africana* in general outline resembles *Admetula gittenbergeri* n. comb. (see above), but is more elongated and lacks the deviated columella.

Cancellaria labrosa Bellardi, 1841, and *C. libassii* Seguenza, 1876, seem to be the only fossil species known from the European or African Neogene closely related to *C. africana*, but the recent species has the last whorl much more expanded.

Genus *Loxotaphrus* Harris, 1897

Loxotaphrus Harris, 1897: 165.

TYPE SPECIES. — *Phos variciferus* Tate, 1888, Miocene, Australia (original designation).

REMARKS

Beu & Maxwell (1987: 6, 48) include this genus in the family Cancellariidae, subfamily Plesiotritoninae; it now groups five fossil species from the Miocene of southern France, northern Italy, Australia and Burma; and one recent species each from northern West Africa, Mozambique and Australia (Beu & Verhecken 2000).

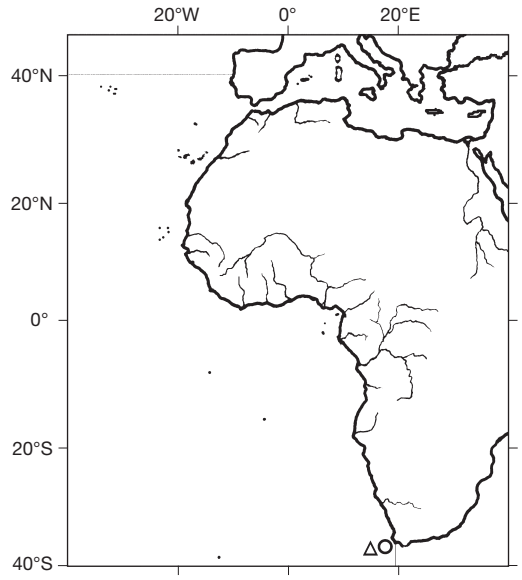

FIG. 35. — Distribution of western South African cancellariid species: *Cancellaria africana* Petit, 1970 (○); and *Nothoadmete euthymei* (Barnard, 1960) n. comb. (△).

Loxotaphrus deshayesii (Duval, 1841) (Figs 36; 65A, B)

Cassidaria deshayesii Duval, 1841: 278; 1863: 70, pl. 1, fig. 9. — Marche-Marchad 1958: 23.

Loxotaphrus deshayesii – Beu & Maxwell 1987: 49, pl. 26, figs f-o.

TYPE MATERIAL. — Holotype: "30 × 30 mm" [*sic*] (Duval 1841), corrected to 32 × 20 mm (Duval 1863), shell not located (Beu & Maxwell 1987).

TYPE LOCALITY. — Off African west coast; the holotype was obtained together with shells from Senegal and Gorée (Duval 1841).

MATERIAL EXAMINED. — **Senegal.** Gorée, 3 specs (MNHN, Jousseaume). — Sud Gorée, 40-42 m, 1 spec. (MNHN, Marche-Marchad). — M'Bour region, 40-45 m, 2 specs (MNHN); 1 spec. (AV 0015). — 20-25 m, 1 spec. (MNHN), 1 spec. (KBIN). — Joal, 50 m, 1 spec. (AMNH 269194).

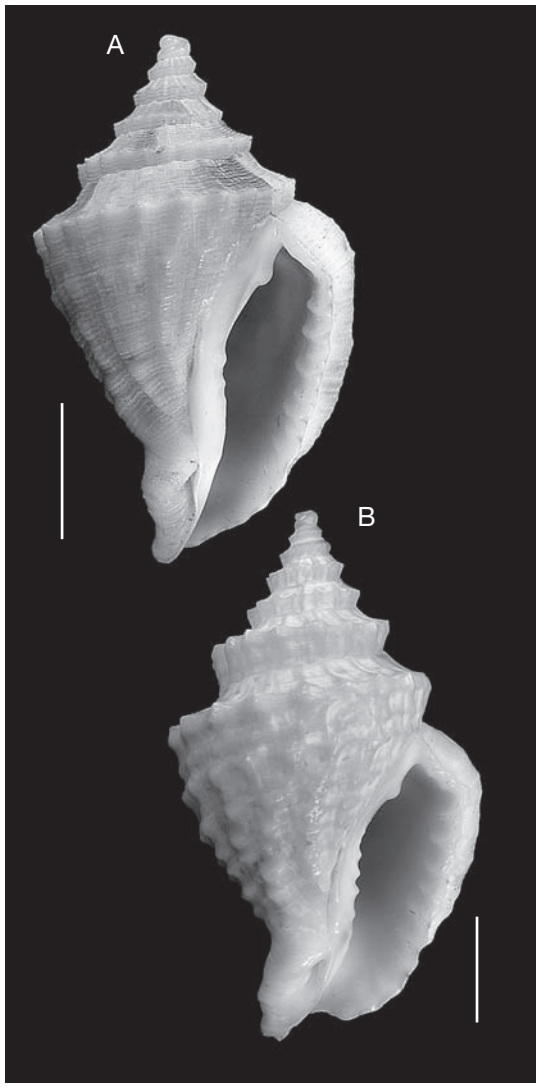

FIG. 36. — *Loxotaphrus deshayesii* (Duval, 1841): **A**, Senegal, Dakar, Gorée, 40-42 m (MNHN); **B**, Guinea, off Conakry, 10-20 m (AV 0070). Scale bars: 5 mm.

Guinea. Off Conakry, 10-20 m, 1 spec. (AV 0014). — 100-120 m, 1 spec. (AMNH 269195). — NO *André Nizéry*, SEDIGUI II, stn B21CH, 9°06'N, 14°35'W, 52 m, 1 spec. — Stn B11CH, 9°30'N, 15°9.6'W, 45 m, 3 specs. — Stn 518 CH, 10°00'N, 15°53'W, 32 m, 1 spec. (all MNHN, up to 29.2 × 19.4 mm).

DISTRIBUTION (Fig. 37). — Senegal, Guinea, Ivory Coast (Beu & Maxwell 1987: 49), between 32 and 120 m.

DESCRIPTION

Shell biconical, with a spire height about one third of total shell height. Dimensions (ignoring the Duval 1841 measurements which cannot be verified now): up to 28.9 × 18.3 mm (AMNH 269195).

Protoconch smooth, pale fawn, paucispiral with up to 1 3/8 rounded whorls; maximum diameter 1.3-1.4 mm, exposed height 1.1-1.5 mm (Fig. 65A, B). Transition to teleoconch clearly marked. A well preserved shell (AV 0015) shows one smooth whorl, ended by a narrow orthocline line, then follows 3/8 rounded whorl showing smooth spiral lines and some axial growth lines. Then the teleoconch starts abruptly with its carinated whorl and clearly marked sculpture.

Teleoconch with 5 1/2 keeled whorls; the sutures are placed slightly lower than the carina of the preceding whorl. Sutural plane sloping well downward towards the periphery. Axial sculpture consists of 17 non-collabral axial ribs on 1st-2nd whorl, 20 on 3rd and 21 on last two whorls; they are well marked on the early whorls, rather faint on the younger whorls, but clearly marked when crossing the periphery of the whorls. Spiral sculpture: seven broad spiral bands, with four microscopic lines in between.

Aperture elongate, ending in a rather long, recurved siphonal canal. Outer lip thickened into a varix, with 7-11 broad short rounded lirae, and a posterior notch. Columellar callus white; no columellar folds, at most some coarse granulations on the ventral part of the callus. A rather strong tooth occurs near the posterior end of the columellar side. A narrow umbilical chink is present.

Shell AMNH 269195 has a colour pattern of brown points and blotches, sometimes V-shaped and pointing spirally in the direction of the aperture.

REMARKS

Beu & Maxwell (1987: 49) considered this species as one of the rarest recent West African gastropods in collections. Some years ago, the late Senegal-based dealer M. Pin obtained about 30 shells from an unspecified research vessel (G. Poppe pers. comm.), so that now this species is present in many institutional and private collections.

Beu & Maxwell (1987: 9) included the genus *Loxotaphrus* in their new cancellariid subfamily

Plesiotritoninae, mainly based on the non-collabral costae.

Apparently, Beu & Maxwell (1987: 49) erroneously copied from Duval (1841: 278, 279) the dimensions of *Marginella petitii* for those of *Cassidaria deshayesii*.

Species more or less closely related to *L. deshayesii* are: *L. subtaurinensis* (Vergneau, 1965), Rupelian, Lower Oligocene of SW France; *L. aturensis* (Peyrot, 1926), Chattian, Upper Oligocene of SW France; and *L. taurinensis* (Bellardi, 1872), Middle Miocene of Italy (Beu & Maxwell 1987: 48-50). The still older *Varicohilda turriculata* Newton, 1922, of the middle Eocene of Nigeria (cf. Beu & Maxwell 1987: pl. 4a-k), is also rather similar but has strong columellar folds. Beu & Maxwell (1987: 23) distinguish *Loxotaphrus* from *Varicohilda* by the former's lack of columellar plaits, and its paucispiral protoconch (the latter is not considered a generic character by the present author).

The species name should not be confounded with *Plesiotriton deshayesianus* Beu & Maxwell, 1987, from the Eocene of the Paris Basin.

Genus *Nothoadmete* Oliver, 1982

Nothoadmete Oliver, 1982: 15.

TYPE SPECIES. — *Nothoadmete tumida* Oliver, 1982, South Orkney Islands, 60°43'S, 43°38'W, 40-80 m (by monotypy).

REMARKS

This genus was proposed in the cancellariid subfamily Admetinae to accomodate the radulate type species, other species in Admetinae being aradulate.

Nothoadmete euthymei (Barnard, 1960) n. comb. (Fig. 38)

Cancellaria euthymei Barnard, 1960: 438, fig. 1b. — Bouchet & Warén 1985: 261.

?"*Tromina* b" – Clarke 1961: 366.

Iphinopsis euthymei – Lussi *et al.* 2004: 6.

TYPE MATERIAL. — Holotype: 9.3 × 6.1 mm (SAM A9888) (Fig. 38).

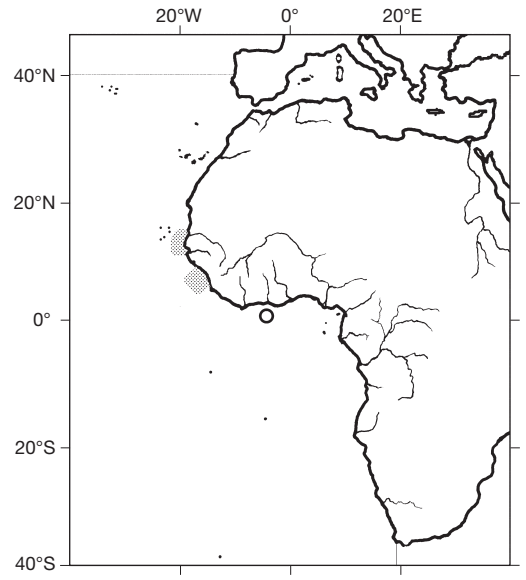

FIG. 37. — Distribution of *Loxotaphrus deshayesii* (Duval, 1841).

TYPE LOCALITY (Fig. 35). — South Africa, off Cape Point, 34°36'S, 17°00'E, 2745-3240 m.

MATERIAL EXAMINED. — Holotype, only shell known.

DESCRIPTION

Shell thin-walled, elongately globose, colour pale yellowish-white. Teleoconch has about three whorls left. Whorls inflated, suture impressed. Sculpture: many very fine microscopic axial ribs; spiral threads: 12, 15 and about 40 on 1st to 3rd whorl respectively, these threads are very narrow posteriorly but gradually become broader anteriorly on the whorl. Aperture: outer lip (partly broken away, together with end of siphonal canal) translucent, no inner lirae. Columella straight, with one very faint fold; very thin columellar callus.

Animal pale cream, eyes distinct, gill blackish, showing through the shell, radula normal for cancellariids (Barnard 1960: 439).

REMARKS

The holotype has the top of the shell, including the protoconch, missing. The "umbilical chink" mentioned by Barnard is actually the result of a slight deformation of the shell.

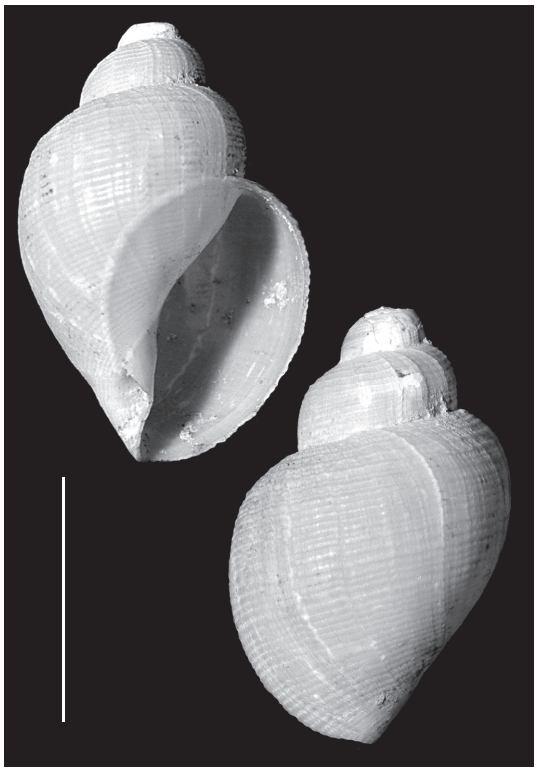

FIG. 38. — *Nothoadmete euthymei* (Barnard, 1960) n. comb., holotype, South Africa, off Cape Point, 2700-2170 m (SAM A9888). Scale bar: 5 mm.

Bouchet & Warén (1985: 261) discussed the genus *Iphinopsis* Dall, 1924, and transferred it from Trichotropidae to Cancellariidae. Four of the species they included in it were studied anatomically and were found to be aradulate. In their list of species resembling the type species *Iphinopsis kelseyi* Dall, 1908, they also cited *Cancellaria euthymei* but gave no further comments on the latter. Since shell morphology is unreliable for supraspecific determination of deep water and polar gastropods, only the presence of a radula can be used as generic character. Therefore, this species is here tentatively included in *Nothoadmete* because of its cancellariid radula (Barnard 1960: 439).

The shell of the holotype also closely resembles *Iphinoella choshiensis* Habe, 1958 (p. 35, fig. 7) from Japan, for which no radula data are given.

Genus *Solatia* Jousseaume, 1887

Solatia Jousseaume, 1887: 222.

TYPE SPECIES. — *Solatia solat* Jousseaume, 1887 (original designation) (= *Buccinum piscatorium* Gmelin, 1791, see Verhecken 1989: 665).

Solatia piscatoria (Gmelin, 1791) (Figs 39A, B; 60A, B)

Buccinum piscatorium Gmelin, 1791: 3490.

Murex semilunaris Gmelin, 1791: 3549.

Voluta piscatoria – Brocchi 1814: 308.

Cancellaria nodulosa Lamarck, 1822: 113.

Cancellaria piscatoria – Deshayes 1830: 186.

Cancellaria brocchii Crosse, 1861: 248.

Solatia solat Jousseaume, 1887: 222.

Solatia piscatoria – Sacco 1894: 26.

TYPE MATERIAL. — Neotype (Verhecken 1989): 20.2 × 14.3 mm (MNHN, unnumbered).

TYPE LOCALITY. — Mauritania, NW of N'Diago, 20°00'N, 17°08'W, 20 m.

MATERIAL EXAMINED. — The neotype and:
Spain. Punta Humbria, leg. W. Onverwacht, 3 specs (AV 1107; colln Wils, Antwerp).
Morocco. Rabat, mouth of Bou Regreb river, beach, 3 specs (MNHN, Gofas). — El Jadida, 1 spec. (MNHN, Pallary colln). — Mogador (= Essaouira), 1 spec. (KBIN, Pallary colln).
Mauritania. Off Banc d'Arguin, MAU stn 78, 20°00'N, 17°21'W, 41 m (RMNH). — MAU stns 065-069, 20°0'N, 17°11'W, 25-32 m, muddy sand, 41 specs, many juveniles (RMNH). — NO *N'Diago*, stn 324, 19°54'N, 17°9'W, 22 m, 3 juv. specs (MNHN). — NO *N'Diago*, stn 328, 20°0'N, 17°8'W, 20 m, 5 specs (MNHN). — NO *N'Diago*, stn 329, 20°0'N, 17°11'W, 24 m, 5 juv. specs (MNHN).
Senegal. Dakar, 4 specs (MNHN). — Gorée, 5 specs (MNHN). — 12°40.5'N, 17°10.5'W, 18 m, 1 spec. (MNHN). — Between Rufisque and Hamm, 6-9 m, 5 specs (KBIN, Gruvel). — Casamance, 10-20 m, leg. M. Pin 1987, 6 specs (MNHN).
Cape Verde. 10 specs (MNHN, Mauny colln).
Ivory Coast. Grand Bassam, 1 spec. (MNHN). — Abidjan region, 15-30 m, 2 specs (MNHN, Le Loeuff/ORSTOM).
Benin. Cotonou, 1 spec. (MNHN).
Principe Island. 2 specs (MNHN).

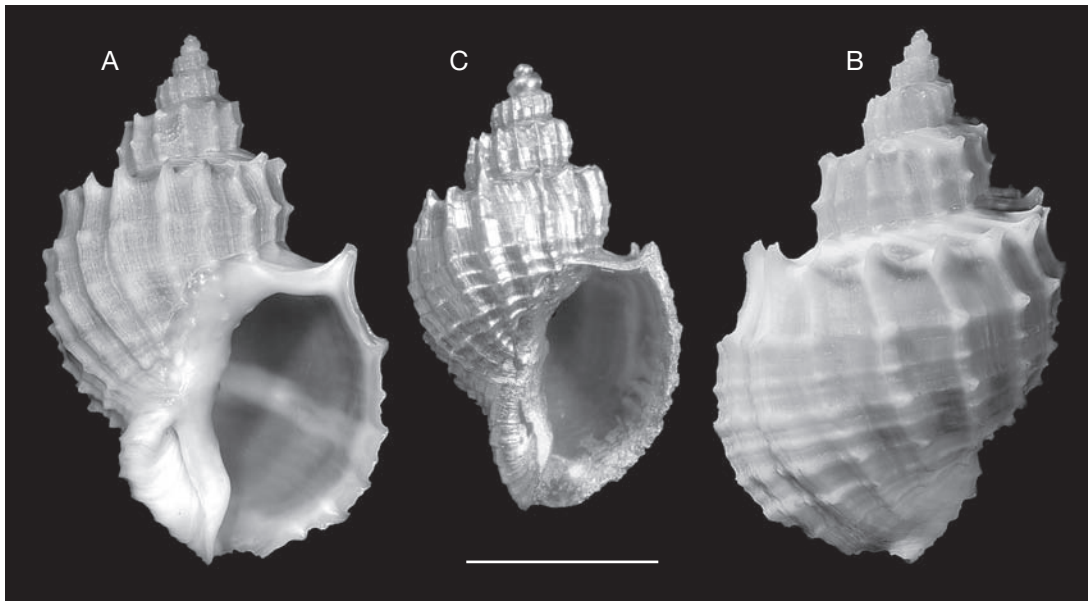

FIG. 39. — W African *Solatia* species: **A**, **B**, *S. piscatoria* (Gmelin, 1791), Senegal, Joal, 10-20 m (AV 0070); **C**, *Solatia* sp. with paucispiral protoconch, Ivory Coast, Grand Bassam (Mission Gruvel) (MNHN) (optical photo of gold-coated shell). Scale bar: 5 mm.

DISTRIBUTION (Fig. 40). — Morocco to Bénin (Nicklès 1950: 116), Principe Island; between 6 and 41 m. Punta Humbria, Spain, is the northernmost locality but needs confirmation: the material may have been accidentally transported by fishermen. Also the locality "Canary Islands" based on 1 spec. (AV 0073) needs confirmation. A single shell labelled "Benguela, Baie des Éléphants" from an old collection (MNHN) is insufficient evidence for establishing Angola as the southern limit for this species. However,

DESCRIPTION (of neotype)

Shell with turriculate spire, body-whorl globose ornamented with small spines.

Protoconch naticoid, multispiral with 2 1/4 smooth, rounded whorls. Maximum diameter 0.9 mm, exposed height 1.0 mm.

