

Taxonomy of Tropical West African Bivalves V. Noetiidae

by P. Graham OLIVER and Rudo VON COSEL

Abstract. — Five species of Noetiidae are described from tropical West Africa, defined here as between 23° N and 17° S. The Noetiidae are represented by five genera, and four new taxa are introduced : *Stenocista* n. gen., erected for *Arca gambiensis* Reeve; *Sheldonella minutalis* n. sp., *Striarca lactea scoliosa* n. subsp. and *Striarca lactea epetrima* n. subsp. *Striarca lactea* shows considerable variation within species. Ecological factors and geographical clines are invoked to explain some of this variation but local genetic isolation could not be excluded. The relationships of the shallow water West African noetiid species are analysed and compared to the faunas of the Mediterranean, Caribbean, Panamic and Indo-Pacific regions. *Stenocista* is the only genus endemic to West Africa. A general discussion on the relationships of all the shallow water West African Arcoidea is presented. The level of generic endemism is low and there is clear evidence of circumtropical patterns of similarity between species. The greatest affinity is with the Indo-Pacific but this pattern is not consistent between subfamilies. Notably the Anadarinae have greatest similarity to the Panamic faunal province.

Résumé. — Description de cinq espèces de Noetiidae d'Afrique occidentale tropicale, ici définie entre 23° N et 17° S. Les Noetiidae sont représentés par cinq genres. Quatre taxa nouveaux sont décrits : *Stenocista* n. gen. (espèce-type *Arca gambiensis* Reeve); *Sheldonella minutalis* n. sp., *Striarca lactea scoliosa* n. subsp. et *Striarca lactea epetrima* n. subsp. *Striarca lactea* montre une variabilité intraspécifique considérable. Pour l'explication de quelques aspects de cette variabilité, sont évoqués des facteurs écologiques et des clines géographiques mais on ne peut pas exclure une isolation génétique locale. Les espèces de Noetiidae du plateau continental ouest-africain sont analysées sur le plan de leurs relations et comparées avec les faunes de la Méditerranée, des Caraïbes, du Pacifique panaméen et de l'Indo-Pacifique. Le seul genre endémique en Afrique occidentale est *Stenocista*. Une discussion générale sur les relations de toutes les espèces d'Arcoidea du plateau continental ouest-africain est présentée. Le niveau de l'endémisme générique est bas, mais on retrouve toute évidence des motifs de répartition similaires entre les espèces circumtropicales. L'affinité la plus marquée existe avec l'Indo-Pacifique mais ce fait n'est pas constant entre les sous-familles. Notamment les Anadarinae ont la similitude la plus grande avec le Pacifique panaméen.

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INTRODUCTION

This is the second and final part of a revision of the tropical West African Arcoidea. The first part included the Arcidae (OLIVER & COSEL, 1993), and this part deals with the Noetiidae and includes a general on the zoogeographical patterns of the Arcoidea as a whole.

Abbreviations used in the text

BMNH : British Museum (Natural History) (now : The Natural History Museum), London, U.K.
MNHN : Muséum national d'Histoire naturelle, Paris, France.
NMWZ : National Museum of Wales, Dept. of Zoology, Cardiff, U.K.
SMF : Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt/M., Germany.
USNM : United States National Museum, Smithsonian Institution, Washington, D.C., USA.
ZMB : Zoologisches Museum der Humboldt-Universität Berlin, Berlin, Germany.
ZMC : Universitets Zoologisk Museum, Copenhagen, Denmark.

leg. : legit, collected by; sh. : shell, shells; spm. : specimen, specimens; sta. : sampling station;
v. : valve; RV : right valve; LV : left valve.

Family NOETIIDAE

Genus **SHELDONELLA** Maury, 1917

TYPE SPECIES : *Sheldonella maoica* Maury, 1917 (OD).

REVISED DIAGNOSIS : Small shells to about 30 mm in length. Equivalve. Moderately to strongly inflated. Inequilateral, beaks well in front of the midline. Outline modioliform-arciform, posterior area expanded. Posterior angle initially carinate, later may be rounded. Anal ridge weak or absent. Ligament mostly anterior to beaks, posterior growth small, extensive growth in gerontic examples only. Sculpture radial, dominated by the secondary riblets. Adductor scars with myophoric ridges.

SPECIES OF *Sheldonella* : *S. maoica* Maury, 1917 [Miocene, Dominican Republic]. *S. centrola* (Guppy, 1867) [Miocene, Trinidad]. *S. bisulcata* (Lamarck, 1819) [Recent, Southern Caribbean, Brazil]. *S. delgada* (Lowe, 1935) [Recent, Panamic Pacific province]. *S. minutalis* n. sp. this paper [Recent, West Africa]. *S. cafria* (Bartsch, 1915) [South Africa (from Jeffreys Bay eastward), western Indian Ocean]. *S. lateralis* (Reeve, 1844) [Recent, Indo-Pacific].

REMARKS

MACNEIL (1938) considered that the Caribbean species possessing a carinate posterior angle should be placed in the genus *Eontia*. The anal ridge shared by these species and the type species of *Sheldonella* he considered of secondary importance but did note that these species may constitute a subgenus of *Sheldonella*. Conversely when considering the Indo-Pacific species he noted the absence of the anal ridge but then gave them subgeneric status under *Sheldonella* (*Paranoetia*) Thiele. We consider that the epibyssate species included by us in *Sheldonella* cannot be placed within the infaunal genus *Eontia* and that the modioliform shape links these species together. We have examined juveniles (pl. II, 4) of the so-called non carinate species such as *S. lateralis* and find that they are carinate at this stage and that the loss of carination depends on the degree of posterior expansion. Similarly the expression of the anal

ridge is greatest in the more arciform species. Consequently we conclude that there is a continuum of degree of expression of the anal ridge and posterior carina and that *Sheldonella* is best defined on its modioliform shape and epibyssate habit.

***Sheldonella minutalis* n. sp.**

(Pl. I, 5A-B; pl. II, 1-2; fig. 1; map 1)

TYPE MATERIAL : Holotype (6.7 mm), MNHN, Cabo Ledo, Luanda province, Angola, 10-40 m, leg. GOFAS. Paratypes : MNHN, plage ORSTOM, Pointe-Noire, R. P. Congo, 5-7 m, 1 spm, leg. VON COSEL, XI-XII.1985; NMWZ, Palmeirinhas, Luanda province, Angola, 30 m, 2 v., leg. GOFAS, 1985.

TYPE LOCALITY : Cabo Ledo, Luanda province, Angola.

DESCRIPTION

Shell to 10.95 mm in length. Equivalve. Strongly inflated. Inequilateral, beaks in the anterior quarter, directed posteriorly (opisthogyre).

Outline modioliform-arciform, posterior expanded but not greatly so. Posterior area broad demarcated by an initially sharply carinate posterior ridge; anal ridge weakly elevated, situated slightly above the midline of the posterior area; posterior margin biangulate, initially inclined at about 45° but turning to 90° or greater beyond anal ridge. Median area not sulcate, ventral margin gently curving, only rarely indented at the narrow and short byssus gape which is in an antero-ventral position. Anterior area very small, anterior margin rounded but not angled with ventral margin. Dorsal margin long, straight.

Dorsal area flat, becoming wide; umbos widely separated. Ligament symmetrical about the beaks but confined to the anterior part of the dorsal area. First lamellar band between

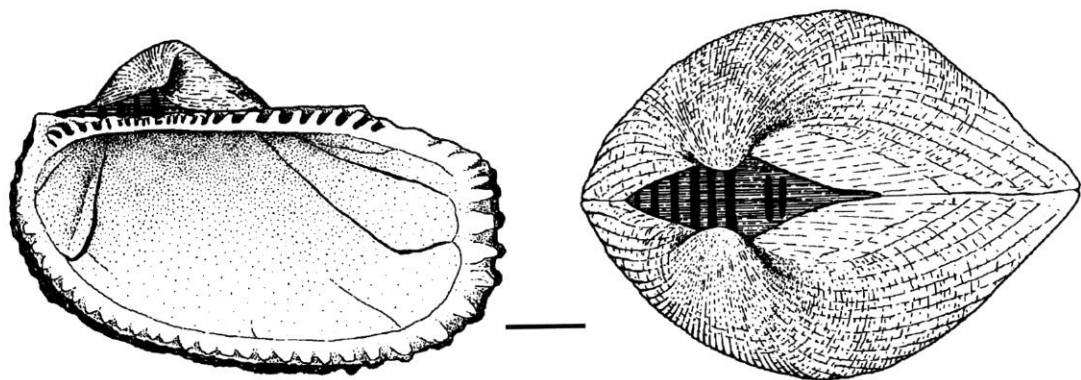


FIG. 1. — Internal view of right valve and dorsal view of *Sheldonella minutalis* n. sp. Holotype. Angola. (Scale bar = 1 mm.)

beaks, then added anteriorly and only in the largest specimens do posterior bands appear. Hinge plate narrow. Teeth in two series but these are barely discernable as median teeth are frequently eroded; anterior set up to 15 teeth, posterior set up to 15 teeth. Teeth small, straight, anterior set more or less vertical, posterior set becoming progressively oblique.

Sculpture primarily of radial riblets and raised threads. Primary riblets narrow, secondaries developing early and forming the dominant sculpture. 36-39 dominant riblets; anterior 3-4 moderately broad; median riblets narrow, closely spaced, evenly nodulose; posterior riblets variable, some broadening rapidly but rarely bifurcate, ridged or weakly nodulose. Primary riblets fading to raised threads anteriorly; becoming obsolete medially; remaining prominent on posterior area, narrower than secondaries although usually higher, nodulose.