Teleoconch with 4 1/4 whorls. Axial sculpture: 15, 14, 11 and 14 narrow ribs on 1st to 4th whorl. Two spiral cords on the spire whorls, nine on the last whorl. Whorls shouldered; axial ribs produced into pointed spines when crossing the shoulder of the younger whorls. Aperture semicircular, truncated posteriorly. Outer lip crenulated, no lirae inside. Columellar callus relatively thick, whitish, covering half of the narrow umbilicus. One broad diffuse fold in the middle of the columella, a very faint one may be visible between this one and the faint siphonal canal. Siphonal fasciole well developed. Sutural area wide, flat, sloping down towards outside.

REMARKS

For extensive data, including statistical biometric data based on 89 shells, and figured radula, see Verhecken (1989).

At Banc d'Arguin, Mauritania, the species has often been found on muddy sand, 24-32 m (RMNH).

Pallary (1920: 26) introduced the name *Cancellaria piscatoria* var. *minor* for a small but normal shell from Rabat; this name is invalid as a junior homonym of *Cancellaria minor* Grateloup, 1847.

Solatia piscatoria and related species are known from the Italian Miocene on (Davoli 1982: 60). Malatesta (1974: fig 27) illustrated the geographical distribution of Miocene, Pliocene and Recent forms.

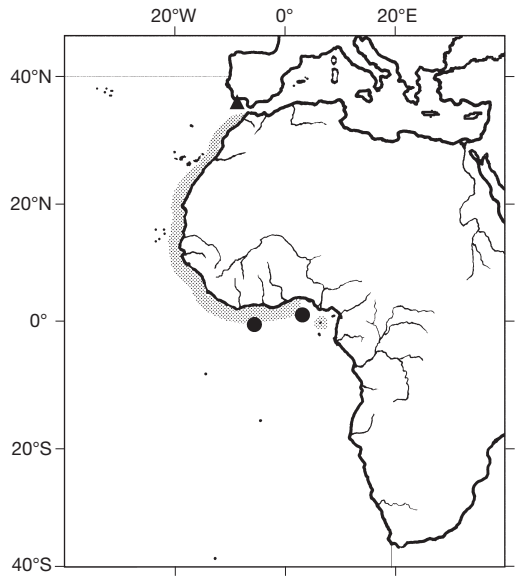

FIG. 40. — Distribution of W African *Solatia* species: *S. piscatoria* (Gmelin, 1791) (grey areas and ▲ to be confirmed); and *Solatia* sp. (●).

Solatia sp.
(Figs 39C; 60C, D)

Solatia piscatoria – Verhecken 1984b: 19, fig. 7a, b; 1989: 667, figs 2, 7a, b.

REMARKS

A single shell (KBIN IG 10591) with paucispiral protoconch from Cotonou, Benin, has been interpreted as suggesting that the protoconch type is not necessarily constant within a species (Verhecken 1984b: 19), a position which cannot be maintained. Another similar shell (MNHN) from Grand Bassam, Ivory Coast, was reported later; these two shells were then (Verhecken 1989: 667) interpreted as probably belonging to a species distinct from *S. piscatoria*. This case was discussed by Bouchet (1989: 73), who concluded as a working hypothesis that *S. piscatoria* and *Solatia* sp. are reproductively isolated, have distribution areas at least partly overlapping, and represent two distinct species.

This species is distinguished mainly by its paucispiral protoconch, versus the multispiral one of *S. piscatoria*; but also its biometric data (Verhecken 1989: fig. 8) are situated eccentrically to those of *S. piscatoria*. Its formal description is postponed until more and better material becomes available. These two shells occur in the atypical tropical hydroclimatic region (Le Loeuff & Cosel 1998), from where also a few verified *S. piscatoria* shells are known (off Abidjan, Ivory Coast, 15-30 m, 2 specs [MNHN]; see also Nicklès [1950: 116, Bénin, cited as Dahomey]).

Malatesta (1974: 373) described the protoconch of seven shells from Ficulle (Pliocene, Italy) he identified as *S. piscatoria* (translation): "Smooth and small, with only one whorl, slightly eccentric". The relation between recent and fossil paucispiral *Solatia* cf. *piscatoria* shells remains to be studied, awaiting the availability of more material with intact protoconch.

Genus *Sveltia* Jousseaume, 1887

Sveltia Jousseaume, 1887: 214.

TYPE SPECIES. — "*Sveltia varicosa* Brocc." (= *Voluta varricosa* Brocchi, 1814), by original designation, Miocene to Pliocene of Europe.

REMARKS

For the type species *Voluta varricosa* Brocchi, 1814, Deshayes (1830: 182) first introduced the orthography *varicosa* in the combination "*Cancellaria varicosa* Brocc.". Practically all authors, except e.g., Rossi-Ronchetti (1955: 274) and Pinna & Spezia (1978: 174), used *varicosa* when referring to this species, and attributed it to the publication of the original spelling. Because of this prevailing usage from 1820 on, as documented e.g., by Chirli (2002: 70), to Landau *et al.* (2006: 77), the incorrect subsequent spelling *varicosa* is deemed to be a correct original spelling (ICZN 1999: art. 33.3.1).

Sveltia lyrata (Brocchi, 1814)
(Figs 41; 43; 65E, F)

Voluta lyrata Brocchi, 1814: 311, pl. III, fig. 6.

Voluta spinulosa Brocchi, 1814: 309, pl. III, fig. 15.

Sveltia lyrata – Sacco 1894: 59.

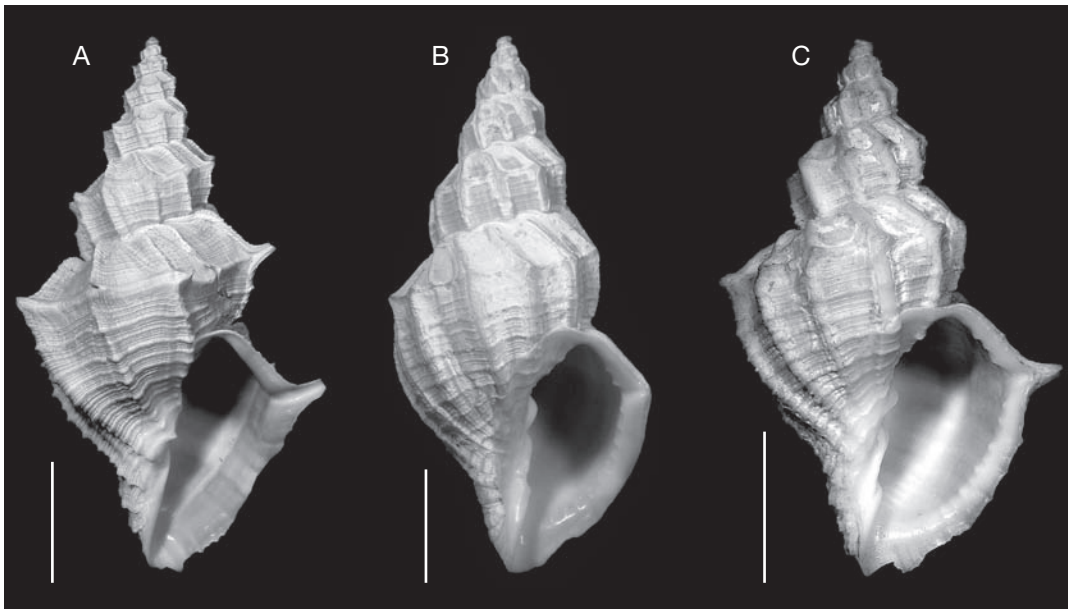

FIG. 41. — *Sveltia lyrata* (Brocchi, 1814): **A**, Mauritania, NW of N'diago, 17°57'N, 16°38'W, continental flat, 200 m (MNHN); **B**, Senegal, St. Louis, 600-1000 m (MNHN); **C**, Namibia, Cape Frio, 300 m (AV 0060). Scale bars: 10 mm.

Cancellaria turricula Lamarck, 1822: 116 (*fide* Deshayes 1843: 419).

Narona (*Sveltia*) *lyrata* – Davoli 1982: 46.

TYPE MATERIAL. — Brocchi (1814: 311) did not mention the number of shells on which his new species is based. He mentioned six localities, all Pliocene (Garassino *in litt.*), and commented on the carina in "alcuni individui" (some individuals), thus clearly indicating more than one type shell; no holotype was selected. Rossi-Ronchetti (1955: 270) figured and fully described shell MSNM no. inv. 89 as "holotype". The Brocchi collection in MSNM holds two shells, indicated (Pinna & Spezia 1978: 169) "holotype" (no. i 4850, same shell as Rossi-Ronchetti's inv. no. 89) and "paratype" (no. i 4851). Based on the Brocchi publication the type statements by cited authors are unfounded; moreover they do not agree with the *Code* (ICZN 1999: arts 74.5, 74.6) for lectotype designation. Consequently, the two shells MSNM no. i 4850, 4851 are syntypes. They are both labeled "Parlascio" (Garassino *in litt.*).

In order to clarify the type locality, specimen MSNM no. i. 4850, with dimensions 42.3 × 20.5 mm, is here designated lectotype; MSNM no. i 4851 becomes paralectotype. The lectotype was figured as "olotipo" by Rossi-Ronchetti (1955: 255) and by Pinna & Spezia (1978: pl. LXIV, figs 2, 2a), and has the number "89" (if the shell is viewed like in Brocchi's pl. III figure 6) written on the anterior outer part of the last whorl.

TYPE LOCALITY. — Brocchi mentioned six localities; the present lectotype designation fixes as type locality the Pliocene of Parlascio, Toscana, Italy. This agrees with the locality given by Rossi-Ronchetti (1955: 272).

MATERIAL EXAMINED. — **Mauritania.** 1 spec. (AV 0068). — NW of N'Diago, 400 m, 1 spec. (MNHN). — Off Cap Blanc, 280-350 m and 400-750 m, MAU, stns 60, 61, 132, 20 specs (RMNH).
Senegal. Off N'Gor, 100 m, sandy mud, 2 specs (RMNH). — Off Cap Vert, 170-200 m, 2 specs (MNHN). — St. Louis, 80-100 m, 1 spec. (AV 1121). — 300-400 m, 1 spec. (AV 0817). — 600-1000 m, 14 specs (MNHN).
Guinea. Baie Sangarea, NO *André Nizéry*, SEDIGUI I, stn 322 CH, 9°42'N, 16°27.5W, 189 m, 1 spec. (MNHN).
Ivory Coast. Abidjan, 1 spec. (AMNH 183182).
Ghana. ATLANTIDE stn 84, 5°37'N, 0°35'E, 150-175 m, 1 spec. (ZMUC).
Congo. Off Pointe Noire, 300 m, 2 specs (MNHN); 1 spec. (ZMA).
Angola. ATLANTIDE stn 135, 7°55'S, 12°38'E, 235-460 m, 1 spec. (ZMUC). — Off Ambriz, 30 m, 1 spec. (AV 0066).

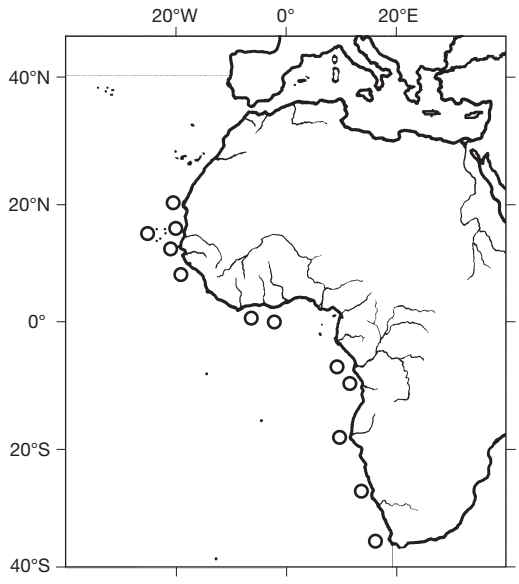

FIG. 42. — Distribution of recent *Sveltia lyrata* (Brocchi, 1814).

Namibia. Cabo Frio, 144-300 m, 5 specs (AV 0060-0062, AV 0064, AV 0069); 1 spec. (MNHN).
South Africa. Off Cape Town, "trawled in deep water", 1 spec. (AMNH).

DISTRIBUTION (Fig. 42). — Recent: from Mauritania to Cape Town, South Africa, between 30 and 1000 m. Moreover, material is cited from off Senegal, Maio, Cape Verde Islands, 628 m (Dautzenberg & Fischer 1906: 17); Ivory Coast, 313-366 m (Graham 1966: 134); Zaire: off Banana, 145-230 m (Adam & Knudsen 1955: 16); Namibia: off Lüderitzbucht, Fisheries Survey vessel *Africana* (Barnard 1959: 12), to 174 m (Kensley 1973: 194). Fossil: Miocene: continental Europe; Pliocene: Mediterranean Basin (Davoli 1982: 47-48); Pleistocene: no records (Malatesta 1974: 372).

DESCRIPTION

Shell pale brownish, biconical, with conspicuous spines on the axial ribs at the carina of the whorls. Dimensions up to 56.6 mm high and 29.3 mm wide.

Protoconch (Fig. 65E, F): multispiral with 2 1/2 smooth, naticoid whorls, sutures impressed; its axis clearly deviated from teleoconch shell axis. Maximum diameter 1.3-1.4 mm, exposed height 1.1 mm.

Teleoconch with up to about seven strongly keeled whorls. Axial sculpture: 8-10 strong, narrow ribs, forming sharp long spines at the keel. Spiral sculpture less pronounced: on the posterior part of the whorls, fine bands of about equal strength; on the anterior part: up to the penultimate whorl, generally two spirals, with between them one secondary spiral and 1 or 2 spirals of third order. Last whorl may have solid pointed spines on the crossing-over of axial ribs and carina. Aperture oblong, with a relatively long siphonal canal. Two strong columellar folds, posterior one the strongest, and a third, faint one on the edge of the siphonal canal. Number of lirae inside outer lip: none, or 12-15. No umbilicus.

Sometimes, the ribs and spiral line at the carina are paler in colour than the rest of the shell. There is also a paler colour band at half height on the anterior part of the body-whorl.

The soft parts have been described by Adam & Knudsen (1955: 18). Graham (1966: 140), mentioning the external features of *Bivetiella cancellata* and *S. lyrata* animals, states that "there are no points in which the two species seem to be significantly different from one another".

REMARKS

This is the largest living eastern Atlantic cancellariid. In most shells, the protoconch is missing and the early teleoconch whorls are heavily corroded, so that the number of whorls cannot be counted exactly. A large number of shells have repaired breaks, suggesting unsuccessful predation. CANCAP stn 2.060, off Mauritania, where four of the seven shells were taken alive, may give an idea of the habitat of this species: "400-750 m, canyon slope, macrourids, pennatulids, crabs, gastropods, asteroids".

A single shell was trawled off Cape Town (AMNH), but Lussi *et al.* (2004: 11) state that this species does not form part of the South African fauna.

This species is rather common in Miocene and Pliocene strata of Central and Southern Europe. In 1901 the first (broken) recent shell was found off Maio, Cape Verde Islands, 628 m (Dautzenberg & Fischer 1906: 17). The first specimens taken alive were described by Adam & Knudsen (1955: 16, pl. 19, fig. 4), who also figured the optical microscopic aspect of the radula, as did Barnard (1958: 243). Recent shells with a protoconch in relatively good condition are rarely found; the protoconch

of both fossil (Davoli 1995: pl. 3, figs 1a, b, 4) and recent shells is multispiral (Fig. 65E, F). Although questioned by Old (1968: 288), there is no doubt that recent and fossil specimens belong to the same species; generally the recent shells are thinner. The correlation line for recent shell height/width data (Fig. 43) is very close to those for two sets of Miocene shells studied by Davoli (1982: 48): the general shell form of this species has changed very little from the Miocene until now. The fossil shells, almost without spines, give a higher correlation factor ($r^2 = 0.96$, $p < 0.005$ for each fossil set) than the recent ones ($r^2 = 0.89$, $p < 0.005$).

Sveltia spinulosa (Brocchi, 1814) is accepted by most authors as a synonym of *S. lyrata*; the precedence of the latter name was established by Michelotti (1847: 223), acting as first reviser.

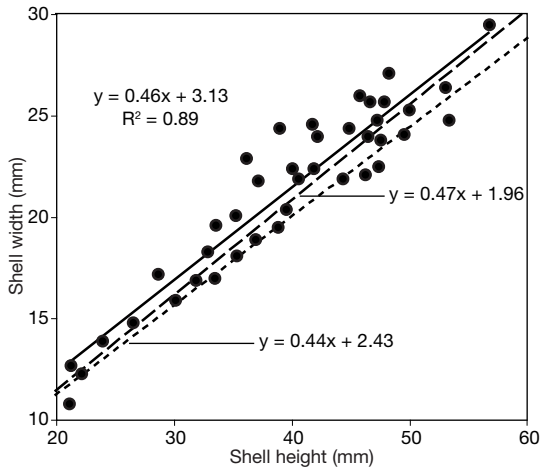

FIG. 43. — Dispersion diagram and linear correlation line for shell dimensions of *Sveltia lyrata* (Brocchi, 1814) (●); and linear correlation lines for fossil shells from the Miocene (Tortonian) from Montegibbio (dotted line) and Tortona (dashed line), Italy (after Davoli 1982: 48, fig. 14).

Genus *Tribia* Jousseaume, 1887

Tribia Jousseaume, 1887: 221.

TYPE SPECIES. — *Cancellaria angasi* Crosse, 1863, Recent, West Africa (by original designation).

REMARKS

Differences between *Sveltia* and *Tribia*, as indicated in their original descriptions, are given in Table 2. Notes: the sculpture of *T. angasi* can also be spirally striated, although generally less than in *Sveltia*. Anterior channel: not very pronounced in both groups. The difference in columellar side is rather unclear, especially given the size differences of mature shells. Callus: difference very unclear. Conclusion: only the form of spire whorls and aperture, and the columellar folds give a meaningful differentiation between *Sveltia* and *Tribia*.

Tribia angasi (Crosse, 1863)
(Figs 44; 49; 61A, B)

Cancellaria angasi Crosse, 1863: 64, pl. 2, fig. 8.

Tribia angasi – Jousseaume 1887: 221.

Cancellaria eudeli Sowerby, 1893: 27.

Cancellaria (*Tribia*) *uniangulata* – Dautzenberg 1910b: 210 (non *Cancellaria uniangulata* Deshayes, 1830).

TYPE MATERIAL. — Lectotype, here designated: BMNH 1896.12.I.II, 14.7 × 8.4 mm (Fig. 44A). This shell was labelled "holotype", but Crosse's description does not allow this conclusion since it does not state nor imply the presence of only one shell (ICZN 1999: Recommendation 73F). This lectotype designation is necessary in order to clarify the taxonomic position of *T. angasi*, especially in relation to *T. coronata* Scacchi, 1835.

TYPE LOCALITY. — Unknown to Crosse; restricted to Gorée, Senegal, by Dautzenberg (1891: 16).

MATERIAL EXAMINED. — **Mauritania.** Cansado, 6-8 m, Mission Gruvel, 5 specs (KBIN). — Off Banc d'Arguin, MAU stn 122, 20°27'N, 17°15'W, 32 m, 1 spec. (RMNH).
Senegal. Dakar Port, 2 specs (MNHN). — Baie de Rufisque, 18-37 m, 2 specs (HUJ); 1 spec. (RMNH); 1 spec. (NMWZ); 1 spec. (AV 0050); 1 spec. (AV 0578). — Baie de Gorée, 1 spec. (BMNH); 2 specs (MNHN); 1 spec. (AV 0049); 2 specs (AV 0051). — Petite Côte, 27-32 m, 2 specs (MNHN). — Cap Vert, 4 specs (MNHN).
Sierra Leone. ATLANTIDE stn 49, 07°29'N, 13°38'W, 74-78 m, 1 spec. (ZMUC).

DISTRIBUTION (Fig. 45). — Mauritania, Senegal, Sierra Leone, 6-78 m. A shell from the Alboran Sea, 220 m, figured under the name *Narona coronata* by Ardovini & Cossignani (1999: 66) is a *T. angasi*, but this locality should be confirmed by more specimens.

TABLE 2. — Differences between *Sveltia* Jousseaume, 1887 and *Tribia* Jousseaume, 1887, as indicated in their original descriptions.