Periostracum spicate from primary riblets but lamellar from secondary riblets, bristles larger along posterior angle. Bristles dark brown, lamellae paler.

Shell white.

Inner margin strongly crenulate posteriorly, becoming finer anteriorly and may almost fade completely along the byssal gape.

Adductor muscle scars subequal, the posterior slightly larger, both with myophoric ridges on either side and extending into umbonal cavity. Byssus retractor scar elongate oval, lying under end of posterior hinge plate, length more or less = width of posterior adductor.

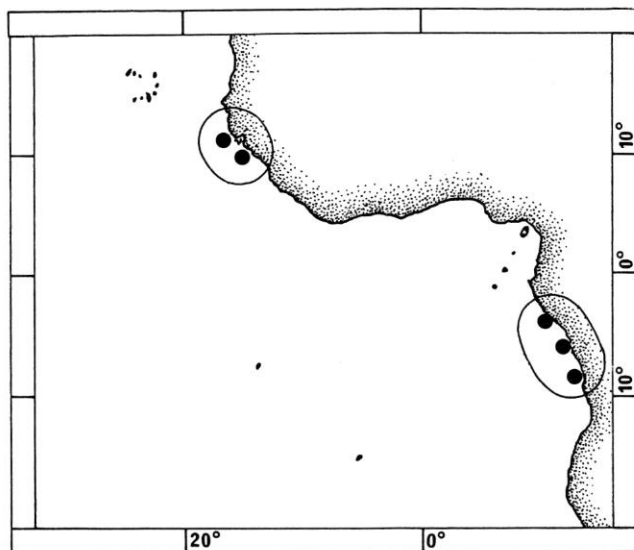
SELECTED SHELL MEASUREMENTS (mm)

Length	Height	Tumidity	Ant. margin to beak	Length	Height	Tumidity	Ant. margin to beak
6.7	4.3	5.0	1.8	5.0	2.9	3.6	1.4
6.0	3.5	4.2	1.4	5.2	3.1	3.8	1.4
5.7	3.2	3.6	1.5	8.4	5.3	6.5	2.3
6.0	3.4	4.1	1.8	7.8	4.6	5.4	2.4

DISTRIBUTION : This species has a widely disjunct distribution with a northern range around Guinea-Bissau and Guinea and then a southern range along the coasts of R. P. Congo and Angola. The reasons for this are not known.

MATERIAL EXAMINED : **Guinea-Bissau** : no precise locality, 7 v., leg. mission L. GAIN; îles Bissagos, 1 spm. + 2 v., coll. L. GAIN, 1913; both MNHN. **Guinea** : Capken, île Tristão, 1 v., coll. NICKLÈS, 1947; Conakry, 1 v., 9°18' N/13°41,5' W, 20 m, 1 v., dredged R/V « André Nizery », leg. VON COSEL, 16.V.1988; both MNHN. **Gabon** : Cap Esterias-Pointe Idolo, 1 v., leg. VON COSEL, 14.XI.1985, MNHN. **R. P. Congo** : Pointe-Noire, 9 v., coll. ORSTOM; Pointe-Noire, Plage Mondaine, many v.; Plage ORSTOM, 5-7 m, 1 spm., both leg. VON COSEL, XI-XII.1985; all MNHN. **Angola** : Ambrizete, Zaire province, on beach, 8 v.; Ambrizete, 07°17'49" S/12°53'05" E, 8 v.; 07°20'19" S/12°55'09" E, 30 v.; 10 km S of Ambrizete, 1 v.; Cabo Ledo, Luanda province, 40 m, 7 spm.; Cabo Ledo, 1 v.; Cabo Ledo, 10-40 m, 1 v.; Barra do Dande, Bengo province, 0-2 m, 3 v.; off Mussulo, Luanda province, 90-100 m, 1 v.; Punta do Mussulo, Luanda province, on beach, 1 v.; Palmeirinhas, Luanda province, 30 m, 2 v., all leg. GOFAS; all MNHN.

BIOTOPE : This species lives byssally attached to hard objects in areas of muddy sand and fine sand. From the limited material at hand it is restricted to depths of 5-40 m and is quite rare.



MAP 1. — Distribution of *Sheldonella minutalis*.

DERIVATIO NOMINIS : *minutalis*, Latin, « insignificant », referring to the small size and grubby appearance of the shells when the periostracum is intact.

REMARKS

Sheldonella minutalis was compared with the Indo-Pacific species *S. cafrina*, *S. lateralis* (pl. II, 4) and the Caribbean *S. bisulcata* (pl. II, 3). The much larger (to 40 mm) *S. cafrina* and *S. lateralis* differ in lacking the anal ridge when adult, are more expanded posteriorly, and the posterior dominant riblets widen rapidly and are consistently bifurcate. *S. bisulcata* is also a larger species reaching 30 mm in length and is less inequilateral. It has fewer dominant riblets, 33-34, and these are wider and more strongly sculptured especially on the posterior area. The persistent primary riblets on the posterior angle are lower than the dominant riblets.

There does appear to be some regional variation in *S. minutalis* in that the few examples available to us from the north of its range around Guinea-Bissau differ as follows : the anterior reduction is greater, the median riblets are narrower and the narrow primaries on the posterior angle are lower than the adjacent secondaries. These differences further separate the West African species from its closest counterpart, *S. bisulcata*. LAMY (1923) listed the specimens collected by the mission L. GAIN from Guinea-Bissau as *A. martini* Recluz (= *S. bisulcata*) but he also stated that he could scarcely separate them from *S. cafrina* from Pt. Alfred, S. Africa. We consider that they fall within the range of *S. minutalis*.

Genus **STENOCISTA** n. gen.

TYPE SPECIES : *Arca gambiensis* Reeve, 1844.

DIAGNOSIS : Small shells to 35 mm in length. Thin shelled. Equivalve. Compressed. Subequilateral, beaks just in front of the midline, orthogyre. Outline subquadrate, oblong. Dorsal area narrow, ligament amphidetic covering entire dorsal area, lamellar bands narrow and numerous. Primary riblets outgrown by secondary ribs which become broad and flat. Adductor scars lacking myophoric ridges or with a faint line only on the ventral edge of the posterior scar. Endobysate, byssus of a few narrow threads adhering to sediment particles.

SPECIES OF *Stenocista* : This genus is so far monotypic.

REMARKS

« *Arca* » *gambiensis* has been previously referred to *Noetia* and *Sheldonella* but it differs from these and all other Recent species which have dominant secondary sculpture in possessing orthogyre beaks and an amphidetic ligament. The compressed form of the shell is also unusual and resembles a few similarly rare species of Anadarinae such as *Anadara deyrollei* and *A. jousseaumei* all of which are considered to be infaunal inhabitants of soft muds or sandy muds. This form contrasts with the inflated, umbonate infaunal species of *Noetia* and *Eontia*. To find any species with the orthogyre beaks and amphidetic ligament one must return to the Eocene fauna of Nigeria described by NEWTON (1922) and EAMES (1957). *Protonoetia nigeriensis* (Newton, 1922) despite being a quadrate inflated form does have wide smooth ribs, orthogyre beaks and an almost amphidetic ligament. *Stenocista* may therefore be derived from that lineage and is part of a regional radiation represented in its early stages by the Nigerian fauna.

DERIVATIO NOMINIS : *Stenocista*, Greek, f., from *steno* meaning narrow or compressed and *cista*, a small box.

***Stenocista gambiensis* (Reeve, 1844)**

(Pl. I, 1, 2A-B, 3; fig. 2-3; map 2)

Arca gambiensis Reeve, 1844 : pl. 6, fig. 36.

TYPE MATERIAL : In BMNH.

TYPE LOCALITY : Gambia, but with no details.

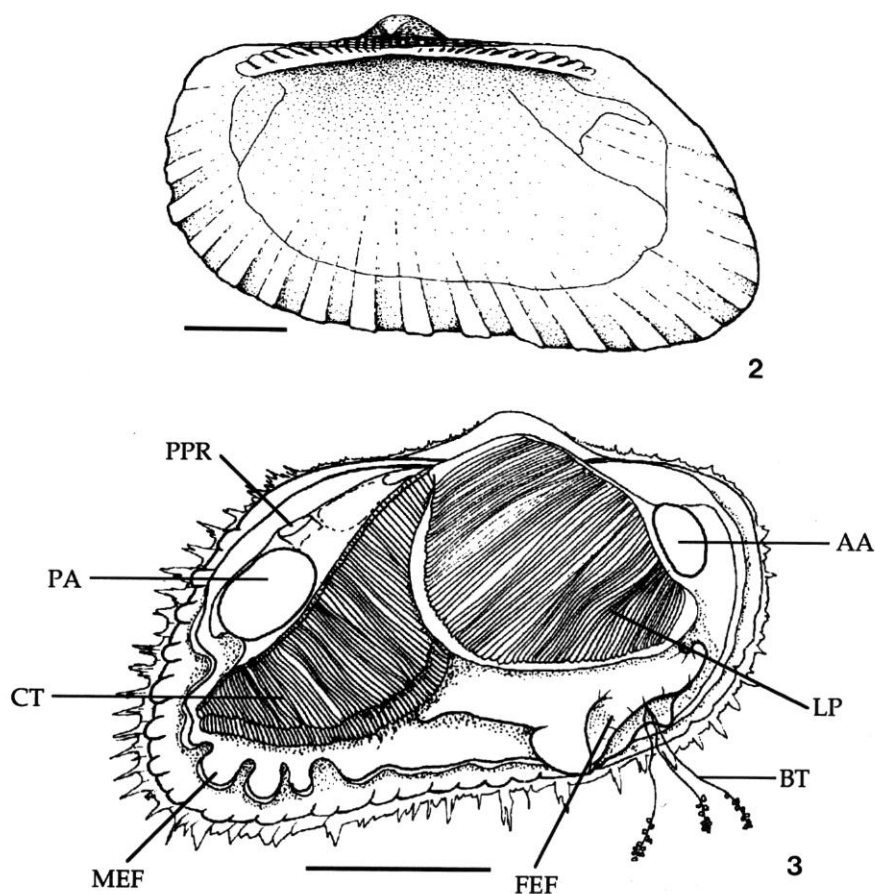


FIG. 2. — Internal view of right valve of *Stenocista gambiensis* (Reeve). Gambia. (Scale bar = 5 mm.)