	Sveltia	***Tribia***
Sculpture	costulated and striated	costulated
Spire	convex	largely flattened near the suture
Aperture	suboval	subtriangular
Anterior channel	superficial indenting of peristome	indenting extremity of peristome
Columellar side	bending obliquely abaxially	straight, thin
Columellar folds	two, rather sharp	three, weak
Callus	rather thin, continuing on columellar border	rather thick, not outside aperture

DESCRIPTION

Shell small, elongated, with turriculate and scalate spire. Dimensions: up to 18.7 mm high and 9.7 mm wide (Senegal, Rufisque; RMNH). Colour white to pale brownish, sometimes with a single or double pale-brown spiral band at about 1/3 of the height of the whorl, and one on the last whorl, just posterior to the second carina; narrow dark brown blotches near the suture between the axial ribs on the posterior part of the whorl.

Protoconch paucispiral, fawn to pale brown, slightly inclined with respect to teleoconch axis, almost without sculpture, sometimes a few faint growth lines (Fig. 61A, B). Number of protoconch whorls: $\bar{x}$ =1 3/8 (σ = 1/8, n = 34), max. diameter: $\bar{x}$ = 0.88 mm (σ = 0.07, n = 34), max. visible height $\bar{x}$ = 0.96 mm (σ = 0.09, n = 32).

Teleoconch with up to 5 1/4 whorls. Suture deeply impressed. Axial sculpture very marked; number of axial ribs on 1st-5th whorl: 1st, $\bar{x}$ = 10.88 (σ = 0.71, n = 34); 2nd, 9.74 (σ = 0.89, n = 34); 3rd, 9.38 (σ = 0.94, n = 29); 4th, 9.44 (σ =1.82, n = 15); 5th, 5 (n = 3). Spiral sculpture mostly rather diffuse, especially on the younger whorls; number of spiral ridges (including secondaries) on 1st-4th whorl: 1st, $\bar{x}$ = 3.85 (σ = 0.53, n = 27); 2nd, 5.17 (σ = 1.17, n = 29); 3rd, 8.32 (σ = 2.85, n = 22); 4th 9.16 (σ = 2.99, n = 6). However, two spirals are well marked: the one on the shoulder of the whorl is narrow but relatively high; and the spiral in the prolongation of the sutural line on the body-whorl is quite conspicuous (Fig. 44): this may confer to the aperture a somewhat trapezoidal from. The spirals are best visible when crossing the axial ribs; in the areas between these ribs they are often very faint. The teleoconch has a microsculpture of tiny pits (Fig. 58B).

Aperture trigonal to trapezoidal; no lirae inside outer lip; no parietal teeth. Columella straight, parallel to shell axis, with two folds (which may be brown), posterior one the strongest. The rim of the siphonal canal might be interpreted as a third fold (the original description of *Tribia* mentions "trois plis peu saillants"); in young shells this rim almost coincides with the anterior fold. Siphonal fasciole poorly developed. Umbilicus closed in younger specimens, in older ones it is half covered by a whitish to brownish callus.

As far as could be judged on a dried specimen, the animal had the foot speckled with reddish-brown dots.

REMARKS

This species has sometimes (e.g., Nicklès 1950: 116; Malatesta 1960: 188) been referred to as *Tribia uniangulata* (Deshayes, 1830), the name of a Neogene fossil from e.g., Northern Italy. Crosse (1863: 65) mentioned the resemblance, but did not specify a difference, except possibly the double carina of *T. angasi*. Study of several specimens of *T. uniangulata* in European museums has shown that this fossil species has a multispiral protoconch, it grows much larger (up to 25 mm), and has a much more solid shell than *T. angasi*.

Tribia coronata also bears a rather close resemblance to *T. angasi*, especially in the juvenile state when the whorls of *T. angasi* have more a *coronata*-like profile but lack the coronations shown in Figure 46D. Recent shells collected in the Mediterranean, reported by Dautzenberg (1910b: 210) as

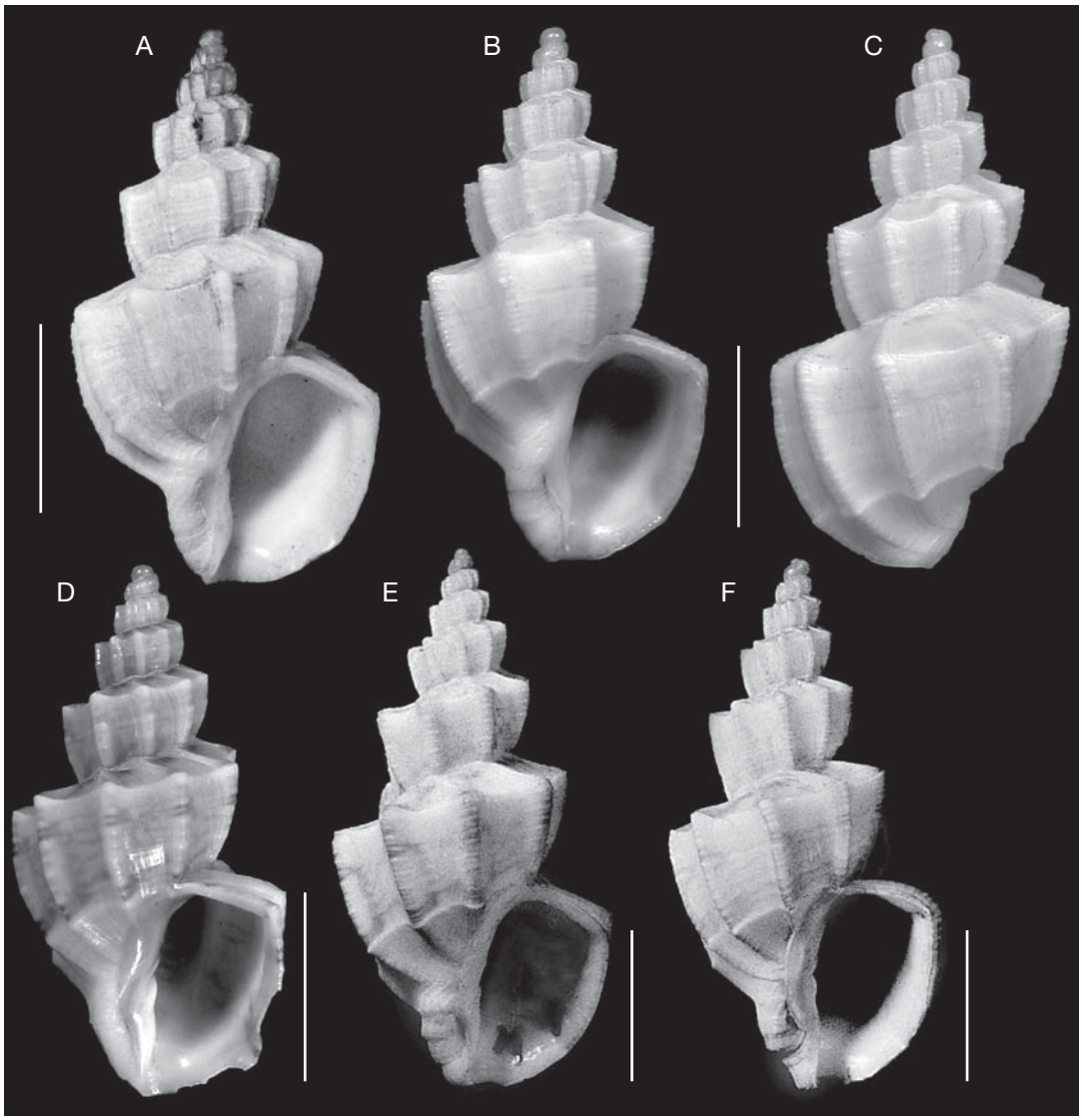

FIG. 44. — *Tribia angasi* (Crosse, 1863): **A**, lectotype, locality unknown (BMNH 189612111); **B**, **C**, shell showing second carina, Gorée, Senegal (MNHN, ex colln Jousseaume); **D**, fresh shell with colour pattern, outer lip slightly chipped, Senegal, Joal, 10-20 m (MNHN); **E**, Senegal, Baie de Rufisque (RMNH, ex Mulder colln); **F**, syntype of *Cancellaria eudeli* Sowerby, 1893, locality statement: "Penang, Malaysia" (NMWZ 1955.158.1429, ex Melvill-Tomlin colln [McAndrew]). Scale bars: 5 mm.

T. uniangulata and also as *T. angasi* (1910a: 32), are in fact *T. coronata* (see below).

In the more than 40 shells seen, the spiral sculpture was found to be very variable: some have very weak spiral striae, only visible when crossing the axials; others have a rather strong spiral sculpture, clearly visible in the area between the axials.

Cancellaria eudeli Sowerby, 1893 is to all evidence a name introduced for a shell of *T. angasi* with the incorrect statement of type locality "Penang,

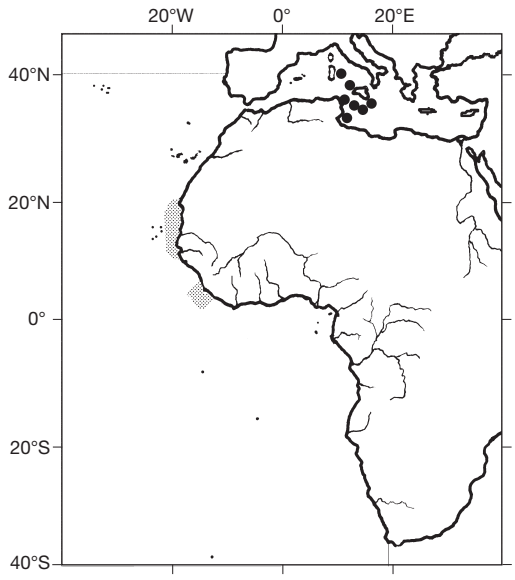

FIG. 45. — Distribution areas of *Tribia* species of western Africa: *T. angasi* (Crosse, 1863) (grey areas); and *T. coronata* (Scacchi, 1835) (●).

Malaysia" (see Verhecken 1986a: 61). The label of the single syntype (NMWZ 1955.158.1429; Fig. 44F) states "unique", but this is not mentioned in the description; its dimensions are 18.4 × 9.5 mm (description: 20 × 9 mm). Sowerby (1893: 27) stated: "There is only one species which seems to bear anything like a close resemblance to *C. Eudeli*, viz., *C. Angasi* Crosse. With this species I am unacquainted, excepting from the figure and description [...]; its habitat is unknown". He gave as differences: "*C. eudeli* is one-fourth larger, has a proportionately longer and sharper spire, and the area between the angle and the suture is flatter, and not sloping". However, the largest shell here studied of *T. angasi* measures 18.7 mm (Fig. 44E); the relative height of the spire (39% of total shell height for *T. eudeli*) agrees completely with that of *T. angasi* shells of similar size. The statement that the sutural plane of the *T. eudeli* type is not sloping is incorrect (see Fig. 44F): it has the same slope as the *T. angasi* shells.

Consequently, there is no reason to separate both taxa, except for the locality statement, which is thought to be incorrect (see also Petit & Harasewych [2005: 49]). Sowerby (1893) gave no further details on collector, date, habitat or any other information allowing a verification; the NMWZ label shows this shell came from MacAndrew's (probably J. J., see Trew 1990: iii) collection, a not always reliable source of information. Sowerby (1893) also stated that the surface of the shell of *T. eudeli* is finely cancellated; this does not apply to the NMWZ shell: together with the dimensions and the slope of the sutural plane this raises doubts as to this shell being the Sowerby type.

The relation of this species with the Neogene fossil *Cancellaria uniangulata* is mentioned above.

Tribia coronata (Scacchi, 1835)
(Figs 46-49; 61C, D)

Cancellaria coronata Scacchi, 1835: 5, pl. 1, fig. 15; 1836: 34, 35. — Philippi 1844: 177, pl. 25, fig. 24 (error for 27).

Cancellaria taeniata Sowerby, 1849a: 137; 1849b: 445, pl. 95, figs 75-76.

Tribia coronata – Jousseaume 1887: 221.

Narona (*Tribia*) *coronata* – Sabelli 1969: 6, 7, fig. 3.

Narona coronata – Grasso 1985: 12.

Cancellaria (*Sveltia*) *coronata* – Micali & Quadri 2001: 170, figs 7, 8. — Cretella *et al.* 2005: 121, fig. 1b.

TYPE MATERIAL. — Very recently, Cretella *et al.* (2005: 121) designated a lectotype: Museo di Paleontologia dell'Università degli Studi di Napoli Federico II, Naples (M.17224), 12.5 × 6.1 mm (Fig. 47).
Syntype of *Cancellaria taeniata*: BMNH 1968412, 13.8 × 6.7 mm (Fig. 46A); the old label has on the back in handwriting: "Tunis – fide old coll. B. M.".

TYPE LOCALITY. — Italy, Puglia, Albanello near Gravina, "Pliocene inferiore"; but according to Malatesta (1960: 187) the species has never been found in Tertiary deposits; he includes the relevant deposits in the Calabriano (Quarternary).

MATERIAL EXAMINED. — **Sicily.** Off Capo Passero, 50-60 m, leg. S. Grasso, 1 spec. (REP 2277).
Near Tunisian coast. 90-180 m, 1 fragment (USNM 189699, Nares, Jeffreys colln). — Adventure Bank, 165 m, 4 specs (BMNH 1969431, see Sykes 1911: 332). — Gulf of Gabès, 2 specs (KBIN, Dautzenberg colln).

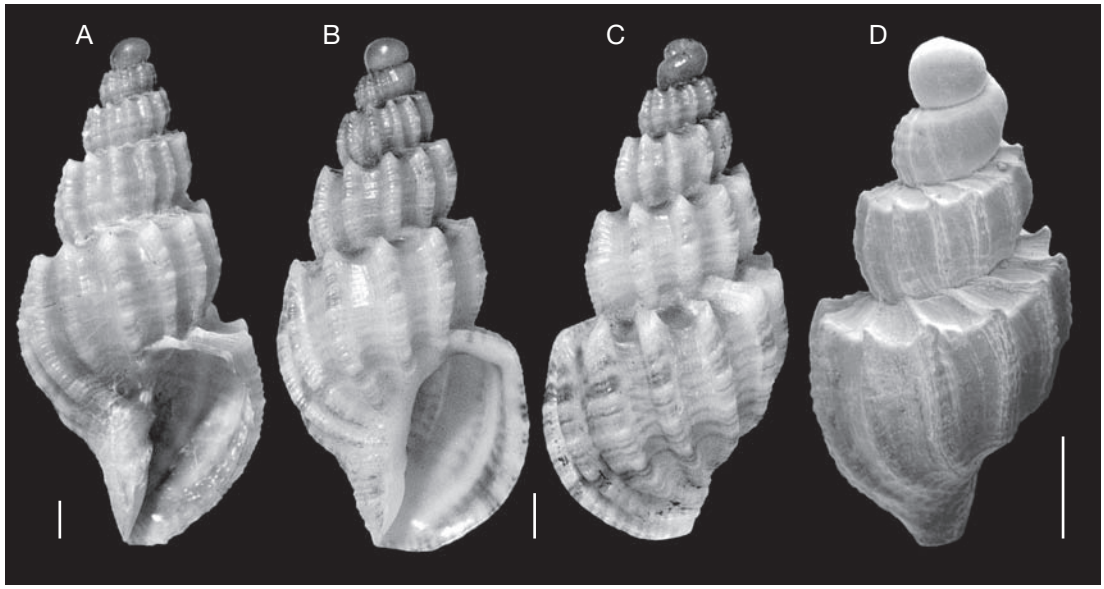

FIG. 46. — *Tribia coronata* (Scacchi, 1835): **A**, syntype of *Cancellaria taeniata* Sowerby, 1849, Tunis (BMNH 1968412); **B**, **C**, Sicily, off Cape Passero, 50-60 m (REP 2277); **D**, juvenile shell showing coronations, Adventure Bank, PORCUPINE, 165 m (BMNH 1969341/3). Scale bars: 1 mm.

Malta. 1 spec. (BMNH, Cuming colln, possibly the shell mentioned by Mamo *in* Caruana (1867: 49) and by Despott (1931: 94).

DISTRIBUTION (Fig. 45). — Central southern Mediterranean. Sicily, off Cape Passero: 1 spec. lv (Piani, in stomach of *Astropecten*: Grasso *in litt.*), 2 specs lv, 50 m, 85-90 m (Grasso 1985); off Palermo (D'Angelo & Gargiullo 1978: 148); off Lampedusa, 1 spec., 11 × 5.4 mm, in stomach of *Astropecten aurantiacus*, 70-100 m, 1975 (Spada *in litt.*); 5 specs d (Micali & Quadri 2001: 172); Malta, 16 km E of Malta (Caruana 1867: 49) and off Ras il-Qammieh and Popeye's Village, 60 m (Cachia *et al.* 2001: 45). Near Tunisian coast: Korba, 1 spec. lv (Sabelli 1969: 6) at 35-40 m (Grasso 1985: 13); Gulf of Gabès, 2 specs d (KBIN, Dautzenberg colln, labelled "*Cancellaria angasi* Crosse, éponges, colln. Bouvier").

Northern Mediterranean: Corsica, 1 spec. d, oriental plain off Campoloro Port, 30 m, Van Veen grab (Verneau *in litt.*).

A specimen from the Alboran sea, 220 m, is figured by Ardovini & Cossignani (1999: 66) under the name *Narona coronata*, but this shell is a *T. angasi*. Also the statement by Micali & Quadri (2001: 170) that "*Cancellaria* (*Sveltia*) *coronata*" is a species with prevalent Atlantic distribution (NW coast of Africa), very rare in the Mediterranean, must be based on the same confusion between the two recent *Tribia* species.

Bathymetry: 30-180 m.

The geographic range figured by D'Angelo & Gargiullo (1978: 148) as "Mediterraneo meridionale", from Gibraltar to Israel is not confirmed by the above data.

DESCRIPTION

Shell small, elongated; its slender appearance is stressed by its pronounced axial ribs. Dimensions 11.0 × 5.6 mm. Colour very pale brown, with lines of pale brown patches on the axial ribs: dark brown blotches on the sutural area between the axial ribs. The spiral lines are whitish.

Protoconch very pale brown, relatively large, paucispiral; consists of one whorl with a maximum exposed height of 1.2 mm and a maximum diameter (measured in a plane perpendicular to shell axis) of 1.1 mm. It has some very faint growth lines on the last half whorl; the first half is too eroded to show any delicate sculpture.

Teleoconch with four slightly rounded whorls; suture impressed, sutural ramp slightly sloping down outward. Axial sculpture starts abruptly at rim of protoconch; it consists of well defined ribs, width 0.5 mm; 12, 11, 10, 10 in number of 1st-4th

FIG. 47. — *Tribia coronata* (Scacchi, 1835), lectotype (MPN M.17224). Photo provided by P. Crovato, reproduced with permission. Scale bar: 5 mm.

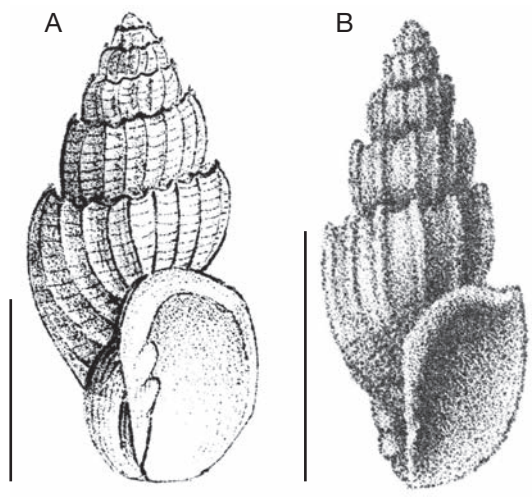

FIG. 48. — Literature figures of *Cancellaria coronata* Scacchi, 1835, reproduced at the same size: **A**, Scacchi 1835: pl. 1, fig. 15; **B**, Philippi 1844: pl. 25, fig. 27. Scale bars: 1 cm, referring to the size of the figures, not to the shell size.

teleoconch whorl respectively. Spiral sculpture of rather vaguely indicated spiral ribs: 5, 8, 11 in number on 1st-3rd teleoconch whorls and 25 on last whorl. The spirals are most prominent when crossing the axial ribs, especially on the younger whorls; they are only vaguely indicated in the area between the axials, where there is also a confuse axial growth-line pattern. Spiral cord near periphery is the most marked, but still not very conspicuous. The upper part of the axial ribs surmounts the sutural ramp, crossing it obliquely as a wedge ending adapically in a lamella with a slightly concave profile. The shoulder of the axial ribs forms a soft coronation.

Aperture rounded trapezoidal, height 5 mm, width 2.6 mm; no parietal tooth, no inner lirae on outer lip which is slightly flared out. Columella straight, with two rather oblique brown folds near its middle, contrasting with the white columella. The white rim of the siphonal canal might be interpreted as a third columellar fold. Umbilicus completely closed by a very thin columellar callus.

Dimensions: verified on shells: up to 14.5 × 7.3 mm (Grasso 1985); Nordsieck (1968: 151) repeats the height of 18 mm given by Scacchi, and D'Angelo & Gargiullo (1978: 148) mention 21 mm.

Lirations inside the outer lip of recent shells have also been reported (Parenzan 1970: 195).

The animal has been figured and described by Grasso (1985: 13, 14); it has a dotted colour pattern like *Bivetiella cancellata* and *Tribia angasi.*

REMARKS

The shell described here (REP 2277) is the only one in excellent condition seen by the present author. It was collected alive in 1980 off Capo Passero, Sicily, at 50-60 m on a "floor [which] is typically deep water coralligenous" (Grasso 1985: 14).

Because the original description of this species by Scacchi (1835) is difficult to obtain, it is here reproduced:

"98. Cancellaria coronata. *C. coronata.*

Testa ovato-oblonga; anfractubus (*sic*) *septem, costis longitudinalibus striisque transversis ornatis, prope suturas angulatis costarumque mucronibus coronatis; columella biplicata, subumbilicata; labro surperne angulato intus striato; alta lin: 8*.

Questa cancellaria facilmente si riconosce per l'angolo che ciascun giro della sua spira ha superiormente presso le commissure, e per le coste longitudinali le quali dove toccano l'angolo si prolungano in tante punte elevate, che a somiglianza di corona circondano la parte superiore degli anfratti. Questi poi oltre alle coste longitudinali sono ornati di sottili strie trasversali, e nella parte che rimane interposta fra l'angolo e la commissura, le coste si continuano in tante piccole piegature e mancano le strie trasversali. L'apertura e inferiormente scanalata, il labro destro superiormente angoloso e nell'interna superficie striato, la colonnetta ha due piegature internamente, al di fuori ha un piccolo ombelico ed è ornata di strie oblique".

The 1836 reprint was reset and differs from the 1835 text only in a few minor typographical details.

The name *Cancellaria coronata* Scacchi, 1835 was introduced for a fossil from southern Italy, and has been used in publications for a number of fossil shells. However, the paleontological literature shows that most of these identifications were disputed by subsequent authors. Also, practically all identifications of the fossil shells were based on a figure given by Philippi (1844: pl. 25, fig. 27; here Fig. 48B) and not on Scacchi's figure (1835: pl. 1, fig. 15; reproduced here Fig. 48A) which was published in an obscure Italian journal and remained practically unknown. The figure of *Cancellaria coronata* given by Philippi (Fig. 48B) is rather different from that figured by Scacchi (Fig. 48A). No relevant material figured by Philippi is extant in Berlin Museum (Aberhan *in litt.*). Only very recently the existence of a single shell from Scacchi's collection has become known; it was selected lectotype by Cretella *et al.* (2005), who kindly provided a photograph (Fig. 47). Based on the measurements, this is not the shell figured by Scacchi: it is 12.5 mm high, versus "alta lin: 8" (about 19 mm) indicated by Scacchi; in form it seems intermediate between the cited figures given by Scacchi and Philippi. Instead of the strong columellar folds in Scacchi's figure, the photograph of the lectotype shows very weak folds, as does Philippi's figure. Discussion of the fossil species is not the subject of this paper; in the present context it is only of importance that the recent shells are very much alike the lectotype in general form, sculpture and columellar folds. Only the spiral sculpture of the lectotype is somewhat stronger than on the shell described here.

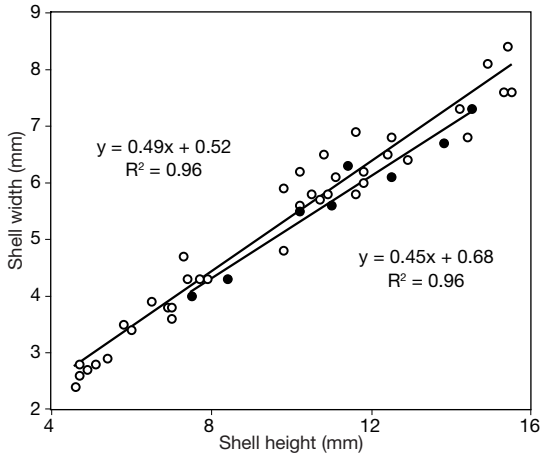

FIG. 49. — Dispersion diagram and linear correlation line for shell dimensions of *Tribia angasi* (Crosse, 1863) (○) and recent *T. coronata* (Scacchi, 1835) (●).

Compared to the recent shells, Scacchi's (1835) figure 15 has the whorls slightly more rounded; and especially the number of axials ribs (7, 9, 10 on last three visible *half* whorls) is higher. The figure also shows two strong columellar folds, a strong siphonal fasciole bordering an umbilical slit, whereas the recent shells have two small folds deep in the aperture, have hardly any fasciole, and no umbilical slit at all.

The photograph of the lectotype of *C. coronata* (Fig. 47) shows a shell tending to *Sveltia* rather than to *Tribia*; however, further study of the cancellariid genera is needed to shed more light on its correct generic classification. Provisionally, *C. coronata* is here left in *Tribia* where it was placed by Jousseaume (1887: 221) when creating this genus.

This Quarternary species is the only endemic Mediterranean cancellariid known. According to

TABLE 3. — Shell characters differentiating *Tribia angasi* (Crosse, 1863) and *T. coronata* (Scacchi, 1835).

	T. angasi	*T. coronata*
Suture	deeply impressed	impressed
Sutural area	sloping down outward	almost horizontal
Whorl side profile	almost straight	slightly convex
Axial ribs	distant	more close-set
Second carina	present	none
Shell colour	white to pale brownish	pale to brownish red

Malatesta (1960: 188) it may be the successor in the Mediterranean of the Mio-Pliocene *T. uniangulata*, while the latter species disappeared from the Pleistocene and Recent Mediterranean but survives off Mauritania and Senegal. Obviously, Malatesta refers here to *T. angasi.* Differences between *T. uniangulata* and fossil *T. coronata* are given by D'Ancona (1872: 138), Cerulli-Irelli (1911: 230), Malatesta (1960: 187), Davoli (1982: 54) and Micali & Quadri (2001: 172); but it must be stressed that many published identifications of these fossil shells have been disputed by subsequent authors. This extensive confusion in the literature is probably due to the fact that only very few authors saw the obscure Scacchi publication.

Caruana (1867: 49), with reference to Philippi only, was the first to report a recent (crabbed) shell from the Mamo collection, Malta. It may well be the shell now in BMNH, ex Cuming colln, labelled "unique, only described as fossil, M.C., Malta" because of the "very intimate relations in which he [Mamo] stood with many eminent conchologists and collectors of shells" (Caruana 1867: 7, 8), this no doubt included Cuming. A spire fragment (USNM 189699) dredged off Tunis Bay coast in 50-100 fathoms was reported by Jeffreys (1870: 83), with reference to Philippi only. Sykes (1911: 332) reported that the species was taken by the PORCUPINE 1870 expedition at Adventure Bank (between Sicily and Tunis), 166 m (BMNH 1969432). He gave as distribution area: "Several deep water localities in the Mediterranean", but without further details; he referred to both Scacchi and Philippi. The figures given by Tryon (1885: pl. 4, fig. 68), Löbbecke (1887: pl. 21, fig. 1) and Kobelt (1904: pl. 79, fig. 17) are based on the Philippi figure.

Two shells without locality data, labelled "*Cancellaria angasi* Crosse, éponges, colln. Bouvier" are in KBIN, Dautzenberg collection. Since there are no other *Tribia* shells from Dautzenberg with such data in KBIN nor in MNHN, they must be those referred to by Dautzenberg (1910b: 211) under the name *Cancellaria uniangulata*, writing: "Nous en possédons deux exemplaires actuels provenant des éponges du Golfe de Gabès (Bouvier)"; but also in the same year (1910a: 32) as *Cancellaria angasi*: "Méditerranée : éponges du Golfe de Gabès (collect. Dautzenberg)". These shells (8.4 and 7.8 mm high) are rather eroded and have the aperture broken, the smaller has at least a whole whorl broken away; but they can be differentiated from *T. angasi* by some of the characters given here, and most probably belong to *T. coronata*.

A single somewhat eroded empty shell (15 mm high), taken by Verneau in detritus at 30 m off Campoloro Port, Eastern Corsica, may indicate the presence of this species in the northern Tyrrhenian Sea, but only a *camera lucida* drawing was available for study.

Recent *T. angasi* and *T. coronata* cannot be distinguished on height/width data only (Fig. 49). Other differences, apart from their different distribution area, are given in Table 3.

The deeply impressed suture of *T. angasi* makes that, for a given whorl, the distance from shell axis to shoulder is larger than from axis to its anterior suture; in *T. coronata* these distances are about the same. This difference is rather striking (Figs 44; 46).

Many citations of Tertiary shells of *T. coronata* (if such shells exist, see Malatesta 1960) pertain to incorrectly identified *T. uniangulata*. Micali & Quadri (2001: 172) correctly state that *T. uniangulata* from the Italian Pliocene has a multispiral protoconch. But they add that this difference in protoconch with *T. coronata* is evident in both fossil (*T. uniangulata* and *T. coronata*) and recent specimens (*T. angasi* and *T. coronata*); however, *T. angasi* has a paucispiral protoconch (see above; and Fig. 61A, B).

Calcara (1845: 281), referring to the obscure journal *L'Occhio*, cited *Cancellaria costata* shells found in Sicily: living off Catania, and fossil near Palermo. But Calcara's findings, copied by Monterosato (1872: 32), have never been confirmed by new recent specimens, and the whereabouts of his material could not be traced. Carus (1893: 412) considered "*C. costata* Calc." related to *T. coronata*; but Aradas & Benoit (1870: 259, 260) mention them separately. Anyway, the name *Cancellaria costata* Calcara, 1845 is invalid as a junior primary homonym of *Cancellaria costata* Sowerby, 1822 (see above, under *Bivetiella cancellata*). The identity of *C. costata* Calcara is unknown; its locality and both fossil and recent occurrence may suggest it is *Tribia coronata*, but this cannot be proven now.

Cancellaria taeniata Sowerby, 1849, described without locality, was considered by Tryon (1885: 76) to be a juvenile *Cancellaria cooperii* Gabb, 1865; but study of Sowerby's syntype (BMNH 1968412; Fig. 46A) shows it is almost certainly a *T. coronata* (see Verhecken 1986a: 7; Petit & Harasewych 2005: 101). The spiral sculpture of this syntype is more pronounced than that of the *T. coronata* shell described here. But other shells of the latter species (e.g., the USNM fragment and the smallest Dautzenberg shell) also have a rather strong spiral sculpture, still clearly visible in the areas between the axial ribs.

Genus *Trigonostoma* Blainville, 1827

Trigonostoma Blainville, 1827: 652.

TYPE SPECIES. — *Delphinula trigonostoma* Lamarck, 1822 (= *Buccinum scalare* Gmelin, 1791), Recent, Indo-Pacific (by monotypy).

REMARKS

The generic placement of the species discussed here is not evident. Petit (1976, 1984) used *Trigonaphera* and *Scalptia* for the species described as *Murex scala* Gmelin, 1791, and stated (1976: 40) that a drawing given by Nicklès (1950: fig. 212) of the species here described as *T. gofasi* "appears to be a *Bivetopsia*"; but the current understanding of cancellariid genera does not warrant a fully founded choice.

Scalptia Jousseaume, 1887 (type species: *Cancellaria obliquata* Lamarck, 1822, by original designation, Indo-Pacific) originally included 30 species, varying from the ovoid type species to rather elongated species like *Cancellaria textilis* Kiener, 1841. This may be difficult to maintain on deeper study of cancellariid genera.

Trigonaphera Iredale, 1936 (type species *Trigonostoma vinnulum* Iredale, 1925, by original designation, from Australia) is distinguished from *Trigonostoma* by "its more compact form, less triangular mouth, which is not free and the minute perforation" (Iredale 1936: 319). Petit (1976: 42) while describing *Trigonaphera withrowi*, stated: "Placement in *Trigonaphera* is tentative pending a complete review of the genus". This remark is still valid today (see Materials and methods above).

The western American *Cancellaria goniostoma* Sowerby, 1832, which superficially looks like *C. rigida* Sowerby, 1832 (both species were often mixed up, see below), was placed in *Ventrilia* by Keen (1971: 658).

Regarding both species here studied, it might seem logical to classify in *Trigonostoma* the species (*T. gofasi* n. sp.) with an umbilicus open almost up to the top, and in *Trigonaphera* the species (*Murex scala*) with a narrower and shallower umbilicus. But for the rest these two species are alike superficially and have been mixed up until now; therefore their placement in different genera would be difficult to defend at present.

Recently Petit & Harasewych (2002: 131) provisionally included their newly described *Trigonostoma mozambicense*, from eastern South Africa, in this genus, commenting "there is some question as to its correct generic placement. The species with which it is compared [*Scalptia scala* (Gmelin, 1791), *Trigonostoma goniostoma* (Sowerby, 1832) and *T. brevis* (Sowerby, 1832); note by present author] appear to comprise a coherent group. Additional material and further study will be required to confirm the monophyly of this group, to define more precisely the limits and relationships of the genera *Trigonostoma* and *Scalptia*, and to determine the relationship of this group to these genera". The same remarks apply to the two species studied here; therefore the present use of the genus *Trigonostoma* is provisional.

Cited authors mention among the features that have been used to diagnose *Trigonostoma*: two columellar folds, a straight columella, an umbilicus. However, large shells of *Scalptia scala*, *T. scalare* and *T. breve* do have a weak anterior third fold at the rim of the siphonal canal, and the columellar lip curves abaxially in *S. scala*, *T. scalare* and *T. goniostoma*. Therefore, it seems justified to include also *Murex scala* in *Trigonostoma*.

The two western African trigonostomids are mainly known from moderate depths (to 60 m).

Trigonostoma gofasi n. sp.
(Figs 50; 62)

Cancellaria rigida – Dautzenberg 1910a: 31, pl. 1, figs 19, 20 (non *C. rigida* Sowerby, 1832). — Nicklès 1950: 116, fig. 212 (*ibid.*).

?*Trigonostoma goniostoma* – Caricati 1973: 237, pl. 4, figs 3, 4.

TYPE MATERIAL. — Holotype: Angola, Ilha de Luanda, dredged in 40-60 m, 1981-1982, S. Gofas, 16.4 × 14.3 mm (MNHN Moll 9497) (Fig. 50A).
Paratypes 1-4, same data as holotype: 1) 17.4 × 15.0 mm (Fig. 50B); 2) 15.9 × 13.9 mm; 3) 13.7 × 12.5 mm; 4) 12.4 × 11.5 mm (MNHN Moll 9494). — Paratypes 5-7, Mauritania, Bilaouak, Mission Gruvel 1908: 5) 23.7 × 18.5 mm, shell figured by Dautzenberg (1910a) and by Nicklès (1950) as *C. rigida* (MNHN Moll 9495) (Fig. 50F); 6) 21.9 × 18.9 mm (KBIN) (Fig. 50E); 7) 21.8 × 17.5 mm (KBIN) (Fig. 50G). — Paratypes 8, 9, off Mauritania: 8) 13.9 × 10.9 mm, 19°05'N, 16°25'W, 20 m, MAU stn 50 (RMNH 56931); 9) 14.1 × 11.4 mm, 19°05'N, 16°25'W, 12-18 m, MAU stn 49 (RMNH 56932). — Paratype 10, Senegal, Baie de l'Ouest, Mission Gruvel 1911-1912, 16.9 × 14.0 mm (KBIN) (Fig. 35H). Paratype 11, Ivory Coast, Abidjan Region, continental flat, ORSTOM, dredged NO *Reine Pokou*, 1965-1977, 23.1 × 19.3 (MNHN Moll 9496) (Fig. 50C).

TYPE LOCALITY. — Ilha de Luanda, Angola, 40-60 m, gravel and rocks.

ETYMOLOGY. — Named in honour of Dr Serge Gofas (formerly MNHN, now Málaga University) who collected part of the type material.

MATERIAL EXAMINED. — The type material, and 16 more specimens:
Senegal. Baie de l'Ouest, Mission Gruvel 1911-1912, 10 specs, all juveniles, but quite eroded (KBIN).
Mauritania. Off Cap Blanc, crabbed and partly broken, MAU stn 04, 20°47'N, 17°02'W, 15 m, sandy mud, 1 spec., 15.8 × 13.9 mm (RMNH).
Liberia. Garraway, leg. Jullien, 3 juvs, mostly juveniles (KBIN).
Ivory Coast. Abidjan area, 60 m, Le Loeuff/ORSTOM, 1spec. (MNHN).
Ghana. Tema Bay, 1 spec. (ZMUC) (Fig. 50D).

DISTRIBUTION (Fig. 52). — Three discrete areas are known: Angola; Liberia to Ghana (northwestern Gulf of Guinea); Senegal and Mauritania.
Bathymetry: between 12 and 60 m.

DESCRIPTION

Holotype: shell 16.4 × 14.3 mm; colour light brownish.

Protoconch (Fig. 62) multispiral, with 2 1/4 whorls (including a brown nucleus of 0.5 whorl, maximum diameter 0.4 mm), exposed height 0.9 mm, maximum diameter 1.1 mm. Protoconch vaguely delimited by start of teleoconch spiral sculpture.

Teleoconch with 4 1/8 whorls. Sculpture on first teleoconch whorl is mainly spiral: two strong spiral cords, a minor one and a strong one at the shoulder. Axial sculpture is hardly discernible. From the second teleoconch whorl on, an axial sculpture of broadly rounded ribs develops, forming pointed coronations (but very often eroded in older shells) on the shoulder of younger whorls. On the body whorl, the axial ribs have a squamose aspect because of the multiple lamellae they are formed of. Sutural ramp (narrower than in *T. scala* n. comb.) bordered on the shoulder by a raised spiral ridge. The axial ribs, on crossing over the sutural ramp, form broad ridges composed of several lamellae reflected adapically on the upper part of the ridges. Near the sutural line, the height of these ridges is almost zero, so that a narrow groove is left between the ridge and the sutural line. Spiral sculpture on later spire whorls consists of three broad bands, with three secondary spirals in between; the second main spiral forms a small carina on the whorl. The last whorl has, apart from a very broad compound spiral band at the shoulder, six primary spirals and 3 or 4 secondaries in between.