FIG. 3. — Gross anatomy of *Stenocista gambiensis*, viewed from the right side after removal of the right valve and mantle. (Scale bar = 5 mm.)

AA, anterior adductor muscle. BT, byssus threads. CT, ctenidium. FEF, frilled edge of foot. LP, labial palps. MEF, mantle edge folds. PA, posterior adductor muscle. PPR, posterior pedal retractor muscle.

DESCRIPTION

Shell to 35 mm in length. Equivalve, compressed, rather thin, very slightly twisted about the weak median sinus. Subequilateral, beaks just in front of the midline, orthogyre.

Outline subquadrate becoming oblong, longer than high, slightly expanded posteriorly. Posterior area weakly demarcated by low rounded posterior angle; posterior margin obliquely truncate; ventral margin more or less straight with a slight sinuation at exit point of byssus but

no gape present; anterior margin broadly rounded, straightening later; dorsal margin long, straight.

Dorsal area narrow, umbos very low and not widely separate. Ligament amphidetic, filling whole of dorsal area; chevrons numerous, closely spaced.

Hinge plate narrow, teeth in two series; anterior set up to 16 teeth, posterior set up to 21 teeth. Teeth small, straight, median teeth vertical, lateral teeth progressively oblique.

Sculpture : of radial ribs and riblets. Primary riblets remaining weak or subobsolete; secondary elements developing rapidly to form 22-25 low, broad ribs, initially these are weakly carinate, later flat,

Periostracum dark brown, lamellar over major ribs with long subtubular blunt bristles arising from the interspace primaries; similar but shorter bristles arise from the carinae of the major ribs.

Shell white.

Inner margin strongly crenulate corresponding to major ribs.

Adductor muscle scars subequal, usually lacking any myophoric ridges but very rarely a raised line ventral to the posterior scar may be present.

ANATOMY

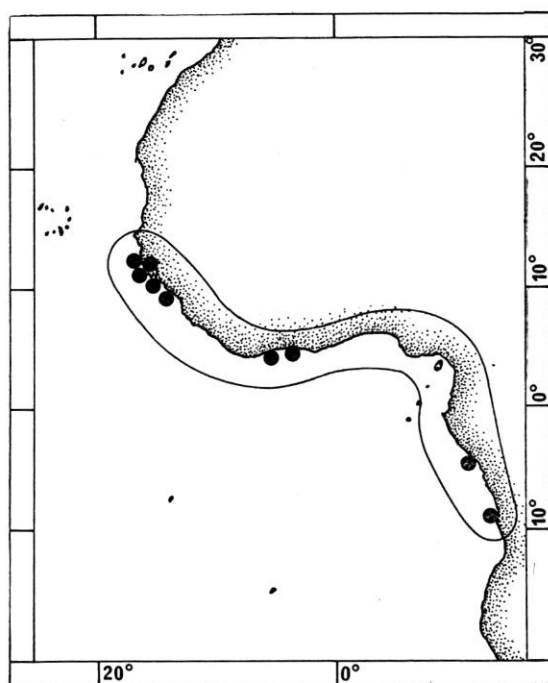
The following brief description is based on a single specimen and concerns the gross features only without dissection.

The mantle edge is entirely unfused and thickened posteriorly where it is thrown into large folds. In the preserved state these folds lie well in from the shell edge and, given their musculature, are probably able to extend to or more likely beyond the shell margin. This situation would be similar to that known for *Estellacar* (OLIVER, 1987b, 1990b). The mantle edge is totally unpigmented and does not bear any eyespots or even the antero-dorsal pigment spot observed in most other infaunal Noetiidae (OLIVER, 1985, 1990c).

The gills are relatively small and restricted to the area behind the umbos, otherwise they are typical of other arcoids. The labial palps in contrast are exceptionally large, semi-circular in outline and have over 100 ridges. These are as yet some of the largest labial palps seen in any arcoid bivalve and even bigger than those of other infaunal noetiids such as *Noetiella* and *Estellacar* (OLIVER 1990a, b).

The foot is not large but the toe is expanded and bears a narrow frilled margin. This type of frill has not been observed in other noetiids but could be expected if there was a need to increase the surface area for crawling across or through the surface of soft sediments rather than burrowing into it. The byssus is active and composed of a few thin threads to which sediment particles are attached. The byssus retractor muscle is small and situated just in front of the posterior adductor.

The gross anatomy described would indicate that *Stenocista* lives in turbid soft sediment sites where the huge labial palps are required for sorting large quantities of material. It is possible that much of the ingested food is resuspended sediment. However the shape of the shell, foot and form of the byssus suggests that it is probably semi-infaunal and may plough through the surface layers rather than burrow deeply as does *Estellacar* (OLIVER 1990b).



MAP 2. — Distribution of *Stenocista gambiensis*.

SELECTED SHELL MEASUREMENTS : See figure 4.

DISTRIBUTION : From Gambia and Casamance south to northern Angola (Luanda).

MATERIAL EXAMINED : **Gambia** : No precise locality, 3 sh., coll. DENIS, MNHN; no precise locality, 2 sh., NMWZ. **Senegal** : No precise locality, 2 v., coll. GRUVEL; Casamance, 8 v., coll. NICKLÈS; Casamance River, Ziguinchor, 3-5 m, 1 v., leg. VON COSEL, 15.III.1988; N Casamance, Abéné-Kafountine, on beach, 4 v.; Kafountine, on beach, 3 v.; Karabane Bôlon, 4 m, 1 v.; S Casamance, Cap Skirring, beach to the south, many v.; Cap Skirring-Diembéring, on beach, many v., S of Cap Skirring, 3-5 m., 8 spm. + 6 v., Elinkine, in creek, 3 m, 1 v., all leg. VON COSEL, 3-17.III.1988; Cap Roxo, 12°20,7' N/16°53,1' W, 15 m, 1 v., dredged R/V "Louis Sauger", leg. VON COSEL, 27.III.1988; all MNHN. **Guinea-Bissau** : Cap Varela, 6 v., coll. MAURY, 1964; Cap Varela, 2 v., coll. MARCHE-MARCHAD, 1953, both MNHN. **Guinea** : 10°21' N/14°35,5' W, 6 m, 2 spm.; 9°42' N/13°50,2' W, 4 m, 2 spm., both dredged R/V "André Nizery", leg. VON COSEL, IV-V.1988; îles Tristão, 3 v., coll. NICKLÈS, 1947, all MNHN. **Côte d'Ivoire** : Bassam, 20 m, 1 sh.; Grand Bassam, 15 m, 1 sh.; 14 m, 5 spm.; Abidjan, 20 m, 1 spm.; Vridi, 20 m, 1 spm.; Vridi, 12 m, 1 spm., all dredged R/V "Reine Pokou" leg. LE LOEUFF, (ORSTOM), 1966-1970; off Abidjan, 4°56' N/5°58' W, 12 m, dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 3.IV.1964; all MNHN. **R. P. Congo** : Pointe-Noire, off Plage ORSTOM, 5-7 m, 1 spm. + 1 v., 3-4 m, 3 v.; Plage Mondaine, on beach, 6 v., all leg. VON COSEL, X-XI.1985; all MNHN. **Angola** : Punta do Mussulo, Luanda province, on beach, 1 v., leg. GOFAS, MNHN.

BIOTOPE : *Stenocista gambiensis* lives in fine sediments of mud or muddy sand in shallow water from 2-20 m. The relative scarcity of this type of habitat render the species only locally common.

REMARKS : *Stenocista gambiensis* is so unique that it should not be confused with any other species of the Noetiidae.

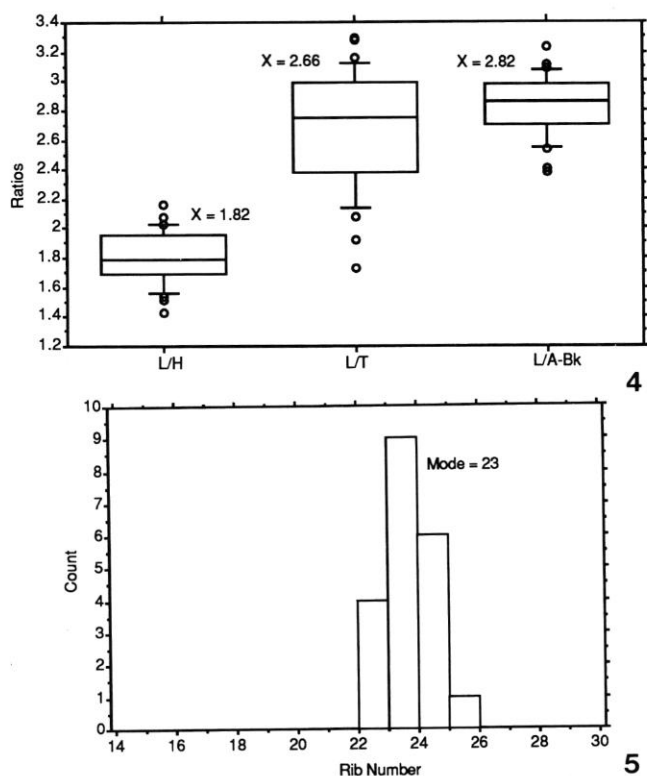


FIG. 4-5. — 4 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Stenocista gambiensis* (n = 30). 5 : Bar chart of Rib Number for *Stenocista gambiensis* (n = 30).

Genus NOETIELLA Thiele and Jaeckel, 1931

TYPE SPECIES : *Arca (Noetiella) congoensis* Thiele and Jaeckel, 1931 (OD).

Noetiella congoensis (Thiele and Jaeckel, 1931) (Pl. I, 4A-B; fig. 6; map 3)

Noetiella congoensis Thiele and Jaeckel, 1931 : 176, pl. 1 (or 6), fig. 11.
Arca lactea Linné; DAUTZENBERG, 1913 : 86 [in part].
Arca lactea Linné; NICKLÈS, 1955 : 116 [in part].
Arca afra Gmelin; DELL, 1964 : 237.

TYPE MATERIAL : Syntypes in ZMB Berlin.

TYPE LOCALITY : Mouth of the Congo River.

DESCRIPTION

Shell to 15 mm in length. Equivalve. Slightly inflated. Inequilateral, beaks slightly to the posterior of the midline, opisthogyre.

Outline subrhomboidal, anteriorly expanded and posteriorly narrowed. Posterior area short, sloping steeply and demarcated by a prominent subacute posterior angle; posterior margin steeply oblique, straight; posterior ventral junction acute. Median area never sulcate, more or less flat; ventral margin more or less straight but slightly inclined towards the posterior. Anterior area expanded, anterior angle obsolete, anterior margin very broadly rounded. Dorsal margin short, straight.

Dorsal area narrow, umbonal separation weak. Ligament initially prosodetic but later secondarily amphidetic, vertical bars numerous, narrow.

Hinge plate narrow, teeth in 2 series, separation obscure, anterior set up to 18 teeth, posterior set up to 12 teeth. Teeth small, laminar, mostly vertical but the marginals rather oblique.

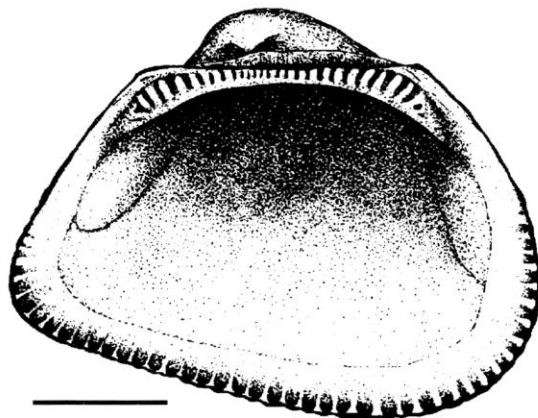


FIG. 6. — Internal view of left valve of *Noetiella congoensis* Thiele & Jaeckel. Côte d'Ivoire. (Scale bar = 2 mm.)

Sculpture of about 60 low, rather indistinct radial riblets or raised lines.

Periostracum persistent, a rather thick coating with dense concentric lines except posteriorly where the radial element is expressed as short hairs and where the concentric element is slightly raised into narrow lamellae. Colour pale brown but often coated with a black or rust coloured deposit.

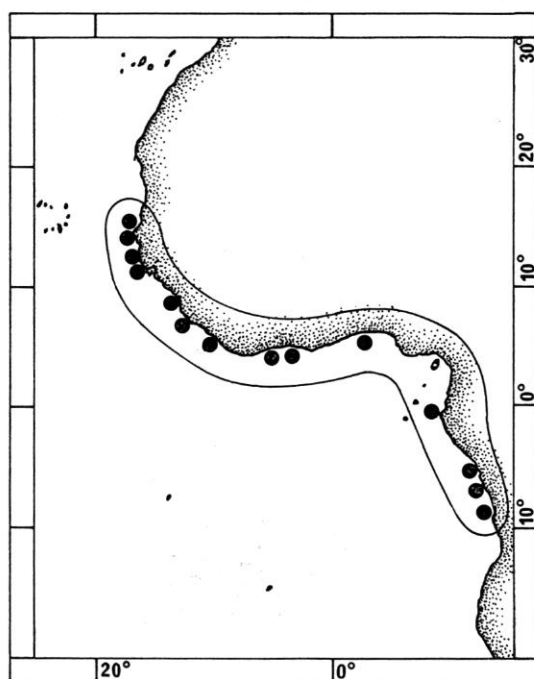
Shell white.

Adductor scars subequal, the anterior a little larger. Inner margin finely fluted.

SELECTED SHELL MEASUREMENTS : See figure 7.

DISTRIBUTION : Senegal (Dakar) to northern Angola.

MATERIAL EXAMINED : **Senegal** : N of Cayar, 15°12' N/15°54' W, 25 m, 1 v., 6.IV.1967; S of Gorée, 65 m, 1 v.; SE of Gorée, 33-34 m, 1 v.; off M'Bao, 20 m, 1 v., all dredged "Gérard Tréca", 1953-1958,

MAP 3. — Distribution of *Noetiella congoensis*.

leg. MARCHE-MARCHAD; SE of Gorée, 14°41' N/17°23,2' W, 17 m, 2 v.; Casamance, 12°32' N/17°28,8' W, 45 m, 1 v.; 12°20,7' N/16°53,1' W, 15 m, 1 spm. + many v.; off Cap Skirring, 12°23' N/16°52,8' W, 13 m, 3 v.; off Cap Skirring, 12°20,7' N/16°53,1' W, 15 m, 2 v., all dredged R/V "Louis Sauger", leg. VON COSEL, III.1988; S Casamance, Elinkine, in creek, 3 m, 1 v.; N Casamance, Karabane Bôlon, 4 m, 3 v., both leg VON COSEL, 17.III.1988; all MNHN. **Guinea-Bissau**: No precise locality, 3 v., leg. L. GAIN, 1913, MNHN. **Guinea**: Conakry, on beach, many v.; off Conakry, 9°40' N/14°05' W, 18 m, 1 v., dredged RV "Calypso", leg. MARCHE-MARCHAD, both MNHN. **Sierra Leone**: Off Freetown, "Atlantide" sta. 141, 15 m, 3 v., MNHN. **Liberia**: 4°34,5' N/8°31' W, 64 m, 2 v., dredged RV "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. **Côte d'Ivoire**: 4°27,5' N/7°09' W, 50 m, 5 v.; 4°52,5' N/5°57,5' W, 40 m, 1 v.; 5°09' N/4°39' W, 20 m, 3 v.; 4°30' N/7°09' W, 35 m, 2 v.; 4°56' N/5°58' W, 12 m, 2 v.; 5°06' N/4°38,5' W, 50 m, 5 v.; 5°04' N/5°18' W, 30 m, 7 v., all dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 1964, all MNHN. Abidjan, 1 sh. + 6 v., leg. MARCHE-MARCHAD; Abidjan region, 20-80 m, many spm. + v. from 9 stations, all dredged R/V "Reine Pokou", leg. LE LOEUFF (ORSTOM), 1967-1970, all MNHN. **Nigeria**: Off mouth of Niger, 4°03' N/6°12' E, 32 m, many v., dredged RV "Calypso", leg. MARCHE-MARCHAD, 26.V.1956, MNHN. **Gabon**: Port-Gentil, 0°42' S/8°47,2' E, 10 m, 1 sh., dredged RV "Calypso", leg. MARCHE-MARCHAD, 16.IV.1956, MNHN. **R. P. Congo**: Pointe-Noire, 7 sh.; Pointe-Noire, 5°56' S/12°07' E, 1 sh., both coll. Office Pointe-Noire; off Conkouati, 4°00' S/10°59' E, 19 m, 9 v., dredged "Kounda", leg. VON COSEL, XII.1985; Pointe-Noire, Plage Mondaine, 1 v.; off Plage ORSTOM, 3-7 m, 2 spm. + 1 v., both leg. VON COSEL, XI/XII.1985; all MNHN. **Angola**: Praia Etambar, Corimba, Luanda province, 1 sh. + 1 v.; Corimba, Luanda province, 10-20 m, 7 v.; Ilha de Luanda, Luanda province, 75-80 m, 7 spm.; Barra do Dande, Bengo province, 0-2 m, 1 v.; Cacuaco, Bengo province, 5-10 m, 5 v., all leg. GOFAS, 1981-85; all MNHN.

BIOTOPE: This species lives in fine or muddy sand from shallow subtidal to well offshore (80 m).

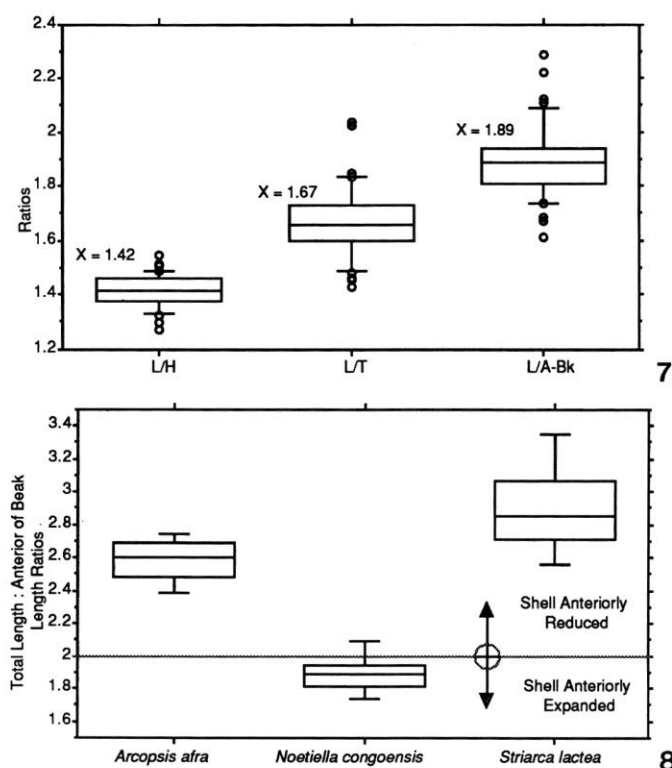


FIG. 7-8. — 7 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/ABk) of *Noetiella congoensis* (n = 38). 8 : Box plots of the ratio Total Shell Length to Anterior to Beak Length for three species of Noetiidae. Infaunal species lie below the ratio 2, epifaunal species above the ratio 2.