Aperture rounded trigonal. Columellar side smooth; two columellar folds (posterior one the strongest), and a very faint one at the rim of the

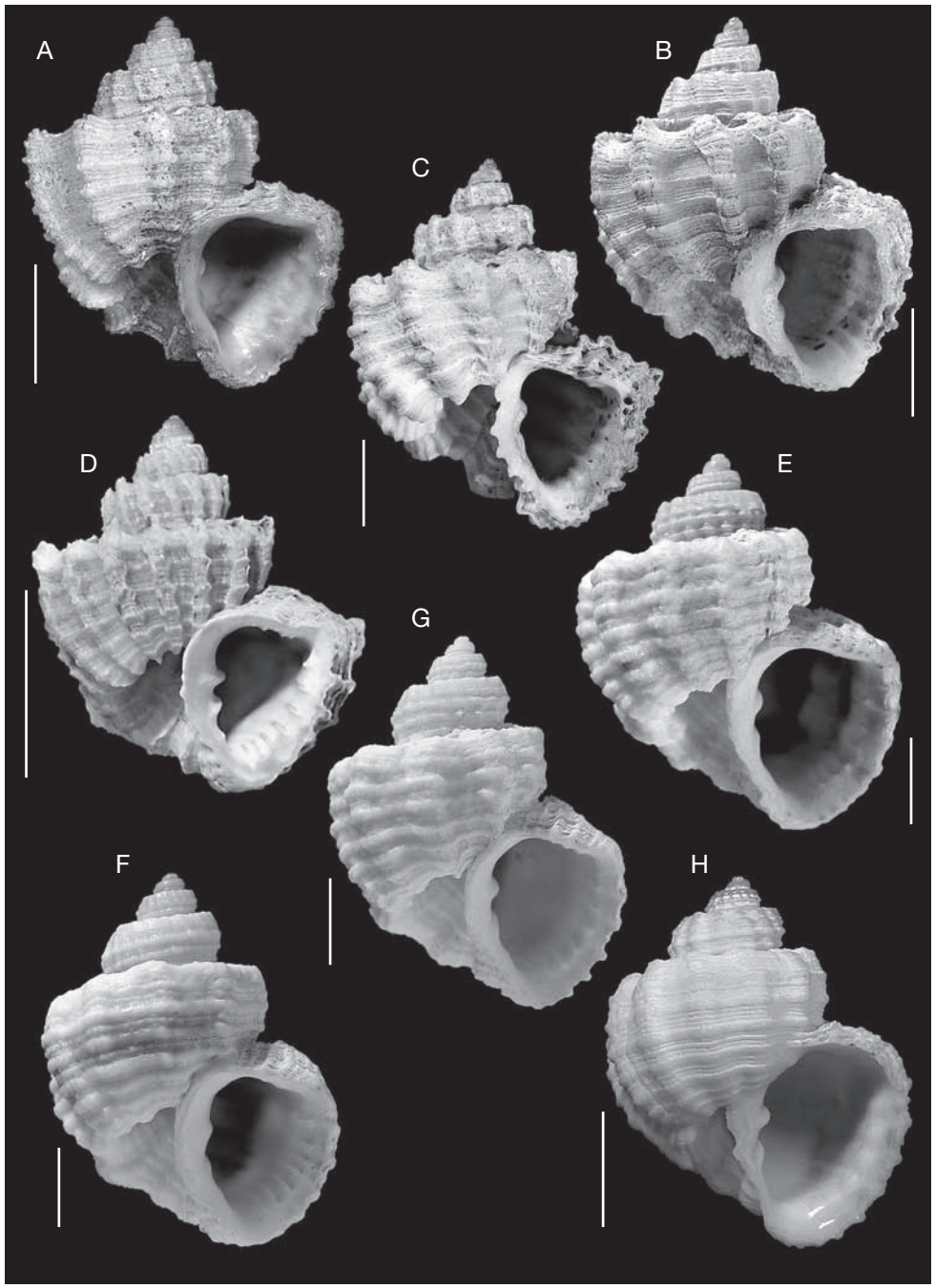

FIG. 50. — *Trigonostoma gofasi* n. sp.: **A**, **B**, Angola, Ilha de Luanda, 40-60 m; **A**, holotype (MNHN); **B**, paratype 1 (MNHN); **C**, **D**, Gulf of Guinea; **C**, paratype 11, Ivory Coast, Abidjan Region, continental flat, ORSTOM, dredged NO *Reine Pokou*, 1965-1977 (MNHN); **D**, Ghana, Tema Bay, 27 m (ZMUC); **E**-**G**, Mauritania, Bilaouak, Mission Gruvel 1908; **E**, paratype 6, Bilaouak (KBIN); **F**, paratype 5, shell figured by Dautzenberg (1910: pl. 1, figs 19, 20) and Nicklès (1950: 116, fig. 212) (MNHN); **G**, paratype 7, Bilaouak (KBIN); **H**, paratype 10, Senegal, Baie de l'Ouest, Mission Gruvel 1911-1912 (KBIN). Scale bars: 5 mm.

vaguely indicated siphonal canal. Outer lip with seven inner lirae; three small parietal teeth on the truncated posterior side of the aperture. Umbilicus widely open almost to the top of the shell; umbilicus depth in function of total shell heigth: $\bar{x}$ = 87% (σ = 4, n = 10).

The largest shell seen, from Mauritania, measures 23.7 × 18.5 mm.

Remarks

Although some of the type specimens (paratypes 5-7, 10) have been known since 1910, they had not yet been formally recognised as a distinct species. This is probably due to the confusion about the western African trigonostomids (cf. Dautzenberg 1910a: 32), and to the scarcity in most collections of material from that region. Only Petit (1976: 40), referring to the figure given by Nicklès (1950: 116, fig. 212), commented on it as "a shell quite distinct from [*T. withrowi*], and appears to be a *Bivetopsia*". The genus *Bivetopsia* Jousseaume, 1887 (type species: *Cancellaria chrysostoma* Sowerby, 1832, by subsequent designation [Cossmann 1888: 784]) has a straight vertical columella with three rather sharp folds, no sutural plane, strong rounded axial ribs and the whorls more rounded than in the species under discussion.

As evidenced by the material now at hand, the species occurs in three (apparently isolated) areas: off Mauritania-Senegal (in the NAR), the North-West coast of Guinea Gulf (in the ATR), and Angola (in the SAR). This distribution pattern suggests a relation between occurrence and hydroclimatic region.

The protoconch surface microsculpture of the Mauritania-Senegal and Liberia shells consists of a great number of slightly elongated nodules about 10 µm long, with a lobed periphery (Fig. 62C). This sculpture remains, even on eroded shells, in protected areas near the protoconch suture.

The best preserved shells are those from Angola: they have an intact multispiral protoconch, clearly distinct from *T. scala* n. comb. paucispiral one, and a rather triangular cross-section of the whorls, with small spines at the shoulder of juvenile shells.

Some shells taken by the Gruvel Mission (1 spec. [MNHN], labelled "*Cancellaria rigida*, figd. Dautzenberg 1910a pl. 1 figs. 19-20" and 2 specs [KBIN], labelled "*Cancellaria costata* Gray") are larger than the Angolan shells but possibly more eroded; this may have resulted in the more rounded outline and different colour: whitish to banded brown (Fig. 50F-H). These three shells are labelled "Mission Gruvel 1908, Bilaouak": this locality is Marsa (former Portandick), N of Nouakchot, Mauritania. Dautzenberg (1910a: 32) cites only two shells from Bilaouak (1908 campaign), but also one for the Gruvel 1909 campaign from "Baie de Rufisque, 18-20 m" which is in Senegal. Dautzenberg (1912: 17) mentioned *C. rigida* also in the report of the Mission Gruvel 1909-1910, but gave no locality there.

Extensive Dutch collecting activity off Mauritania and Senegal resulted in only three shells of this species.

Differences between the Bilaouak and Angola shells are: the rounded whorls of the former, versus the whorls with a much more triangular cross-section and a whitish shoulder carina for the latter. However, this difference may at least partly be due to the more eroded condition of the Bilaouak shells; moreover, material at hand is as yet insufficient to justify a further splitting at species level. But the graph "width versus height" of all known shells from the three areas yields points with a linear correlation (r^2 = 0.98, $p < 0.005$) showing that no distinction can be made based on these data (Fig. 55, black dots).

The shells studied from the Guinea Gulf (Ivory Coast and Ghana) are juveniles, except paratype 11 (Fig. 50C). They have a multispiral protoconch in fine condition, but with an aberrant sculpture. There are no nodules of comparable size as those in typical *T. gofasi* n. sp., but large areas of the protoconch are (still?) covered by a special sculpture (Fig. 62D-F), for which several interpretations are possible. It might be: 1) a thick fibrous periostracum; 2) crystals of aragonite, as figured by Levi *et al.* (1998: fig. 4A, B); 3) the crossed-lamellar structure of a crystal layer under the protoconch surface, after becoming disclosed by erosion of the surface layer, as figured by Davoli (1995: pl. 1, fig. 8c); or 4) it is similar to the "protocrossed-lamellar structure" of the protoconch of some buccinid and volutid neogastropods, as proposed by Togo

(1974: 378). Where this structure is missing, no nodulose sculpture can be seen; this almost rules out point 3 above. The teleoconch does not show any important difference to that of the Angolan or more northern specimens. The single Ghana shell (ZMUC; Fig. 50D) has remains of a similar protoconch sculpture; its teleoconch is somewhat more angular, and the first teleoconch whorl has 18 well defined axial ribs, versus almost none for the typical form. Unfortunately, the single adult shell from Abidjan area (paratype 11, Fig. 50C) has the protoconch surface too eroded for showing its fine structure. Since only three juvenile shells from Liberia with such protoconch sculpture are at hand, it is difficult to judge now if this difference in protoconch characters of the Guinea Gulf shells, together with the geographic isolation (if any), has a taxonomic meaning.

Indeed, it is conceivable that these Guinea Gulf juveniles, if they belong to *T. gofasi* n. sp., may have been transported in the veliger stage from the Senegal area population in the NAR by the winter Guinea current, or from the Angola population in the SAR by the summer current; but may have failed to develop fully in the hydroclimatic conditions of the ATR (see Le Loeuff & Cosel 1998: 310). But this would not explain the different protoconch surface sculpture, unless it would be due to some corrosive property of the Guinea Gulf waters.

A shell taken by a "high-sea fishing boat in the Atlantic at large of the African coast" and tentatively identified as *Trigonostoma goniostoma* by Caricati (1973: 236, figs 3, 4) may belong to the species here described, but it was not available for study. The figure shows a more prominent spiral sculpture.

In the graph of the height/width data of *T. gofasi* n. sp. and *T. scala* n. comb. (Fig. 55), the individual points for both species appear relatively well grouped, but calculation of the 95% confidence area (not shown) for both species shows that these severely overlap. So, these species cannot be distinguished based on those data. Other differences are given in Table 4.

Trigonostoma gofasi n. sp. differs from the Central West American *T. goniostoma* (see discussion under *T. scala* n. comb.) in being less elongate, having a scabrous sculpture, a wider umbilicus and a more deviated columella. Both species have a multispiral protoconch.

TABLE 4. — Shell characters differentiating *Trigonostoma gofasi* n. sp. and *T. scala* (Gmelin, 1791) n. comb.

	***T. gofasi* n. sp.**	***T. scala* n. comb.**
Protoconch	multispiral	paucispiral
Columellar callus	smooth	granulated
Umbilicus	wide, deep	narrow, less deep
Siphonal fasciole	absent	present
Axial ribs on sutural ramp	broad, reflected, do not reach suture	sharp, reach suture

Sacco (1894: 9) suggested a more or less direct descendance of the recent "*Trigonostoma rigidum* Sow" (= *T. gofasi* n. sp.) from *T. ampullaceum* (Brocchi, 1814) of the Italian Pliocene.

Trigonostoma scala (Gmelin, 1791) n. comb.
(Figs 51; 63)

Murex scala Gmelin, 1791: 3551.

Cancellaria rigida Sowerby, 1832: 53; 1833: fig. 41; 1849a: 456.

Cancellaria costata Sowerby, 1833: fig. 42 (non *C. costata* Sowerby, 1822).

Trigonaphera withrowi Petit, 1976: 39, pl. 2, fig. 3a, b.

Scalptia scala – Petit 1984: 58. — Bernard 1984: 90. — Petit & Harasewych 2002: 131.

TYPE MATERIAL. — Neotype, here designated, 32.5 × 25.7 mm, leg. M. Pin, 1987 (MNHN Moll 9486) (Fig. 51A).

The specimen from the Spengler collection, figured in Chemnitz (1780: 1, vign. 37a-c), is not in ZMUC (Schiøtte; Tendal *in litt.*); its actual whereabouts is unknown, so that no specimen is available for lectotype designation of *Murex scala*. Designation of the Chemnitz figures is judged inappropriate: these figures are rather crude, depict a shell with erroneous locality statement, in unusual positions (Petit 1984: 58), and do not allow the rather subtle differenciation in the western African trigonostomids, especially the difference in protoconch type.

The very complex nomenclatural situation (discussed below), the unusual figures in Chemnitz (1780), and the necessity for clear distinguishing characters between this species and *T. gofasi* n. sp., lead to the exceptional need for a neotype designation, with the express purpose of clarifying the taxonomic status as well as correcting the

type locality of *T. scala* n. comb. More details are given below, under Nomenclature.

Lectotype of *Cancellaria rigida*, here designated (see below, under Nomenclature), 20.0 × 15.2 mm (BMNH 1964445) (Fig. 54).

Holotype of *Trigonaphera withrowi*, 21.4 × 15.7 mm (USNM 760635).

TYPE LOCALITY. — *Murex scala*: unknown to Gmelin (1791). The Spengler shell he refers to is said to originate from "the east-Indies" (Spengler *in* Chemnitz 1780: 29); this is here judged erroneous. The neotype originates from Joal, Senegal, 10-20 m.

Cancellaria rigida: the locality statement of the lectotype (Puerto Portrero, western Central America) is here judged erroneous (see below, under Nomenclature); it is corrected (ICZN 1999: art. 76 A.2) to "off western Africa". The lectotype is from the Cuming collection, and it is well known that several Cuming specimens have incorrect locality statements.

Trigonaphera withrowi: off Senegal, 25 m.

MATERIAL EXAMINED. — **Mauritania.** Portandick (= Marsa), 1 spec. (MNHN, as *Cancellaria costata* Gray, ex colln Petit de La Saussaye).

Senegal. 18-20 m, 1 spec. (KBIN), 4 specs (MNHN). — Dakar, 5-10 m, 2 specs (AV 0139). — N'Gor, 8 m, 2 specs (AV 0137). — M'Bour, 10 m, 5 specs (AV 0134, 0138, 0141). — Rufisque, 1 spec. (MNHN, Gruvel 1912). — Gorée, 1 spec. (MNHN, Marche-Marchad). — Joal, 10-20 m, 13 specs (MNHN). — Casamance, 1 spec. (AV 0140). — "Gambia ?", 2 specs (RMNH, H. Cuming). — 3 specs (BMNH, Accn. no. 1822, ex Mrs De Burgh colln, under the name *Cancellaria costata*).

Gabon. "Zone équatoriale", 15-50 m, 2 specs (MNHN, Bernard). — Port Gentil, 3 specs (MNHN, Chevalier 1980-1989); 25 specs (MNHN, Bernard 1980-1989). — 1°40'S, 9°25'E, 150 m, in Reineck sediment core 1 juv. spec. (labelled "Equatorial Guinea", but coordinates refer to Gabon) (MNHN).

DISTRIBUTION (Fig. 52). — Off Senegal, and off Gabon; 5-50 m.

Bathymetry: 5 to 50 m; one juvenile in sediment core at 150 m.

DESCRIPTION (of neotype)

Shell 32.5 mm high and 25.7 mm wide. Colour yellowish-brown with three brown spiral bands on the last whorl. Protoconch pale brown, paucispiral, with 1 1/2 whorl, maximum diameter 1.0 mm, exposed height 0.9 mm. Transition to teleoconch well marked. Teleoconch with 4 7/8 strongly scalate whorls. Axial and spiral sculpture on early teleoconch whorl forms a finely latticed pattern; on later whorls the axial sculpture is more prominent. Sutural ramp wide, with some faint spiral lines. From 2nd teleoconch whorl on, the narrow axial ribs form sharp narrow lamellae when crossing over the sutural ramp; in younger whorls when well preserved, their upper parts are reflected abaperturally. The depressions between the lamellae are often coloured brown. Spiral sculpture consists of 10 spiral bands, narrower bands (one each) of second, third and fourth order are placed in between. Body-whorl with well defined siphonal fasciole. Aperture white, roughly triangular, with 9 lirae inside outer lip. Columella concave, with three folds, the anterior one forming the rim of the siphonal canal, which is curved abaxially. Columellar callus white, with rather strong granulations on the columellar lip and short spiral ridges on the parietal lip, and in frontal view partly covering the rather narrow umbilicus which is open till 65% of shell height but expanding strongly in the last whorl. A sinus in the outer lip at the shoulder of the last whorl is delimited by 3 teeth on the parietal lip and by a marked indentation in the outer lip.

Variability

The neotype is one of the largest shells of this species seen. The shells studied present following variability. Shell up to 33.1 mm high, maximum width 25.3 mm. Colour yellowish-brown to brownish-grey. Protoconch with 1 1/4 to 1 3/4 whorls ($\bar{x}$ = 1.5, σ = 0.15, n = 23), maximum diameter 0.8-1.3 mm ($\bar{x}$ = 1.1, σ = 0.1, n = 23), exposed height 0.6-0.9 mm ($\bar{x}$ = 0.78, σ = 0.19, n = 21); a sculpture of tiny nodules (Fig. 63C, D) remains on a few shells. Transition to teleoconch clearly marked. Teleoconch with up to five strongly scalate whorls. Axial sculpture of 14-20 ribs ($\bar{x}$ = 15.6, σ = 2.9, n = 22) and spiral sculpture of 5-7 bands ($\bar{x}$ = 5.9, σ = 0.7, n = 28) on first teleconch whorl forms a finely latticed pattern; on later whorls the axial sculpture is more prominent. Aperture: 7-11 lirae inside outer lip. Smaller shells have a rather narrow and shallow umbilicus, columella slightly concave, with two folds (posterior one the strongest) and one minor fold forming the rim of the siphonal canal. The sinus in the outer lip at the shoulder of the last whorl is delimited by 1-4 teeth on the parietal lip and, in larger shells, by a marked indentation in the outer

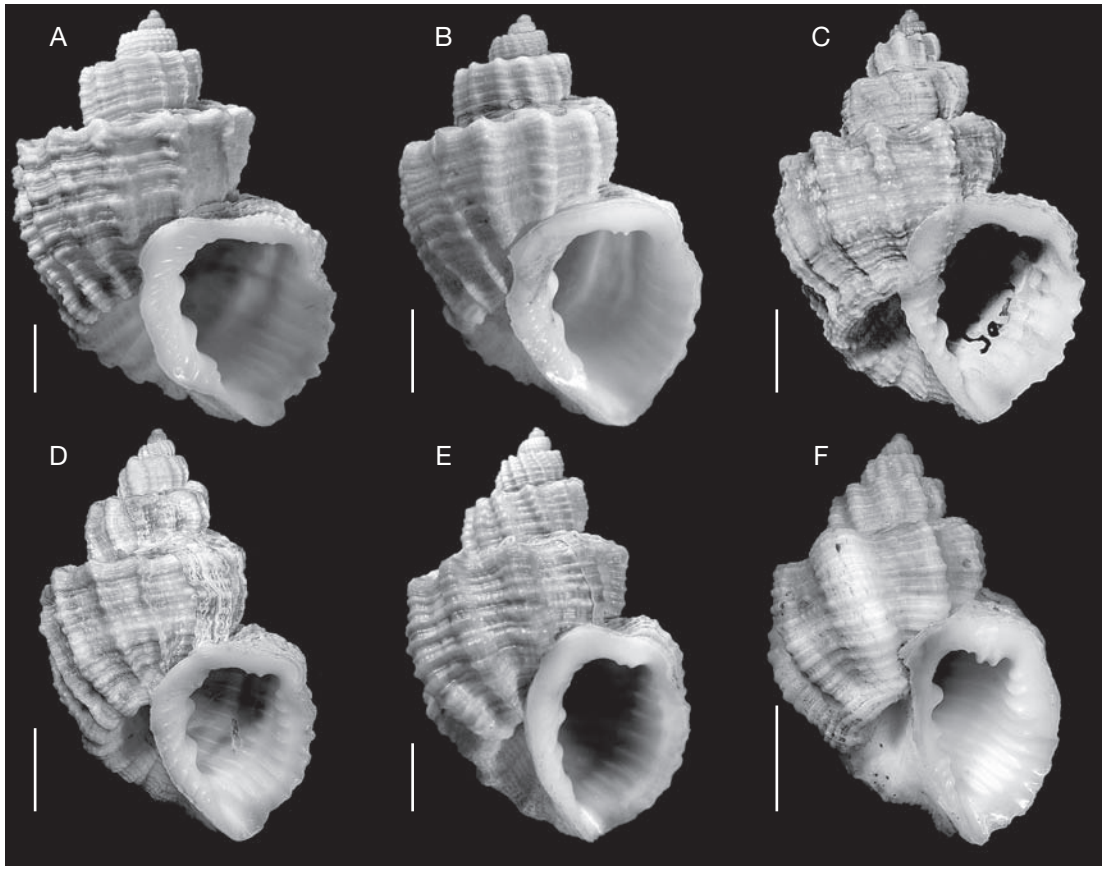

FIG. 51. — *Trigonostoma scala* (Gmelin, 1791) n. comb.: **A**, neotype, Senegal, Joal, 10-20 m (MNHN Moll 9486); **B**, Senegal, Dakar, N'Gor village, dredged on sand, 8 m (AV 0137/1); **C**, Gambia (ZMUC); **D**, Senegal, Joal (MNHN); **E**, **F**, Gabon, Port Gentil, lagoon's beach and sand dredged in the bay, 0°44'S, 8°48'E (MNHN). Scale bars: 5 mm.

lip. The depth of the umbilicus, expressed in % of total shell height is: $\bar{x}$ = 62.8 (σ = 7.1%, n = 31).