REMARKS : This is the only species of West African noetiids to possess a prosodetic ligament and consequently it should not be confused with any other species in this region. The functional morphology and relationships of this genus are described by OLIVER (1987a, 1990b).

Genus **STRIARCA** Conrad, 1862

TYPE SPECIES : *Arca centenaria* Say, 1824 (OD).

Striarca lactea lactea (Linné, 1758)

(Pl. I, 8A-C; fig. 9; map 4)

Arca lactea Linné, 1758 : 694.

TYPE MATERIAL : Syntypes in Linnean Society of London collection (DODGE, 1952 : 148-149).

TYPE LOCALITY : Mediterranean Sea, ("In M. Mediterraneo", LINNÉ, 1758).

We have noted considerable variation in the shells of *Striarca lactea* from throughout its range and have given subspecific status to two of the West African forms. Below we have given a general description of the nominate species and differential descriptions of the new subspecies.

DESCRIPTION

Shell to 20 mm in length. Equivalve, moderately inflated. Inequilateral, beaks in front of the midline, marginally opisthogyre.

Outline subquadrate, longer than high, not or slightly expanded posteriorly. Posterior area demarcated by distinct posterior angle, carinate in juveniles, soon becoming rounded; posterior margin obliquely truncate to slightly curved. Median area slightly sulcate in juveniles, soon not apparent; ventral margin gently curving or straight, rarely indented at short, narrow byssal gape. Anterior margin broadly rounded. Dorsal margin long, straight.

Dorsal area becoming wide, umbos becoming widely separated. Ligament amphidetic expanding symmetrically to cover most of dorsal area in older specimens.

Hinge plate narrow; teeth in two series but gap barely discernable, numbering up to 35 in total. Teeth straight, vertical medially, slightly angled laterally.

Sculpture of numerous radial riblets, these developing interspace riblets over the antero-median and anterior areas. Anterior riblets narrow with equally sized interspaces contrasting with the postero-median riblets which are more closely spaced; posterior riblets widely spaced, narrow but becoming higher and more irregular than other riblets. All median and anterior riblets nodulose, these taking the form of stepped beads; posterior riblets more irregularly nodulose.

Periostracum straw coloured of bristles arising from the riblets on the posterior angle, finer bristles elsewhere and overall with lamellar periostracum in the interspaces.

Shell white.

Inner margin finely crenulate except for stronger teeth on posterior margin and almost absence of serrations at byssal gape.

Adductor muscle scars subequal, both with myophoric ridges. Byssus/posterior pedal retractor scar narrow, elongate, situated below the posterior end of the hinge plate.

DISTRIBUTION : Irish and southern North Sea, south to Morocco and throughout the Mediterranean and Black Sea, except the Azov Sea. Intermediate forms occur off Mauritania and in the Cape Verde Islands.

BIOTOPE : In the intertidal they are usually found byssally attached under rocks which are often partly embedded in sand or silty gravel. Offshore they are attached to stones but the exact orientation of these is not certain. Living from low in the littoral and offshore to about 100 m. Deeper records are of dead shells.

***Striarca lactea scoliosa* n. subsp.**

(Pl. I, 7A-B; fig. 12B; map 4)

TYPE MATERIAL : Holotype (9.7 mm), MNHN, Nigeria, SE of Lagos, Guinean Trawling Survey, R/V "Thierry" Sta. 38/6, 6°02' N/4°16' E, 100 m. 10.X.1963. Paratypes : MNHN, 3 spm. as holotype; NMWZ, 2 spm. as holotype.

TYPE LOCALITY : SE of Lagos, Nigeria.

DESCRIPTION

Shell to 11 mm in length. Equivalve, more inflated. Inequilateral, beaks well in front of the midline, marginally opisthogyre.

Outline subquadrate, somewhat oblique, longer than high, not or slightly expanded posteriorly. Posterior area demarcated by distinct posterior angle, carinate in juveniles and remaining so. Posterior margin obliquely truncate, straight to slightly auriculate. Anterior margin rounded but sloping obliquely. Dorsal margin long, straight.

Sculpture of numerous radial riblets, these rapidly developing interspace riblets over the antero-median and anterior areas. Anterior riblets narrow with equally sized interspaces contrasting with the postero-median riblets which are more closely spaced; posterior riblets widely spaced, narrow and similar to anterior riblets. All median and anterior riblets nodulose, these taking the form of closely spaced regular beads; posterior riblets more irregularly nodulose.

Periostracum rust coloured, of distinct bristles arising from the riblets on the posterior angle, finer bristles elsewhere and overall with lamellar periostracum in the interspaces.

Adductor muscle scars subequal, both with myophoric ridges extending into the umbonal cavity. Byssus/posterior pedal retractor scar narrow, elongate, situated below the posterior end of the hinge plate. Between this scar and the posterior adductor there is a well marked anal groove.

DERIVATIO NOMINIS : *scoliosa* from "skolios", Greek, "oblique" referring to the inequilateral, oblique outline of the shell.

DISTRIBUTION : Senegal to Nigeria.

BIOTOPE : These deep water populations are byssally attached but to small stones or other solid objects in sandy or muddy areas. It is likely that these are not restricted to the undersides of rocks as are the littoral populations of *S. l. lactea* and *S. l. epetrima*. Found offshore from 35-200 m.

***Striarca lactea epetrima* n. subsp.**

(Pl. I, 6A-B; fig. 12C; map 4)

TYPE MATERIAL : Holotype (9.25 mm), MNHN, Angola, Baía do Limagem, Benguela province, 0-2 m.
Paratypes : MNHN, 7 spm. as holotype; NMWZ, 3 spm. as holotype.

TYPE LOCALITY : Baía do Limagem, Angola.

DESCRIPTION

Shell to 13.5 mm in length. Equivalve, moderately inflated. Inequilateral, beaks in front of the midline, marginally opisthogyre.

Outline subquadrate, longer than high, not or slightly expanded posteriorly. Posterior area demarcated by distinct posterior angle, carinate in juveniles, rounded only in the largest individuals. Posterior margin obliquely truncate, straight. Anterior margin rounded. Dorsal margin long, straight.

Sculpture of numerous radial riblets, these rapidly developing interspace riblets over the antero-median and anterior areas; these twice as dense as in the typical form. Anterior riblets narrow with equally sized interspaces contrasting with the postero-median riblets which are more closely spaced; posterior riblets widely spaced, narrow and similar to anterior riblets. All median and anterior riblets nodulose, these taking the form of closely packed regular beads; posterior riblets regularly nodulose.

Periostracum straw coloured, of bristles arising from the riblets on the posterior angle, finer bristles elsewhere and overall with lamellar periostracum in the interspaces.

Adductor muscle scars subequal, both with myophoric ridges extending into the umbonal cavity. Byssus/posterior pedal retractor scar narrow, elongate, situated below the posterior end of the hinge plate. Between this scar and the posterior adductor there is a well marked anal groove.

DERIVATIO NOMINIS : *epetrima* from *epetrimos*, Greek, "closely packed", referring to the closely spaced radial sculpture typical of this species.