REMARKS

This species has a paucispiral protoconch, indicating a direct development of the larva, and has a discontinuous occurrence: both off Senegal and off Gabon (in the two hydroclimatic Alternance Regions, see Le Loeuff & Cosel 1998: 310). Based on the material now available, the Senegal and Gabon populations are well separated geographically. Future finding of specimens from localities in between or further south may be unlikely, due to the different hydroclimatic regions

Egg capsules from a "*Cancellaria* sp." from ATLANTIDE stn 131, 5°58'S, 12°08'E, 27 m, described and figured by Knudsen (1950: 109, 110, fig. 18A), are in the alcohol collection of BMNH; the egg number (30-40) and size indicate a non-pelagic development. Knudsen based his tentative identification as cancellariid capsules on their being "of exactly the same type" as capsules in Swedish collections that had been collected in Japan and identified by M. Eri, then director of the Misaki Biological Station, as produced by *Cancellaria spengleriana* Deshayes, 1830. If we accept this reasoning, then the data on protoconch and distribution for all West African cancellariids, given in Table 1, suggest the Gabon population of *T. scala* n. comb. as the only candidate

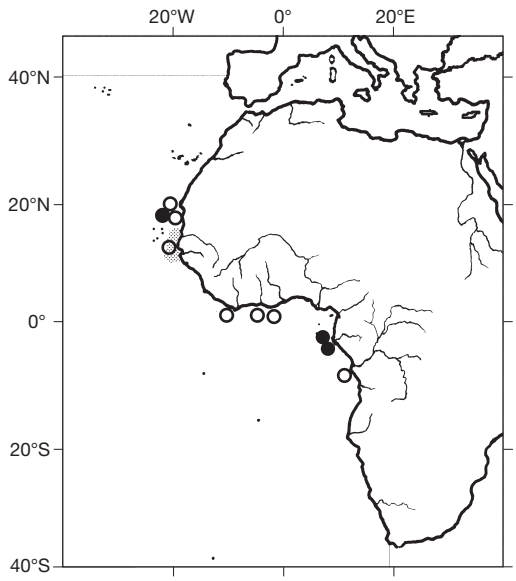

FIG. 52. — Distribution of W African *Trigonostoma* species: *T. scala* (Gmelin, 1791) n. comb. (● and grey area); and *T. gofasi* n. sp. (○).

species for producing these capsules.

The Gabon shells studied generally have a thicker shell; in dimensions they are very close to the Senegal shells, which however tend to be slightly wider (Fig. 53). But both populations cannot be distinguished on their height/width data: the linear regression coefficient for the populations considered together ($r^2 = 0.94$, $p < 0.005$; not figured) is hardly different from those obtained for each one separately (Fig. 53, both with $p < 0.005$).

Both populations have the same protoconch type, but no Gabon shell with a protoconch in condition allowing study of its fine structure was at hand. Protoconchs with remaining nodulous sculpture (Fig. 63C, D) are rare also in the Senegal material: most "well preserved" protoconchs show hardly any sculptural details (Fig. 63A, B).

The juvenile shell from the sediments off "Equatorial Guinea" (MNHN) has a light brown protoconch with a nodulous sculpture, but the three teleoconch whorls are white, which is unique in the material studied. This shell can be distinguished from whitish juvenile shells of *Admetula cornidei* in its much smaller brown protoconch, its broad sutural ramp, and being less slender.

The Mauritania locality, based on a single shell with locality data Portandick (= Marsa), from the old Petit de La Saussaye collection (MNHN) is here ignored until confirmed by more material.

Apart from Senegal, it appears that the two W African trigonostomid species, *T. gofasi* n. sp. and *T. scala* n. comb., are not sympatric. Their geographic distributions, as presently known, appear to be discontinuous, and related to the hydroclimatic regions. From N to S: NAR, Senegal: *T. gofasi* n. sp. and *T. scala* n. comb.; ATR, eastern Liberia-Ivory Coast-Ghana: *T. gofasi* n. sp.; SAR, Gabon: *T. scala* n. comb.; and Angola: *T. gofasi* n. sp.

Trigonostoma scala n. comb. must be the species referred to by Dautzenberg (1910a: 32) when writing about "*Cancellaria rigida*" (referring to *T. gofasi* n. sp.): "Nous possédons dans la collection Petit de La Saussaye des exemplaires dont l'ombilic est bien moins ouvert que chez celui que nous avons représenté". This narrower umbilicus might be an argument for including this species in *Trigonaphera* rather than in *Trigonostoma*, as did Petit (1976) when introducing the specific name *withrowi*.

Nomenclature

Several names have been used for this taxon.

During the 19th century, the name *Murex scala* Gmelin, 1791 remained unnoticed; the present species was referred to as *Cancellaria costata* Sowerby, 1833 (also cited as *C. costata* "Gray" in Sowerby), a junior primary homonym of *C. costata* Sowerby, 1822 (= *C. cancellata* (Linnaeus, 1767)). It is not clear to which species Parenzan (1961: 55) referred when citing "*C. costata* Calc." for the Ionian Sea (see also under *Tribia coronata*).

Sowerby (1832: 53) proposed *Cancellaria rigida* for a shell in the Cuming collection, said to originate from Puerto Portrero, Central West America; he further added that he "has several much larger specimens with whose locality he is unacquainted". In the same publication also *C. goniostoma* was described, from western San Salvador. Although cited descriptions allow a good distinction between *C. rigida* and *C. goniostoma*, there has been considerable confusion about the former name. Some earlier authors (e.g., Sowerby [1849a: 456], citing as locality "the sands of the river Gambia") interpreted *C. rigida* as a W African species,

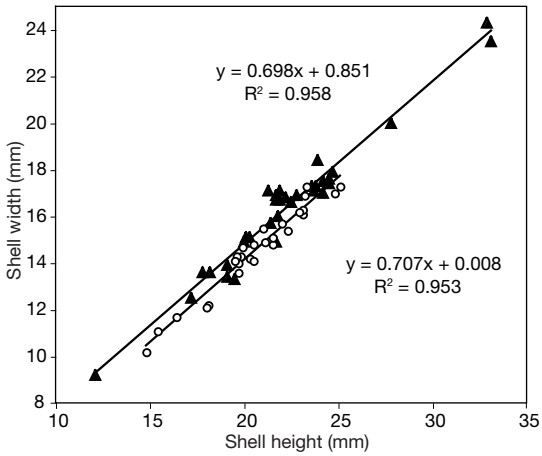

FIG. 53. — Dispersion diagram and linear correlation line for shell dimensions of *Trigonostoma scala* (Gmelin, 1791) n. comb. from off Senegal (▲) and Gabon (○).

FIG. 54. — Lectotype of *Cancellaria rigida* Sowerby, 1832 (BMNH 1964445).

as did Dautzenberg (1910a) and Nicklès (1950) (see above, under *T. gofasi* n. sp.). Tryon (1885: 78, figs 83-85) cited the locality confusion, and synonymized *C. rigida* with *C. goniostoma*; but the value of this is disputable since he also considered *C. brevis* Sowerby, 1832, as synonym of *C. goniostoma*. Löbbecke (1881: 7, pl. 1, figs 5-8) figured W African shells and mentioned the paucispiral protoconch, but copied the W American locality. Authors from the 1950's on (Keen 1958, 1971; Petit 1976) considered *C. rigida* a synonym of *C. goniostoma*. Although the original figure of *C. rigida* is rather unclear, two shells in BMNH (1964445) were identified on BMNH labels as possible syntypes by Keen in 1964. In correspondence with the present author the late Keen wrote: "My purpose in segregating the material was only to bring it to the attention of specialists. [...] I was not at all certain that the specimens matched precisely the first published illustration" (Keen *in litt.* 21.II.1979).

In 1964, Olsson labelled three shells in BMNH as "paralectotypes to be selected" of *T. goniostoma* (never published); one of them (BMNH 1964346, neg no. 51515 cd) is clearly a *T. scala* n. comb. shell. Also this illustrates the confusion reigning at the time regarding *T. goniostoma* and the western African species studied here.

In 1976, Petit (p. 40) believed that the type of *C. rigida* had not been located, and concluded that *C. rigida* is a synonym of *C. goniostoma* (and hence a western American species). He discussed the problem, and introduced the name *Trigonaphera withrowi* for the W African species known until then under the name *C. rigida*. However, both shells identified by Keen as possible syntypes of (what she considered to be the W American) *C. rigida* (and also BMNH 1989031, a Cuming shell recognised by Keen as figured by Reeve 1856: spec. 83) were checked and found to agree completely with the W African *T. withrowi* (= *T. scala* n. comb.), including the paucispiral protoconch (*T. goniostoma* has a multispiral protoconch). Consequently, if these BMNH shells are indeed the syntypes, and if no western American species similar to *T. scala* n. comb. exists, then the latter name is a senior subjective synonym of *C. rigida*, which in that case is not a W American, but a W African species. The western American cancellariid fauna is well known (see Keen 1971: 646-658), therefore the probability of the existence of a species strongly resembling *T. scala* n. comb. is judged very low. Obviously, all depends

on the correctness of the cited identification of the shells in lot BMNH 1964445 as syntypes of *C. rigida*. The description of *C. rigida* was based on one Cuming shell and "several much larger specimens"; both shells in lot BMNH 1964445 are about the same size (22.0 × 16.5 and 20.0 × 15.2 mm). So, only one of them can be a syntype (unless both belong to the "much larger" shells, which is improbable since BMNH 1989031 measures 32.3 × 24.4 mm), or the Cuming shell is not in this lot. A note accompanying this lot correctly states (KMW 1989): "The smaller of these two specimens is probably that figured by Sowerby, Conch. Ill. f. 41 (1833). It is not known how or when the other specimen became associated with it. The former specimen is an ideal candidate for lectotype selection". In order to clarify the identity and locality of *C. rigida*, this specimen BMNH 1964445 (Fig. 54) is here designated lectotype of *Cancellaria rigida* (see above). Based on the discussion above, the original locality statement is here corrected (ICZN 1999: Recommendation 76A.2.) to "western Africa".

In 1976, this western African species appeared to be without a valid name, therefore, rather than proposing a new name for *C. costata* "Gray", Petit (1976: 39) introduced the new species *Trigonaphera withrowi*, so that the species could be based on a holotype, and not on a figure.

Later, Petit (1984: 58) reintroduced for this species the use of the name *Scalptia scala* (Gmelin, 1791), which had remained unused since 1801. Gmelin (1791: 3551) described *Murex scala* from unknown locality, with references to two figures: Meuschen (1767: fig. b) and Chemnitz (1780) "Conch 4. p. 1. vign. 37. f. a. b. c." (in fact p. 3, but the page error is understandable, since the page bears a "1" in the top right corner, probably a binder's signature). The Chemnitz figures represent a shell in the collection of Spengler, referred to by the latter (p. 28) as "37 vign n° 3 lit. a, b, c 'Bordestrap (Treppengelände)'". Gmelin used the same two references also for his *Buccinum scalare* (1791: 3495). Petit (1984: 58) designated the Meuschen figure as representing the lectotype of *Buccinum scalare*, which was till then known as *Trigonostoma trigonostoma* (Lamarck, 1822) or *T. pellucida* (Perry, 1811), and had been referred to under the Dutch vulgar name "Bordes Trap" in the non binominal literature (e.g., Meuschen 1767: 8 no. 156, and figured in frontispiece, b). On behalf of *Scalptia scala* Petit stated that "Bosc (1801), by citing only the Chemnitz vignette, intentionally or unintentionally restricted Gmelin's name to those figures".

Petit's (1976) arguments for identifying *Trigonaphera withrowi* as *Scalptia scala* are: the restriction by Bosc of *M. scala* to the cited Chemnitz figures, and the recognition of these Chemnitz figures as this western African species. Petit states (1984: 58): "Recognition of the three Chemnitz figures is possible only when it is realized that in these figures the shell is oriented with the apex tilted away from the viewer, and the area between the shoulder angle and the suture is not visible. [...] A specimen in the writer's collection matches these Chemnitz figures in details of sculpture and colour, the only difference being that the illustrations are slightly elongated making the shell appear more attenuate. This is an artifact of the tilted position of the shell in the drawings and otherwise the delineation is perfect". The height/width factor for the Chemnitz vignette 37 figures a and b (fig. c shows an unusual position and cannot be relied upon in this context) is 1.35 and 1.55 respectively; if we accept 1.45 as mean value, this agrees rather well with the factor (1/0.72 = 1.39) obtained from the correlation line for *T. scala* n. comb. in Figure 55. This means that the figures in Chemnitz' vignette 37 a-c are not substantially elongated; only the relative height of the spira (44% of the shell length in vign. 37 fig. a) seems exaggerated; the most attenuate shell studied (Fig. 51D) has only 30%.

Chemnitz (1780: 27) mentioned the "Bordestrappe" and gave a figure (pl. 122, fig. 1130), said to be a copy of a very bad figure given by Knorr intended to represent that species. He mentioned the low quality of the figure, and continued (translation):

"Real Bordestrappes count among the number of rarest Cabinet pieces. Our greatest connoisseur in shells, the gentleman Art Intendant Spengler, is here the only one who can show it. This most worthy of my friends I have asked for a precise figure and an extensive description of it. My question was not in vain. The nice figure we see in the 37th Vignette at fig. 2 [*sic*: this is a *Babylonia* spec.] and his description well worth reading we now find here in his own following words.

Description of the so-called Bordestrap (Treppengeländer)

See 37th vignette Nº 3 lit. a. b. c." [there is no no. 3 in this vignette; this error is repeated further on in his text].

Then starts Spengler's text, first discussing the six specimens of *Trigonostoma scalare* then known (till p. 28) and followed by the description of his own shell, ending near the bottom of p. 29. To all indications, this whole text is from Spengler, Chemnitz' text starting again with "Tab. 122. F. 1131 u. 1132 wie auch Tab. 123 F. 1134 u. 1135. In museo nostro" at the bottom of p. 29. This means that the words "my collection" in the description on page 28 refer to Spengler and not to Chemnitz, as might be assumed from a reading of the description only.

Because the text is in somewhat outdated German set in Gothic characters, it may not be easily intelligible to non-European readers; therefore a translation of the description is here given. Remarks between square brackets are from the present author. It must be kept in mind that this shell is figured the apex downward, so that what is now called the last whorl was then referred to as the first one, and our "top whorl" was called "the under most whorl".

"The heart-shaped or triangular aperture, the expanded wide umbilicus, and the sharply deposited conical whorls, that are artfully set with raised and cross-striated sectioned ribs, constitute the main character of this snail [= shell], and this plan applies as a rule to the piece from my collection that I will describe now, although for the rest it really differs in some parts from the Dutch [specimens], as I will demonstrate at the end. In the 37th vignette under n° 3. [*sic*] lit. a. b. c. it is shown from three sides. The lover of nature will remark already from the first sight that the first and largest whorl has a completely different proportion to the other whorls, than one sees in other known snails [= shells]. Indeed it does not taper from above, as it is pushed apart there by the expanded and funnel-like umbilicus. But it is the very broadest at the underside against the second whorl where it is truncated straight, forming a sharp edge, as all the other whorls. Only the first whorl is a little bit rounded, but bent inwards against the border of the regularly coronated umbilicus. The other five whorls are straight, but narrower at the abutting side than at the anterior side. As already said, the aperture is three-sided. The lip is strong and grooved with sharp teeth reaching deep inside, the outer border is expanded, sharp and cutting. The columellar lip is thin and set with three folds and many small nodules. It turns outward against the umbilicus. On the upper side the two long sides of the aperture meet, leaving between them a short canal which is slightly curved outwards. All six whorls and also the umbilicus are adorned with narrow raised ribs set in measured distances according to the length, but the last of which, under the aperture, has double the width as the others. On the truncated horizontal part under each whorl, which could not be apparent in the figure, they are sharper and thinner. Beyond the carina these ribs, and the spaces in between, are crossed by raised lines. The base colour of the snail [= shell] is generally nice yellow, and regularly shadowed with pale brown bands. The umbilicus (which reaches for the most part into the undermost spire whorl, as with the Wentletraps) and the aperture are straw yellow, and the latter is completely transparent. Its native country is Eastindia.

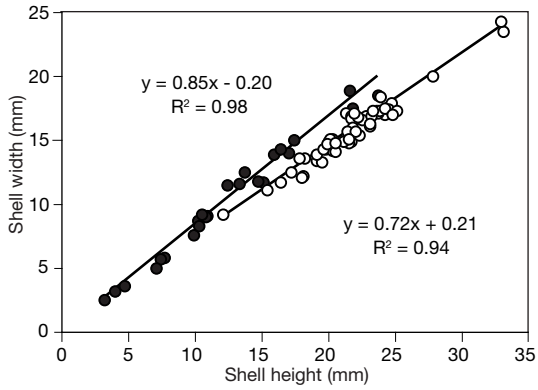

FIG. 55. — Dispersion diagram and linear correlation line for shell dimensions of *Trigonostoma gofasi* n. sp. (●), and *T. scala* (Gmelin, 1791) n. comb. (○) from all localities.

The difference between this [= Spengler's shell] and the above mentioned Dutch "Bordestrap" figured in copper [but all figures are in copper, see title page] is that the latter is more elongated and looks as it has the whorls more torn apart. The umbilicus is slightly wider, and consequently the aperture stands more in front. The colour is white with a slight reddish tinge." (Spengler *in* Chemnitz 1780: 26-29).

In short: Chemnitz stated that Spengler was the only one in Denmark to have a specimen of the "Bordestrap"; he published figures and Spengler's description of it. In it, Spengler stated that his shell has some substantial differences from the real ("Dutch") "Bordestrap" *Trigonostoma scalare*, and gave these differences at the end of the description. Obviously, Spengler's shell is not *Trigonostoma scalare*, but belongs to another species. This shell, type specimen of *Murex scala* Gmelin, 1791 was not in the Chemnitz collection as generally assumed, but in the Spengler collection, reported to be in ZMUC (Dance 1986: 226). However, the figured shell is not in ZMUC (Schiøtte; Tendal *in litt.*), so that no specimen is available for lectotype designation. Gmelin did not copy the East India locality, which is here considered incorrect.

Comparison of the description and figure here given, to those by Spengler (in Chemnitz 1780) shows that the neotype is consistent with what is known of the former name-bearing type, including its dimensions (supposing the Chemnitz vignette 37, figs a-c are real size: a: 35 × 24 mm, b: 33 × 23 mm). One point which is not directly clear regards the depth of the umbilicus that, according to Spengler's description "meistentheils bis in die unterste Spitze reichet" (reaches mostly into the lowest top whorl). "Meistenteils" means: mostly, usually, or: for the greater part; the first meaning cannot be relevant here since, to all evidence, Spengler had seen only his own shell; so the meaning must be "for the greater part". So, the umbilicus in Spengler's shell was open for the greater part of the shell height; in the neotype this value is 65% of the shell height.

Like *T. scala* n. comb., the Indo-Pacific *T. bicolor* (Hinds, 1843) has a paucipsiral protoconch; it also has thin axial ridges on the sutural plane and brown blotches in between; but its spiral sculpture is much weaker, and especially the specimens from Mozambique are thin-walled. Differences between *T. scala* n. comb. and *T. mozambicense* from off eastern Africa, also with a paucispiral protoconch, are indicated by Petit & Harasewych (2002: 131).

Trigonostoma scala n. comb. differs from the following somewhat similar species with a multispiral protoconch: *T. goniostoma* and *T. brevis*, from Central western America, have a wider and deeper umbilicus, the axial ribs have a more rounded profile. *Trigonostoma brevis* is a much more globose shell; *T. goniostoma* has the spiral sculpture much smoother than *T. scala* n. comb.

The Indo-pacific *T. scalare* has the umbilicus much larger than *T. scala* n. comb.; the shell is white, sometimes with a pink or purplish tinge. Its sutural plane is almost unsculptured, and the relative height of the spire is larger. Regarding the differences from *T. gofasi* n. sp. from western Africa, see Table 4.

Several European Mio-Pliocene trigonostomid species from e.g., Aquitaine (France), Italy, and the Vienna Basin, e.g., *T. spinifera* (Grateloup, 1832), *T. umbilicare* (Brocchi, 1814) or *T. geslini* (Basterot, 1825), in form and sculpture are rather close to *T. scala* n. comb., but their exact relations remain to be studied.

DISCUSSION

It is unfortunate that, in spite of plenty of well documented material, there are still no data on the feeding behaviour of the species studied here. In other geographic areas, cancellariids have been found on the spira of larger molluscs (Melvill & Standen 1901: 451; Petit & Harasewych 2000: 150). Together with observations of the West American *C. cooperi* sucking blood from rayfish (O'Sullivan *et al.* 1987) and echinoderms (Buck 1991), this suggests a parasitic feeding behaviour. It is hoped that workers in future campaigns may find the opportunity of studying this aspect too.

Data on the protoconch type, the presence of a cancellariid radula, and the geographic distribution of the N and W African species studied, are given in Table 1.

Bathymetry

The Cancellariidae species here studied occur from shallow waters (e.g., Banc d'Arguin, Mauritania) to bathyal depths. In some cases it could not be determined if the specimen had actually lived at the capture depth: e.g., *Bivetiella cancellata* at 280 m, may exaggerate the real bathymetric range of the species.

Figure 56 gives a graphic comparison of the bathymetry data for all documented species. The vertical dotted line indicates the approximate depth of the continental shelf break. Ten species occur only

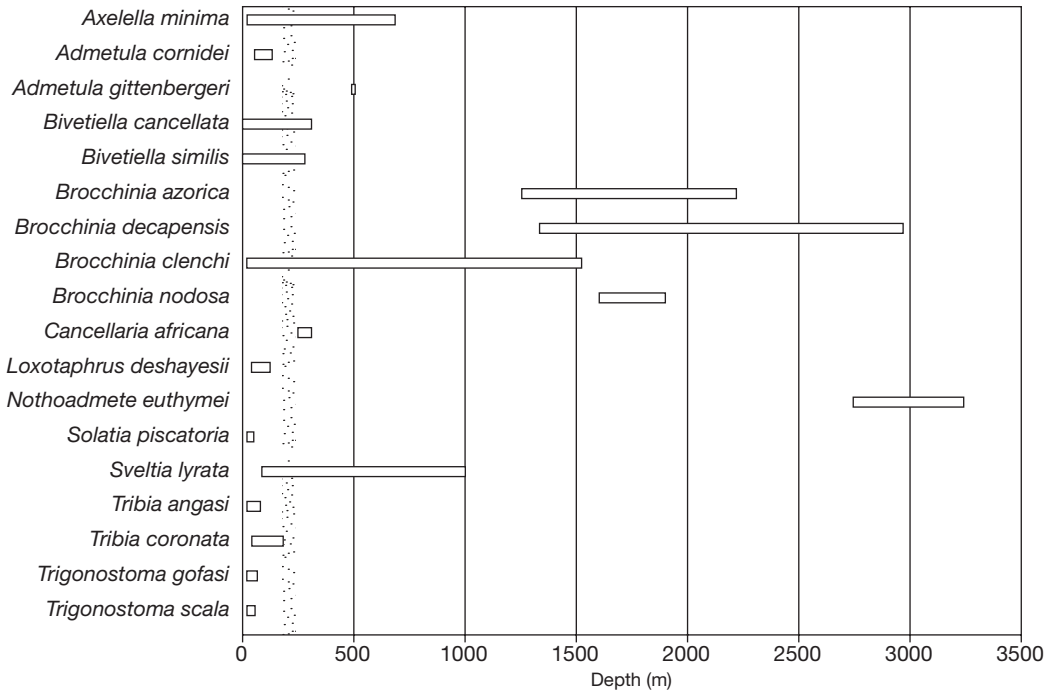

FIG. 56. — Bathymetric data of the Cancellariidae from the studied area. The dotted line represents the approximate situation of the continental shelf break.

on the continental shelf or slightly deeper (a few specimens of *B. cancellata* and *B. similis* till 280 m; *C. africana* at 250-280 m). Six species were taken only on the continental slope or deeper. Three species (*A. minima*, *B. clenchi* and *S. lyrata*) are known from both depth ranges.

GEOGRAPHICAL DISTRIBUTION

Seen on an Atlantic scale, the Cancellariidae from the area here studied form a fairly isolated group. Out of these 20 species only *Brocchinia azorica* and *B. nodosa* have been recorded in the eastern Atlantic N of 40°N, the area studied by Bouchet & Warén (1985), the latter species also off NE USA (see Verhecken 2002: 510). A single shell tentatively identified as *Brocchinia clenchi* from off Pernambuco, Brazil, NMWZ 1955.158.02258, *Challenger* stn 122, 637 m (Verhecken 2002: 510, 511), is the only indication of a possible link between the eastern and western S Atlantic cancellariids. The four species living off western South Africa are all bathyal; their eastward limit may be formed by the Agulhas current which is active to a depth of at least 2300 m (Gyory *et al.* 2004). A few eastern S African specimens found off Cape Town are believed to be incidental intruders (see Material and methods).

The level of endemism of the Cancellariidae of the whole studied area is 85%. For the three cancellariids living in the Mediterranean Sea it is 33%; for the NE Atlantic cancellariids N of 40°N (six species, see Bouchet & Warén 1985) it is 50%.

Distribution within the area studied:

The number of hydroclimatic zones (counting the Mediterranean as an extra zone) in which each species occurs can be deduced from Table 1:

– 7 zones, *Bivetiella cancellata*.
– 6 zones, *Bivetiella similis*.
– 5 zones, *Sveltia lyrata*, *Trigonostoma gofasi* n. sp.
– 4 zones, *Solatia piscatoria*.
– 3 zones, *Axelella minima*, *Loxotaphrus deshayesii*.
– 2 zones, *Admetula cornidei*, *Brocchinia decapensis*, *Tribia angasi*, *Trigonostoma scala* n. comb.
– 1 zone, *Admetula gittenbergeri* n. comb., *A. italica*, *Brocchinia azorica*, *B. clenchi*, *B. nodosa*, *Cancellaria*

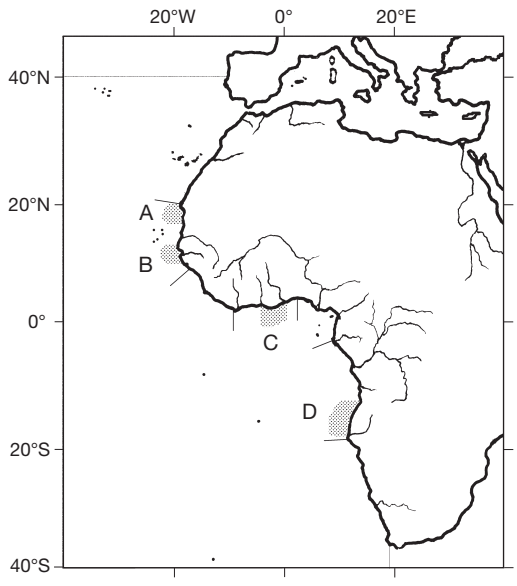

FIG. 57. — Refuge areas on west African coast, after Le Loeuff & Cosel 1998: **A**, Senegal, "Petite Côte"; **B**, upper continental shelf off Casamance; **C**, Ghana probable refuge area; **D**, Lobito to Mossamedes. The hydroclimatic regions (see Fig. 2) are indicated.

africana, *Nothoadmete euthymei* n. comb., *Solatia* sp., *Tribia coronata*.

The five species occurring in four zones or more all have a multispiral protoconch; out of the 15 species occurring in three zones or less, the protoconch of 11 species is paucispiral, two have the protoconch unknown, and two have a multispiral protoconch. The latter two species (*Brocchinia azorica*, known from off NW Ireland and the Azores, and *B. nodosa* found off NW Ireland, in the Bay of Biscay, and off Mauritania) may well be intruders from more northern waters of the eastern Atlantic.

With the exception of three specimens of *Bivetiella cancellata* from Sao Tomé and Principe islands, and two specimens of *Solatia piscatoria* from Principe Island, no material from off Nigeria and Cameroon coasts (the ETTR, see above) was found in collections. This is in keeping with the Le Loeuff & Cosel (1998: 315) finding that species richness (for the whole fauna and for each zoological group they studied) is smallest in cited area.

Except for the Azores, there is no cancellariid material from the islands near the mid-Atlantic ridge in the collections studied. This may be due to their geographic isolation, but also to insufficient collecting activity at these locations.

It is remarkable that *Axelella minima* and *Brocchinia clenchi*, species with non-pelagic larvae as evidenced by their paucispiral protoconch, are present off the Azores, the Canaries, Madeira and NW Africa; but *B. azorica* with pelagic larvae has not been found off Madeira, the Canaries and W Africa. *Bivetiella cancellata*, *B. similis* and *Solatia piscatoria* occur off W Africa, Cape Verde and Canary islands, but have not reached Madeira or the Azores, in spite of their pelagic larvae.

Apart from a few species incidentally occurring in the Cape of Good Hope area, cancellariid species living off W Africa are clearly separated from those of eastern African seas. However, recent discoveries in eastern South-African and Mozambique waters have yielded some species rather closely resembling W African species: e.g., *Admetula afra* and *A. epula* versus *A. cornidei* and *A. italica*; *Loxotaphrus rosadoi* Beu & Verhecken, 2000 versus *L. deshayesii*; and *Trigonostoma mozambicense* versus *T. scala* n. comb. The significance of this is not clear yet. Possibly, they may originate from common Tethys ancestors.

This study also showed the occurrence of some species over large distances. Shallow water species: *Bivetiella cancellata*: Mediterranean to Angola; *B. similis*: eastern Spain to Namibia. Deeper water: *Sveltia lyrata*: Mauritania to South Africa. Deep water species: *Brocchinia azorica*: NW Ireland to Azores, possibly to Angola and South Africa (if *B. azorica* and *B. decapensis* are synonyms); *B. nodosa*: American east coast to Bay of Biscay-Mauritania. As can be deduced from their multispiral protoconch, all these species, except for *B. nodosa* for which no protoconch data are available, have planktotrophic larvae.

The two trigonostomid species were found to have each a distribution area split up according to hydroclimatic regions and not overlapping with each other, except off Senegal. This can be explained by paleozoogeography. "In the Neogene a large tropical eastern Atlantic faunal province stretched out from the North of France southward to Angola. […] Within the northern and southern zones of alternance, particularly species of the Italian Pliocene, or very close descendants, are found on often very short

coastal strips with special hydrological conditions known as 'endemic pockets', 'relict pockets' or 'refuges'" (Le Loeuff & Cosel 1998: 318) indicated on Figure 57. From N to S: the "Petite Côte" of Senegal, between Cape Verde Peninsula and Joal-Fadiouth (A); the vast upper continental shelf (10-30 m) with clean sandy bottom off Casamance (B); probable refuge on the coast of Ghana (C); and the most important refuge, on the coast of southern Angola (Lobito to Mossamedes) in the SAR (D).

In the area studied, several cancellariid species have a distribution closely related to these refuge areas (see Table 5). However, it must be noted that *L. deshayesii* and *Tribia angasi* also occur off the Guinea coast; and that the southernmost populations of *T. gofasi* n. sp. and *T. scala* n. comb. live also outside of a refuge area. Also, no cancellariid was found to occur only or mainly in the (most important) refuge area (Fig. 57D).

Sveltia lyrata is a species well known from the European Mio-Pliocene; it has a wide distribution in deeper water off the W African coast, also in but not restricted to the refuge areas. Its deep habitat should preclude influence of the hydroclimatic regions on its distribution, but material of this species from WTTR and ETTR is absent in the collections studied.

For 17 out of the 20 recent species studied here, fossil species can be considered closely related: these have been mentioned under the relevant Remarks. The others, *Brocchinia azorica*, *B. decapensis* and *Nothoadmete euthymei* n. comb., are bathyal species, related fossil forms of which may be rather unlikely to be found.

A couple of citations of Cancellariidae from the area studied must be disregarded:

1) *Cancellaria exigua* E. A. Smith, 1891 was described for a single specimen from *Challenger* stn 164B, off Sydney, Australia. Because of the great number of "undoubtedly Atlantic forms" in the material from that station, several authors questioned the correctness of that locality; an Atlantic origin of this material has been suggested (Hedley 1901: 23). It has been shown (Verhecken 1991b) that *C. exigua* is indeed an Australian species.

2) *Buccinum aquilarum* Watson, 1882 from the Azores was described as "a perplexing form, in general aspect very like several *Admetae*" (Watson 1882b). Clarke (1962: 27) considered it to be an *Admete*, but this is a turrid (Bouchet & Warén 1985: 257).

TABLE 5. — Western African species with distribution area mainly restricted, or very near to, the refuge areas (see Fig. 57): **A**, "Petite Côte", Senegal; **B**, upper continental shelf (10-30 m) off Casamance; **C**, coast of Ghana.

	A	B	C
Admetula gittenbergeri n. comb.	×		
Brocchinia nodosa	×		
Loxotaphrus deshayesii		×	×
Solatia sp.			×
Tribia angasi	×	×	
Trigonostoma gofasi n. sp.	×	×	×
Trigonostoma scala n. comb.	×	×	

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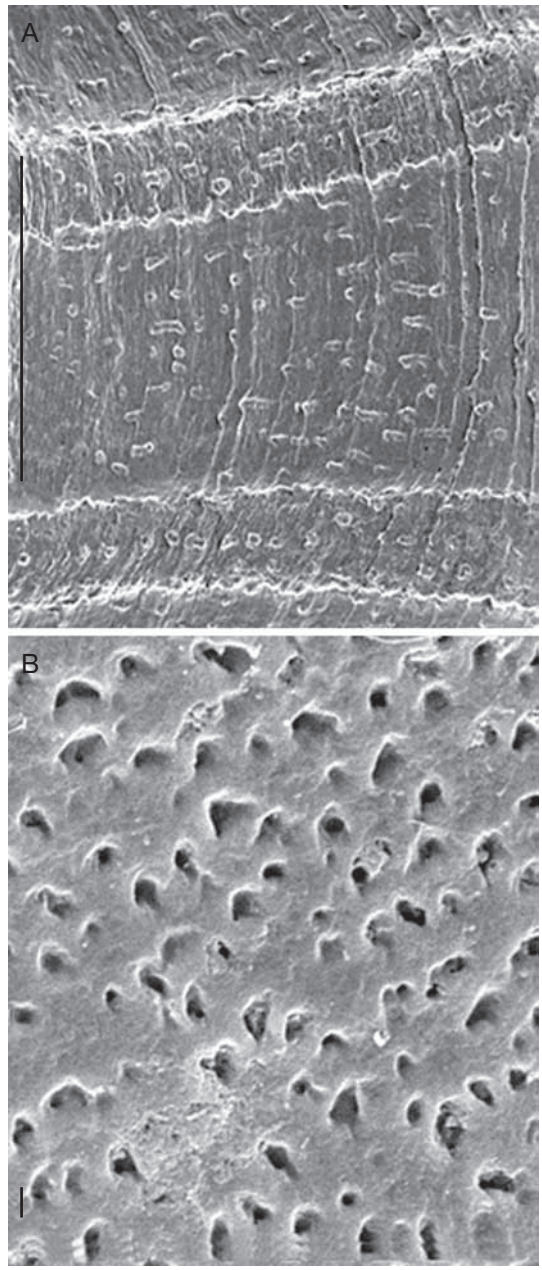

Fig. 58. — Teleoconch microsculpture: **A**, *Axelella minima* (Reeve, 1856), shell of Figure 9F; **B**, *Tribia angasi* (Crosse, 1863), Senegal, Baie de Rufisque, 18-20 m, Gruvel 1909 (KBIN) (see Fig. 61A, B). Scale bars: A, 100 µm; B, 1 µm.

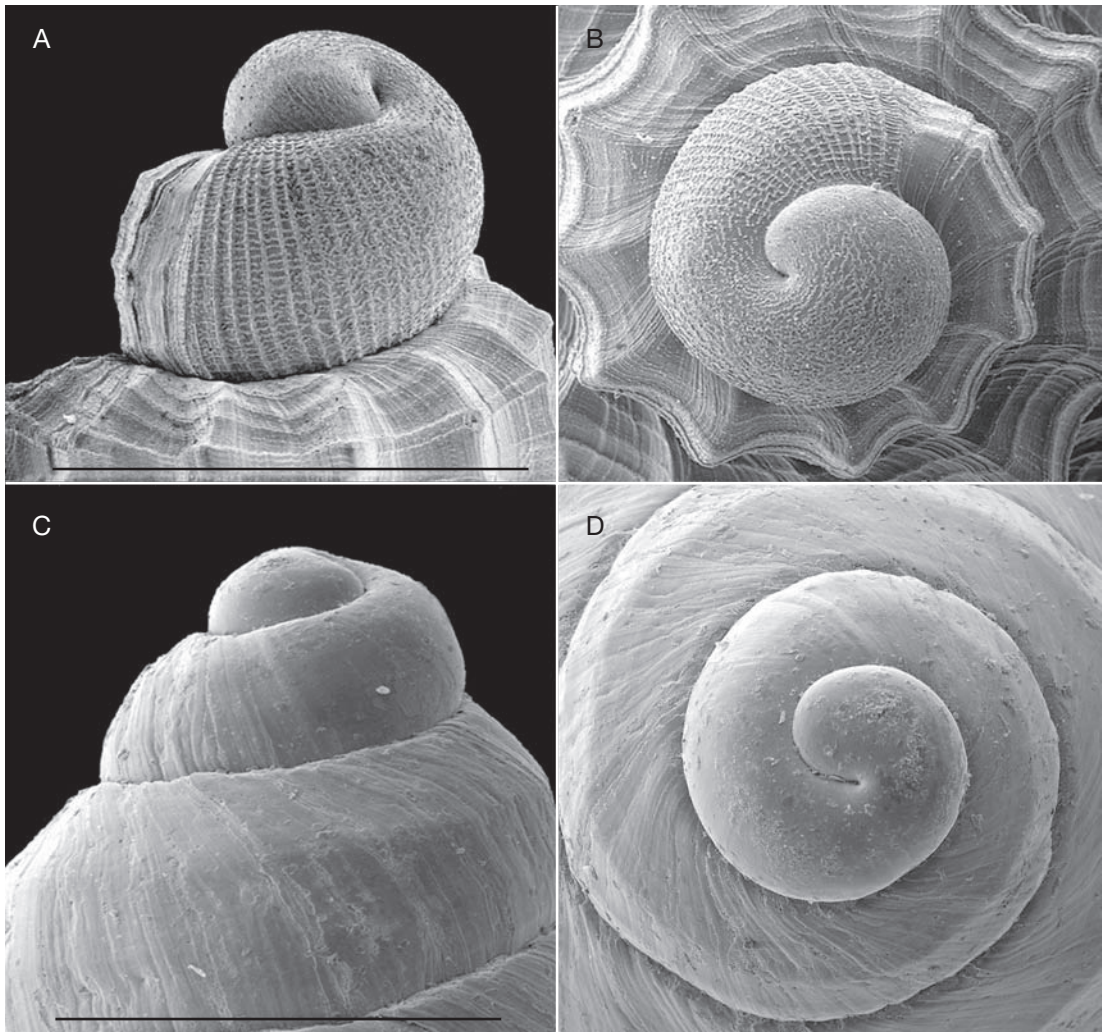

FIG. 59. — Protoconchs: **A**, **B**, *Axelella minima* (Reeve, 1856), shell of Figure 9F; **C**, **D**, *Brocchinia clenchi* Petit, 1986, Azores, S of Terceira, *J. Charcot* BIAÇORES 1971, stn 14, 38°39'N, 27°14.5'W, 27-38 m (MNHN). Scale bars: 1 mm.

FIG. 60. — Protoconchs of West African *Solatia* species, both from Cotonou, Bénin (KBIN IG 10591): **A**, **B**, *S. piscatoria* (Gmelin, 1791), multispiral protoconch; **C**, **D**, *Solatia* sp., paucispiral protoconch. Scale bar: 100 µm.