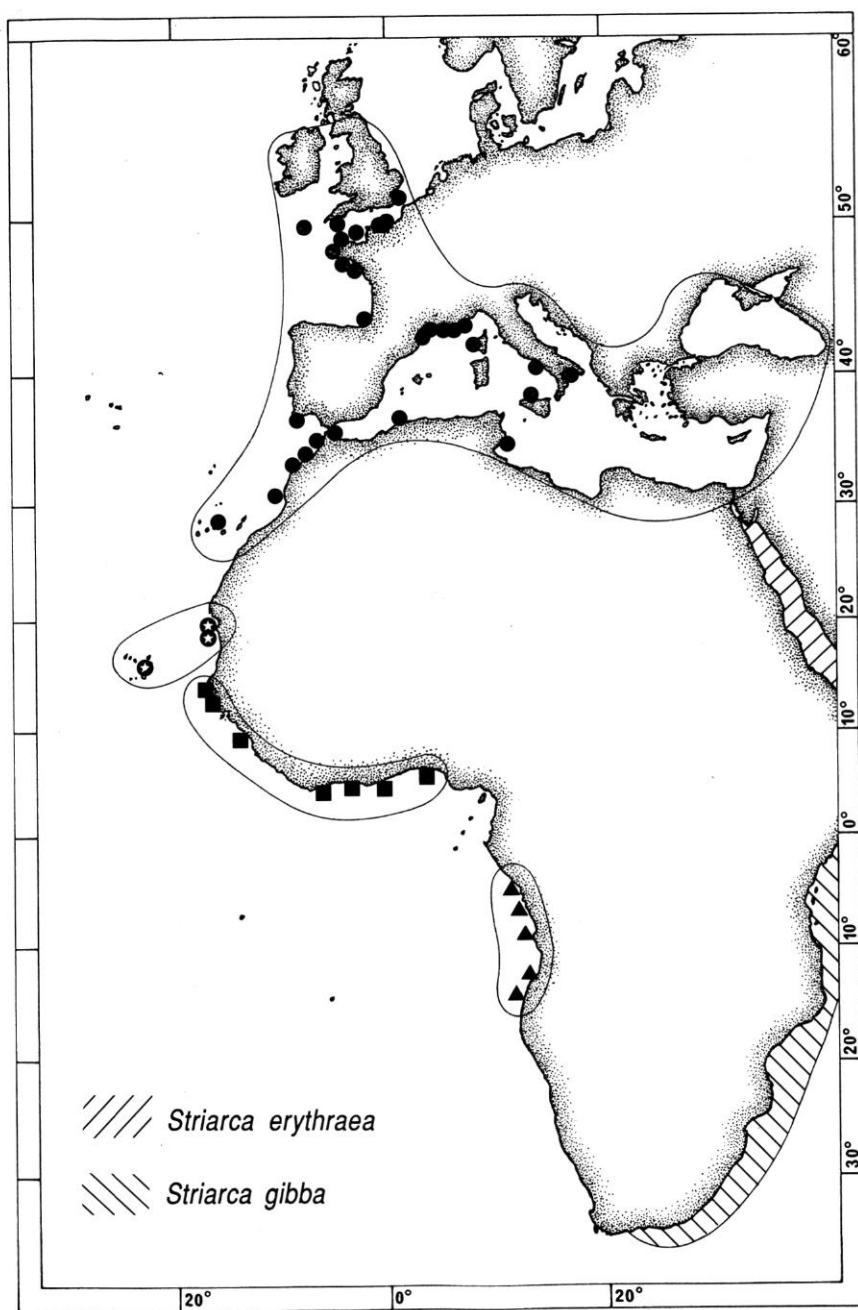
DISTRIBUTION : R.P. Congo to southern Angola (Moçâmedes).

BIOTOPE : The littoral populations from Angola are found byssally attached under rocks which are partly embedded in sand or silty gravel. The offshore samples are byssally attached but to small stones or other solid objects. Found from low in the intertidal to 40 m offshore.

SELECTED SHELL MEASUREMENTS : See in Remarks section.

MATERIAL EXAMINED

Striarca lactea lactea : **British Isles** : Plymouth, 5 spm., Herm, many spm., both coll. MARSHALL, NMWZ; Deal, 2 sh., leg. STAADT; Celtic Sea, between 49°15' N-48°33' N, 95°09' W/05°28' W, 102-112 m, dredged RV "Thalassa", leg. VON COSEL, XII.1983, all MNHN. **Atlantic France** : Étretat, Seine-



MAP 4. — Distribution of *Striarca lactea* agg. : *S. l. lactea* (circles), *S. l. scoliosa* (squares), *S. l. epetrima* (triangles), intermediate form (stars in circles), *S. erythraea* and *S. gibba* (shaded areas).

Maritime, 1 sh., 1 v., coll. H. FISCHER; St. Vaast, Manche, 3 sh., old colln.; Granville, Manche, 7 spm., coll. AUDOIN & EDWARDS; Brest, 3 spm., coll. LOCARD; Roscoff, 3 spm., old colln.; Quiberon, 1 spm., coll. LOCARD; Noirmoutier Is., Vendée, several spm., old colln.; Guéthary, South, Gulf of Gascony, many spm., leg. H. FISCHER, 1898; all MNHN. **Atlantic Spain**: San Sebastian, 2 v., leg. STAADT, 1935, MNHN. **Portugal**: Lagos, Algarve, 2 spm., leg. FISCHER-PIETTE, 1955, MNHN. **Strait of Gibraltar**: Punta Almina, Ceuta, 35°54,1' N/5°16,5' W, 25-40 m, many spm.; Anse Almadraba, Ceuta, 35°52,5' N/5°19' W, 20-26 m, 10 v.; Anse Sarchal, Ceuta, 35°53,4' N/5°17,8' W, 0-3 m, 1 spm., all leg. BOUCHET, GOFAS & LOZOUET, V. 1986; Ceuta, 35°53' N/5°18' W, 50 m, 3 spm., leg. VON COSEL, V. 1986; all MNHN. **Algeria**: Oran, 4 spm., coll. LOCARD, MNHN. **Tunisia**: Sfax, many sh., coll. STAADT, MNHN. **Italy**: Palermo, 2 spm., coll. DEPONTAILLER; Naples, 2 spm., coll. PETIT; Taranto, 10 v., coll. MONTEROSATO; Capri, 3 spm., old colln., all MNHN. **Mediterranean France**: Nice, Alpes-Maritimes, 1 spm.; Cannes, Alpes-Maritimes, 2 spm.; S. Raphael, Var, 3 spm.; Marseille, Bouches-du-Rhône, 10 spm.; Sète, Hérault, 5 spm., all colln LOCARD, MNHN; Banyuls, Pyrénées-Orientales. 0-1 m, many spm., leg. P. G. OLIVER, 1980, NMWZ. **Corsica**: Ajaccio, 5 spm., MNHN. **Atlantic Morocco**: Casablanca, strandline, many v., leg. RIGOTARD, 1917; 34°12' N/7°7' W, 150 m, 10 v.; 34°54' N/7°54' W, 145 m, 3 v.; 33°36' N/7°45' W, 25 m, 3 spm.; 33°24' N/8°25' W, 25 m, many spm.; 30°39' N/10°3' W, 129 m, 1 spm.; 30°35' N/10°5' W, 268 m, 1 v.; 30°26' N/9°55' W, 47 m, 4 v.; 30°23' N/9°55' W, 110 m, 3 v.; off Mazagan, many spm., all dredged R/V "Vanneau", 1923-1929; all MNHN. **Canary Islands**: Las Palmas, Gran Canaria, Playa Las Canteras, 4 v., leg. VON COSEL, X.1965, MNHN.

Intermediate forms: **Mauritania**: 19°28' N/17°01' W, 80 m, 1 spm.; 18°30' N/16°50' W, 240 m, 4 spm.; 18°19' N/16°34' W, 210 m, 12 spm., all dredged R/V "N'Diogo", leg. RICHER DE FORGES, 1983; all MNHN. **Cape Verde Islands**: Boavista, Récif Baixena, 7 m, 1 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1959, MNHN.

Striarca lactea scoliosa: **Senegal**: Dakar, Baie de Gorée, 80 m, many v.; 80-250 m, 3 v.; Off Cap Manuel, 135 m, 7 spm.; S of Gorée, 95-98 m, 6 v.; SW of the Madeleines, 46 m, 5 spm. + 1 v.; 49-51 m, many v.; 60 m, 1 spm. + 1 sh.; SW of Cap Manuel, 50 m, 5 v.; off Gorée, 170 m, 1 v.; off Cap Vert, 150-250 m, 2 v.; SW of Gorée, 110-112 m, 2 v.; all dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 1953-57; Casamance, 12°44,5' N/17°27,3' W, 40 m, 6 v.; 12°32' N/17°28,8' W, 45 m, 5 v., both dredged R/V "Louis Sauger", leg. VON COSEL, 28.III.1988; all MNHN. **Guinea**: 10°49' N/16°39' W, 42 m, 14 spm. sta. 153; 10°40' N/16°44' W, 65 m, 10 spm. sta. 151, both dredged R/V "Atlantide"; both ZMC; off Conakry, 10°19' N/16°34' W, 73-60 m, 4 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956; all MNHN. **Côte d'Ivoire**: 4°16' N/7°30' W, 40 m, 3 spm. + 1 v.; 4°42,5' N/6°35,5' W, 40 m, 1 spm.; 4°35' N/6°29' W, 200 m, 1 spm.; 5°1,5' N/3°23,5' W, 70 m, 1 spm. + 1 v., all dredged R/V "La Rafale" Guinean Trawling Survey, leg. CHERBONNIER, 1964; Abidjan region, 37 m, 2 spm.; 7 m, 2 spm.; 10-15 m, 1 spm.; 80-90 m, 10 spm., all dredged R/V "Reine Pokou", leg. LE LOEUFF (ORSTOM), 1967-69; all MNHN. **Ghana**: Off Cape Coast, 26-31 m, 7 spm., leg. LE LOEUFF (ORSTOM), 10.II.1968, MNHN. **Nigeria**: 6°2' N/4°16' E, 100 m, 6 spm., dredged R/V "Thierry", Guinean Trawling Survey, 10.X.1963 (types of *scoliosa*).

Striarca lactea epetrima: **R. P. Congo**: Pointe-Noire, 7 v., coll. Office Pointe-Noire; Pointe-Noire: Plage Sauvage, strandline, 1 v.; Plage Mondaine, many v.; Plage ORSTOM, 3-4 m, 1 v., all leg. VON COSEL, XI-XII.1985, MNHN. **Angola**: Ambrizete, Zaire province, 45 m, 7 v.; Ilha de Luanda, Luanda province, 40-60 m, 4 spm.; Praia Etambar, Corimba, Luanda province, infralittoral, 9 spm.; Cabo Ledo, Luanda province, 10-40 m, 9 spm.; Pta. das Lagostas, Bengo province, 5-20 m, 4 spm.; Barra do Dande, Bengo province, 0-2 m, 1 v.; Caotinha, Benguela province, infralittoral, 1 spm.; Baia de Santa Maria, Benguela province, 8-10 m, 1 spm.; Baia do Limagem, Benguela province, 0-2 m, 11 spm. (types of *epetrima*); Praia Amelia, Moçâmedes province, 40-60 m, 1 sh., all leg. GOFAS, 1981-1984; all MNHN.

REMARKS

West African *Striarca* have previously been confused with *Arcopsis* and *Noetiella*. *Noetiella* differs in having a prosodetic ligament and is expanded anteriorly (fig. 6). *Arcopsis*

shares the amphidetic ligament but it remains very small throughout ontogeny (fig. 15), and the sculpture is distinctly coarse (pl. I, 10A).

We have encountered considerable difficulty in assessing the variation shown between the samples of *Striarca* from the Eastern Atlantic and Mediterranean and have concluded that with the present data are unable to distinguish specific differences from ecophenotypic or geographical variation. In this respect *Striarca* resembles the pattern shown by *Anadara polii* (see above). However we have a considerable amount of material and have attempted to elucidate patterns in the variation observed.

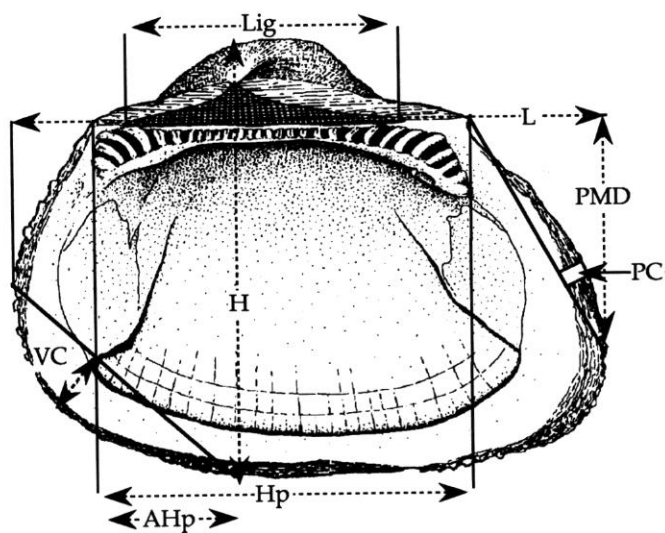


FIG. 9. — Internal view of right valve of *Striarca lactea* (L.). Guéthary. (Scale bar = 2 mm.) Linear parameters are those used in the morphometric analysis, for explanations see text.

Subjectively the West African shells appear more inequilateral and more trapezoidal than the shells from more northerly warm temperate localities. To quantify these observations, shells from seven regions were measured : Guéthary (GTY), 0 m, this is approaching the northern limit of the range of the species; Gibraltar (GIB), 25-40 m; Mediterranean (MED), Banyuls, 0 m; Atlantic Morocco (MOR), 25 m; Mauritania (MAU), 80-210 m; Gulf of Guinea (GUI), 40-200 m; Angola (ANG), 0-40 m. All shells were measured for nine parameters : Length (L), Height (H), Tumidity (T), Hinge plate (Hp), Anterior Hinge plate (AHp), Ventral Curve (VC), Posterior Curve (PC), Posterior Margin Distance (PMD) and Ligament length (Lig.). These are shown in figure 9 and the data is presented as a set of box plots (fig. 10) for the following ratios $L : H$, $L : T$, $L : VC$, $Hp : AHp$, $L : PC$, $L : PMD$ and as a graph (fig. 11) for L against Lig.

Length/Height : This ratio shows little variation between groups except that the Gulf of Guinea sample shows greater variation with a tendency to be narrower.

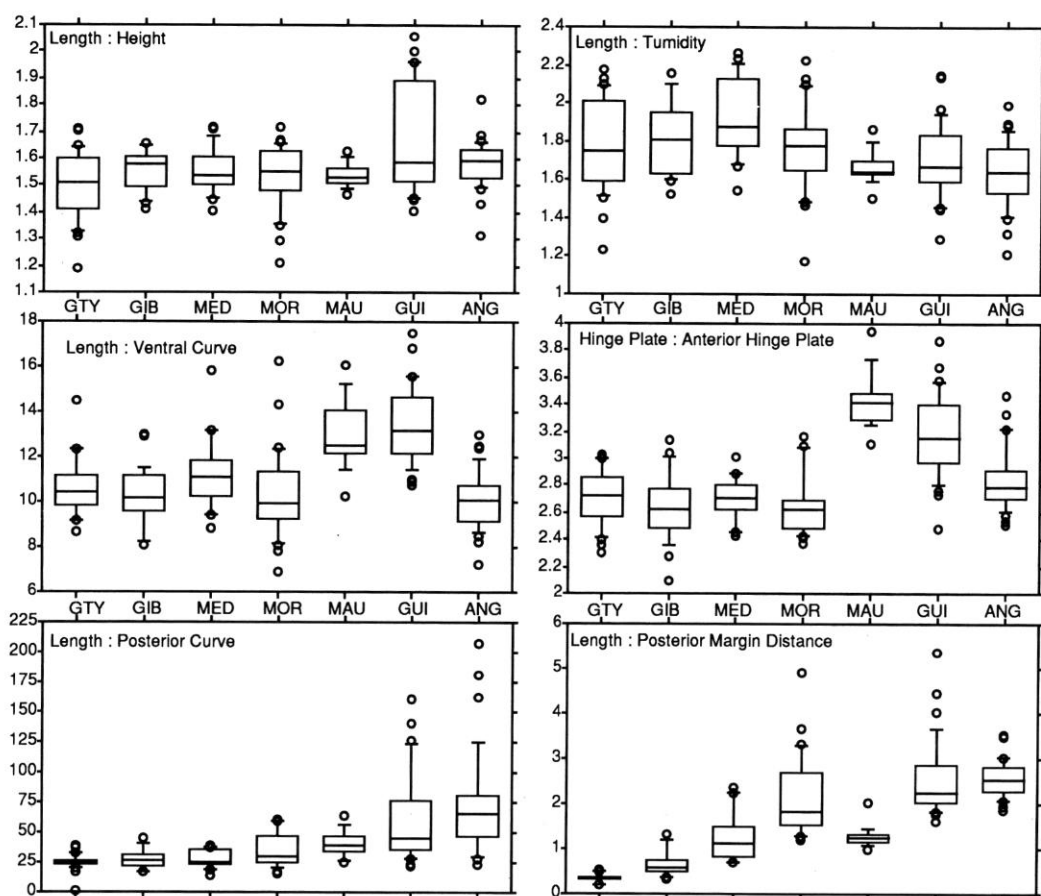


FIG. 10. — Box plots of six ratios of shell dimensions of *Striarca lactea* agg. from seven localities throughout its range. For key to dimensions see figure 9.

GTY = Guéthary (n = 27) : GIB = Gibraltar (n = 25) : MED = Mediterranean (n = 19) : MOR = Atlantic Morocco (n = 26) : MAU = Mauritania (n = 15) : GUI = Gulf of Guinea (n = 30) : ANG = Angola (n = 33).

Length/Tumidity : This ratio indicates that all tropical West African samples have shells which are more tumid.

Length/Ventral Curve : This ratio is a measure of the obliqueness of the anterior ventral margin. The Mauritanian and Gulf of Guinea samples separate clearly from the remainder with the Angolan sample the same as the northern warm temperate samples.

Hinge plate/Anterior Hinge plate : This is the most accurate measure of the inequilateral condition and the pattern shows again clear separation for the tropical samples but only slightly for the Angolan material.

Length/Posterior Curve : This is a measure of the shape of the posterior margin with large values indicating this margin to be almost straight. This pattern again shows the tropical

material to be distinct except that it is the Mauritanian sample which is intermediate and not the Angolan sample as in the previous two ratios.

Length/Posterior Margin Distance : This is a measure of the trapezoidal shape of the posterior outline with high values indicating a stronger distinction between the posterior margin and the posterior ventral margin. There is considerable variation in the warm temperate samples, the Gulf of Guinea and Angolan shells generally have the highest values but the Mauritanian shells are intermediate.

ANOVA does not reveal a consistent pattern whereby the tropical West African samples are alike and all differ from the northern warm temperate samples. On outline alone one would not consider the tropical West African shells to belong to a separate species. An analysis of the tropical West African samples compared to the combined northern warm temperate reveals that as indicated in figure 10 the Gulf of Guinea and Angolan material are discernable from typical *Striarca lactea*. Of the six ratios compared, the Gulf of Guinea and Angolan samples differ in four at the 90 % significance level, but the sample from Mauritania in only one.

Table of the means of the ratios (X) computed for the data set used in figure 10 and the F statistic for ANOVA of the Temperate sample with the others. The Temperate sample consists of the combined data from the Guéthary, Mediterranean and Moroccan samples.

REGION	L/H		L/T		L/VC		Hp/AHp		L/PC		L/PMD	
	X	F stat	X	F stat	X	F stat	X	F stat	X	F stat	X	F stat
Temperate	1.54		3.63		11.6		2.67		33.8		1.18	
Mauritania	1.54	.003	3.34	1.95	12.9	0.131	3.43	45.3*	41.0	0.017	1.30	0.55
G. of Guinea	1.68	7.88*	3.42	1.65	13.4	0.424	3.17	33.7*	122.0	4.52*	2.53	12.6*
Angola	1.58	0.634	3.28	5.60*	10.1	0.305	2.84	4.39*	100.1	2.75*	2.56	13.9*

* Significant at 90 %

The comparison of the relative size of ligament (figure 11) shows that the slope of the growth curve is similar for the Mauritanian, Gulf of Guinea and Angolan samples but that these differ from the other more northern warm temperate samples.

The sculpture of the samples also differs with a trend for decreasing coarseness from north to south (compare A-B on plate III).

Therefore in outline, ligament growth and shell sculpture the Gulf of Guinea material differs from typical *S. lactea* from northern warm temperate waters. The Angolan material also differs in sculpture but to a lesser degree in outline whereas the Mauritanian sample is intermediate in form.