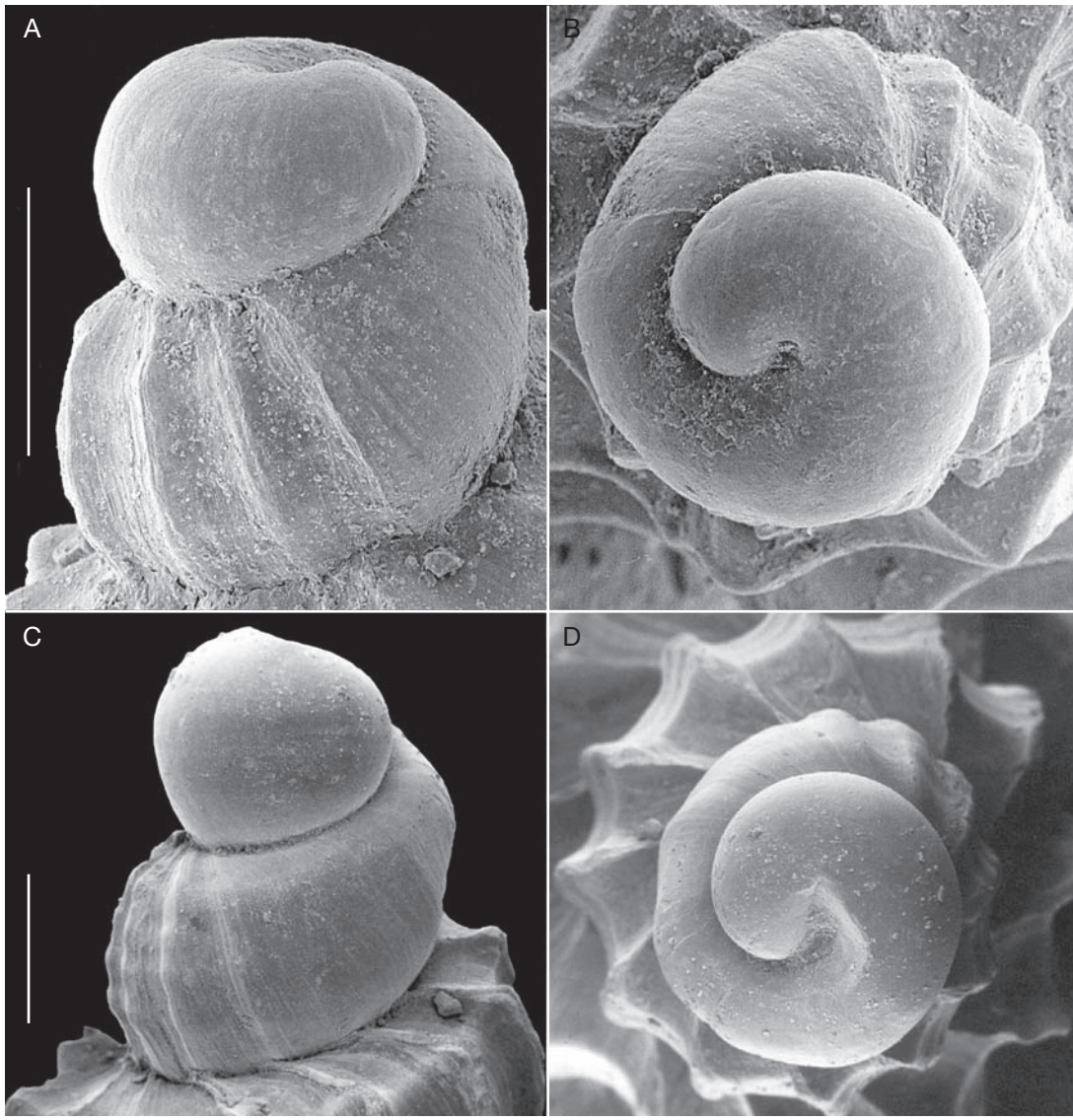

FIG. 61. — Protoconchs of North-West African *Tribia* species: **A**, **B**, *T. angasi* (Crosse, 1863), Senegal, Baie de Rufisque, 18-20 m, Gruvel 1909 (KBIN) (see Fig. 58B); **C**, **D**, *T. coronata* (Scacchi, 1835), protoconch of shell of Figure 46D (photos C, D: SEM Laboratory, University of Basel, M. Düggelin, operator). Scale bars: 500 µm.

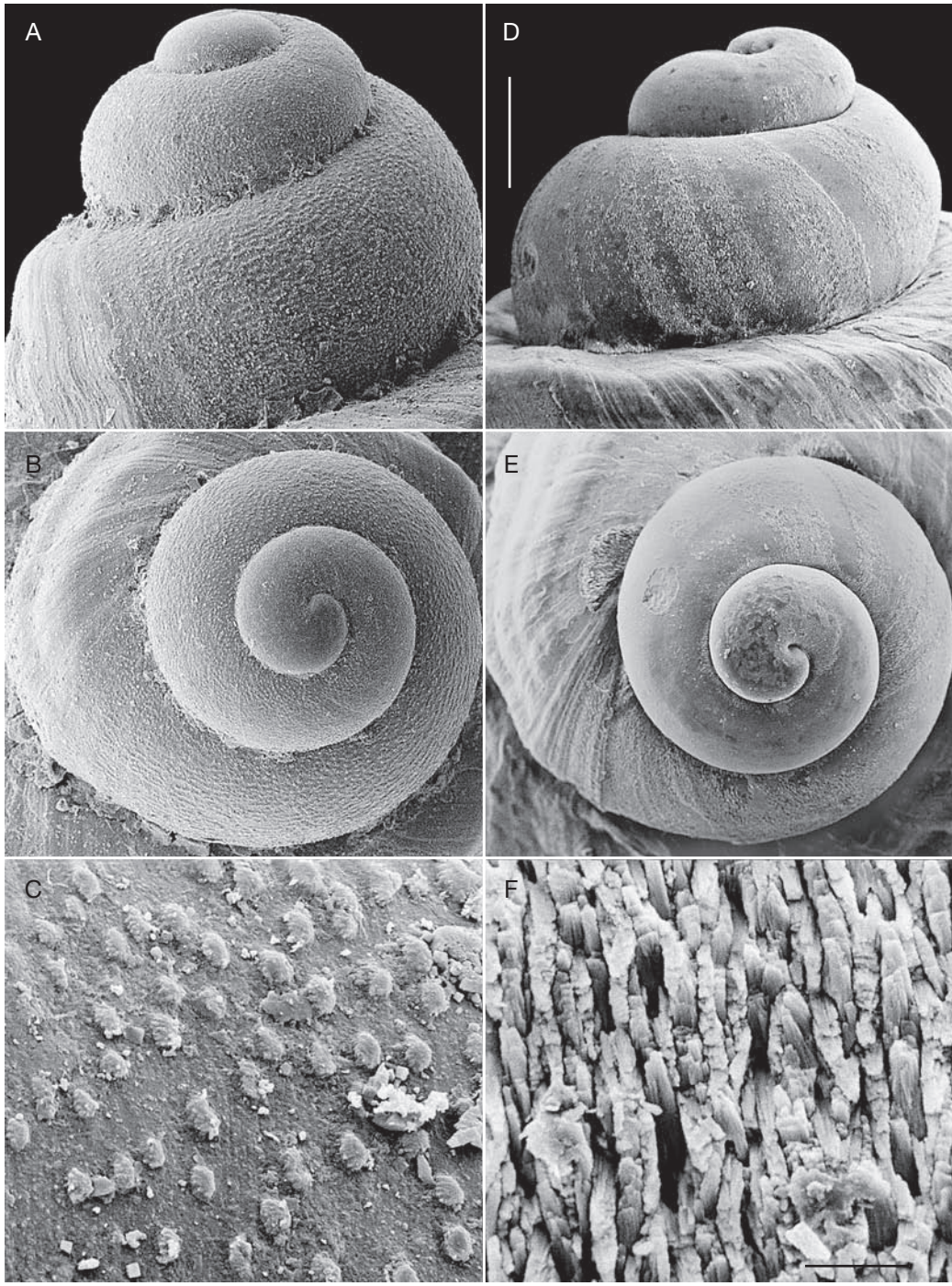

FIG. 62. — *Trigonostoma gofasi* n. sp., different types of protoconch sculpture: **A**-**C**, granular protoconch sculpture, Liberia, Garraway (KBIN); **D**-**F**, non-granular protoconch sculpture, Ivory Coast, Abidjan region, 60 m, Le Loeuff (MNHN). Scale bars: A, B, D, E, 250 µm; C, F, 10 µm.

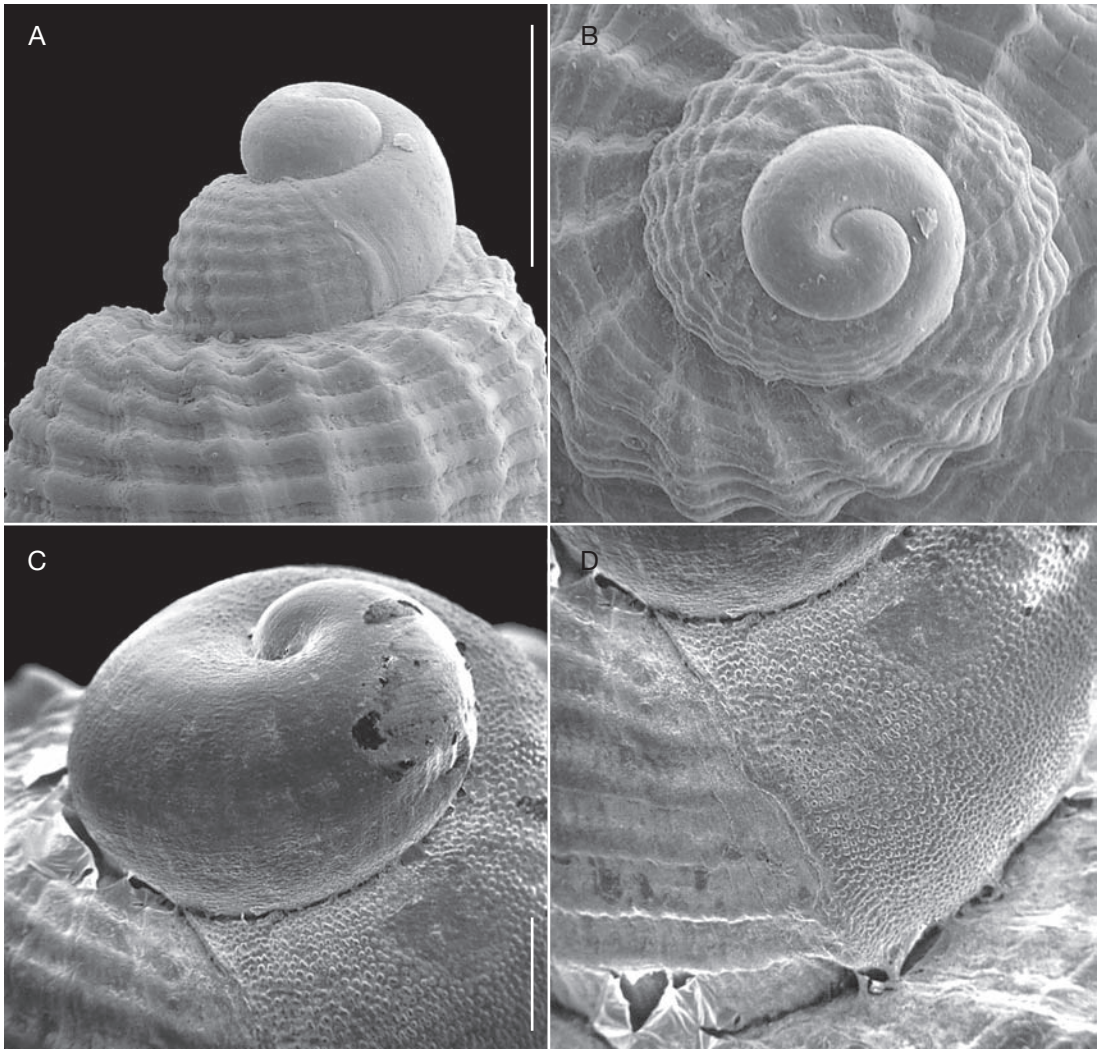

FIG. 63. — Protoconchs of *Trigonostoma scala* (Gmelin, 1791) n. comb. from Senegal (MNHN): **A**, **B**, Joal; **C**, **D**, with granulated surface. Photos: C, D, SEM Laboratory, University of Basel, M. Düggelin, operator. Scale bars: A, B, 500 µm; C, D, 100 µm.

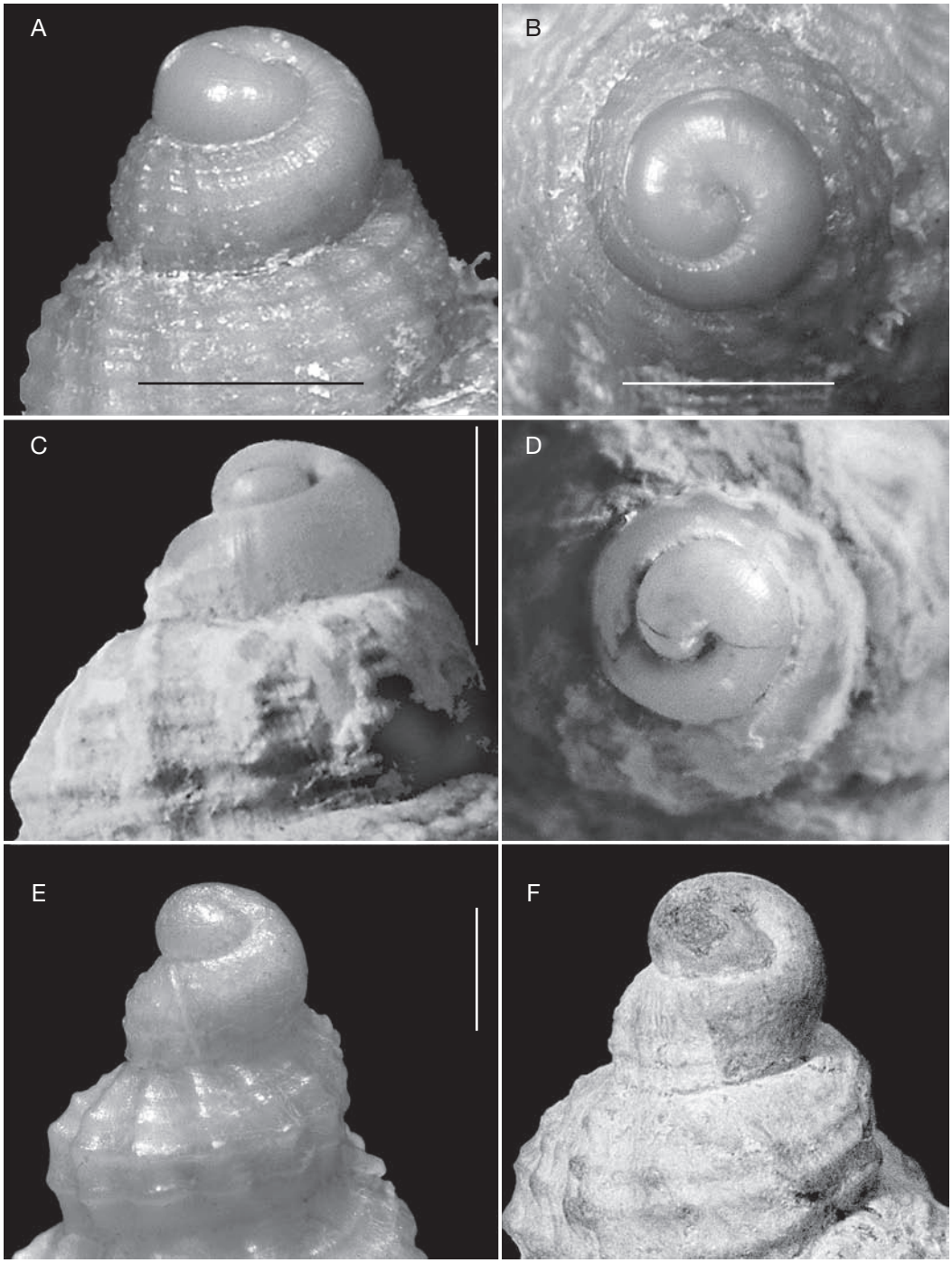

FIG. 64. — Protoconchs: **A**, **B**, *Admetula cornidei* (Altimira, 1978), off Western Sahara, 50-60 m (AV 0047); **C**, **D**, *Admetula gittenbergeri* (Verhecken, 2002) n. comb., paratype 3, from type locality (RMNH); **E**, **F**, *Cancellaria africana* Petit, 1970; **E**, protoconch of fresh shell of Figure 34B; **F**, protoconch of corroded shell of Figure 34E. Scale bars: 1 mm.

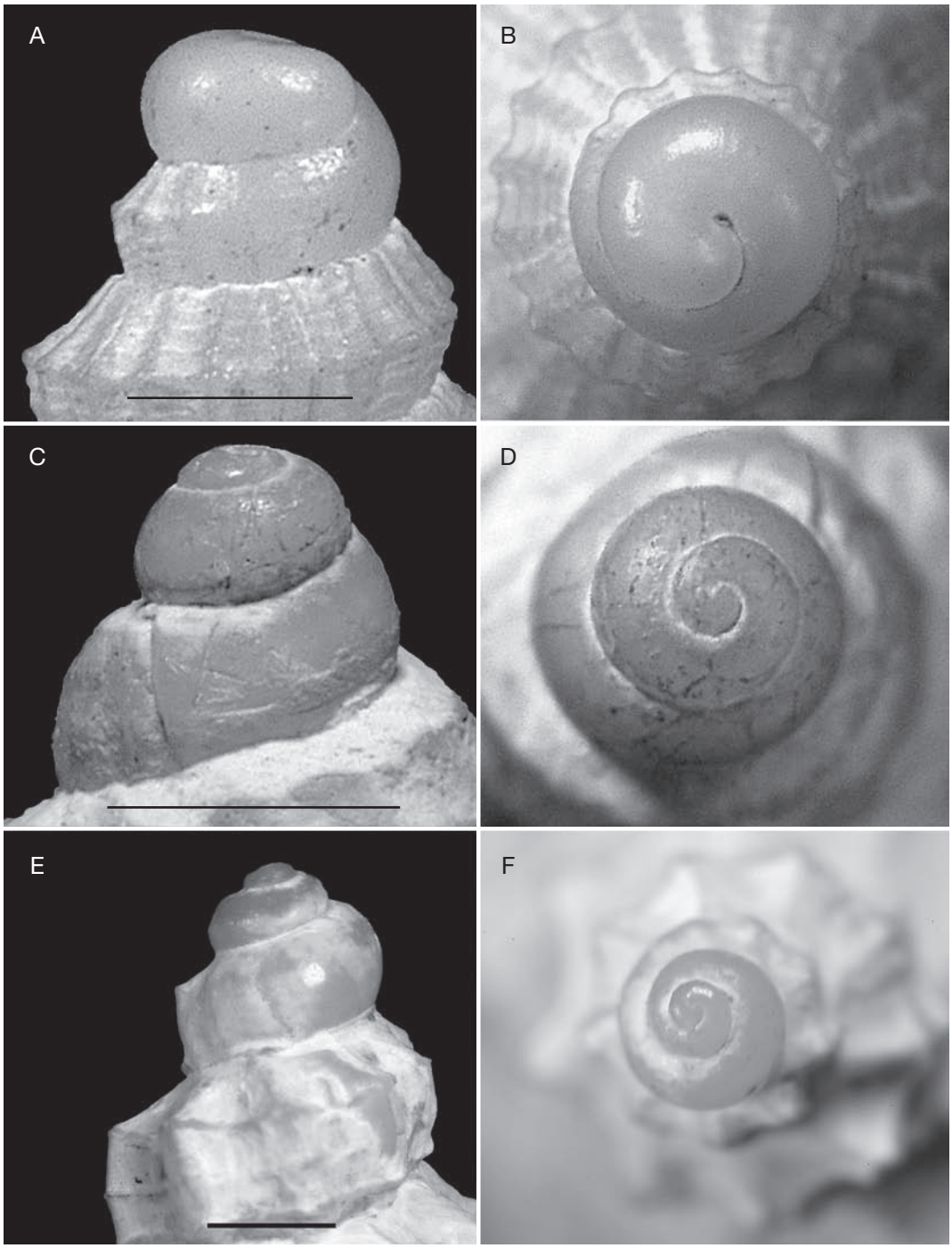

FIG. 65. — Protoconchs: **A**, **B**, *Loxotaphrus deshayesii* (Duval, 1841), shell of Figure 36A (MNHN); **C**, **D**, *Brocchinia azorica* (Bouchet & Warén, 1985), shell of Figure 26; **E**, **F**, *Sveltia lyrata* (Brocchi, 1814), shell of Figure 41A. Scale bars: 1 mm.

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