The distribution of all the material studied is plotted on map 4 and shows that there are discontinuities along the West African coast, at the Saharan region and at Cameroon-Gabon (including the offshore islands of São Tomé and Annobon). These isolate the Angolan form from that of the Gulf of Guinea and the latter from the typical northern warm temperate form. Consequently, because of the differences in shell form and their coincidence with geographic patterns we have given subspecific status to the Angolan (*S. l. epetrima*) and Gulf of Guinean (*S. l. scoliosa*) forms. We have refrained from giving separate status to the

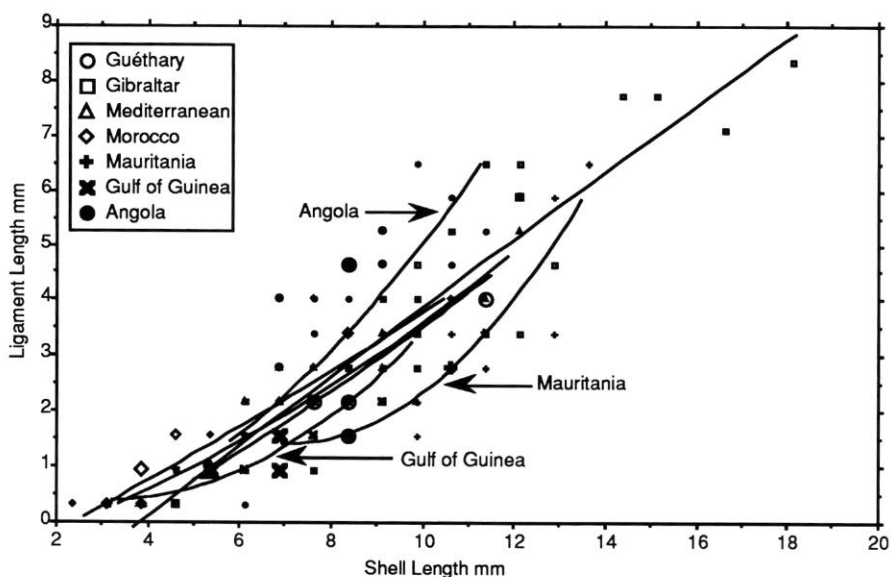


FIG. 11. — Graphs of Ligament Length plotted against Shell Length for seven samples of *Striarca lactea* from throughout its geographical range. Overlapping points are shown as larger symbols.

Mauritanian material because of its intermediate nature. If only Gulf of Guinea material was available for comparison with Mediterranean material we are certain that species level separation would have seemed to be appropriate.

The dilemma of assessing variation in shell form in the Bivalvia is graphically illustrated by *Striarca lactea* and warrants further discussion.

The causes of the variation cannot be regarded as random as we do observe a geographic pattern. There may be genetic separation of the populations involved but at this stage we cannot investigate these. Other cause could be ecophenotypic variation and clinal variation. With clinal variation one would expect to observe changes in parameters coinciding with latitudinal or longitudinal gradients. This is not the case with the majority of outline parameters because in the Angolan material these frequently reverse the trend seen in the Mauritanian and Gulf of Guinea samples. A similar pattern is observed for the changes in ligament growth. Clinal variation would however seem to apply to the radial shell sculpture with its increasing density towards the south of its range. One factor other than latitude which is common to the Mauritanian and Gulf of Guinea samples is the depth range. In the northern part of its range *S. lactea* is typically littoral or sublittoral, only occasionally extending to about 100 m. The Mauritanian and Gulf of Guinea samples range from 40-210 m and there are likely to be associated changes in habitat. In shallow water and littoral sites *S. lactea* lives under large stones and rocks but in the deep water samples they are attached to small stones, pebble or shell gravel and are likely to live on the surface of, rather than beneath, these small objects. It is not inconceivable that this change in habitat could result in changes in shell shape. Unfortunately nowhere from a single region do we have a range of samples from a

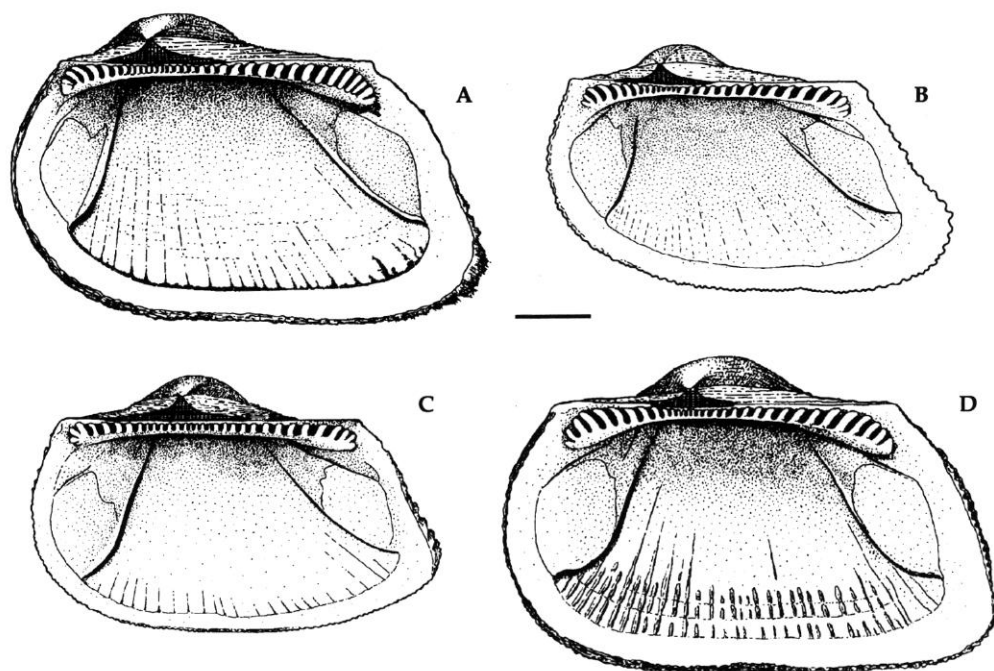


FIG. 12. — Internal views of right valves of *Striarca*: A, *S. lactea* (L.) intermediate form from Mauritania. B, *S. l. scoliosa* n. ssp. from Gulf of Guinea. C, *S. l. epetrima* n. ssp. from Angola. D, *S. gibba* (Kraus) from Natal. (Scale bar = 2 mm.)

bathymetric gradient. Furthermore from our present samples it appears that *S. lactea* agg. is absent from the littoral and sublittoral of the Senegal-Cameroon coast. A functional result of the greater anterior reduction is to move the byssal gape forward. This tends to raise the posterior and with the greater angulation of the posterior and straightening of the posterior margin combine to raise the posterior inhalent and exhalent apertures above the sediment surface. Anterior reduction also allows attachment in smaller crevices which may fit with the inferred habitat.

Without carrying out some form of genetic or protein analysis we cannot properly distinguish the underlying causes of the variation observed but we can recognize its presence. It can be argued that such variation should not be recognized at the subspecies level because we cannot demonstrate genetic isolation and that there is an intermediate form in the Mauritanian samples. One of the major problems with *Striarca* in general is that nowhere are the species highly distinct and a similar pattern of regional variation is present in the Indo-Pacific *Striarca symmetrica* (Reeve, 1844) complex (OLIVER, 1985), *Striarca* is ecologically conservative, consistently inhabiting the same niches throughout its range. This would account for the lack of radiation in shell form which then leads to problems in species discrimination which in reality is currently based on geographic provenance. A comparison of the *S. symmetrica* complex with *S. lactea* agg. would reveal similar difficulties as there are overlapping morphologies [for example *S. erythraea* (Reeve), from the Red Sea and *S. oyamai*

Habe, 1953 from Japan]. The differences between the subspecies of *S. lactea* described here are as large as those between *S. lactea* agg. and *S. symmetrica* agg. As an example the south east African *S. gibba* (Krauss, 1848) is figured (fig. 12D). Given the current state of the systematics of *Striarca* we feel that discreet quantifiable units of morphological variation should be recognised nomenclaturally and that this must be at the subspecies level. The varietal level has no value as it is primarily employed to recognize individuals within populations.

Genus **ARCOPSIS** Koenen, 1885

TYPES SPECIES : *Arca limopsis* Koenen, 1885 (SD Reinhard, 1935).

Arcopsis afra (Gmelin, 1791)
(Pl. I, 10A-C; fig. 13; map 5)

Arca afra Gmelin, 1791 : 3308.

TYPE MATERIAL : MNHN, 4 syntypes from the ADANSON collection. This is Le Jabet of ADANSON, 1757 : 250.

TYPE LOCALITY : Senegal.

DESCRIPTION

Shell to 13 mm in length. Equivalve. Moderately inflated. Inequilateral, beaks between the midline and anterior third.

Outline subquadrate, oblong, longer than high. Posterior area short, demarcated by strong posterior angle which is carinate initially but soon just sharply angled; posterior margin gently curved, obliquely subtruncate. Median area more or less flat, some very weakly sinuous; ventral margin more or less straight some a little indented at byssus exit, byssal gape obsolete. Anterior margin broadly rounded. Dorsal margin long, straight.

Dorsal area relatively narrow, flat, umbonal separation slight. Ligament amphidetic, small, restricted to a narrow shallow resilifer between the beaks.

Hinge plate moderate, teeth in two series, separated by a small edentulous gap corresponding to the resilifer, anterior set up to 11 teeth, posterior set up to 18 teeth. Teeth moderate, minutely serrated, more or less straight, central teeth vertical, lateral teeth slightly oblique.

Sculpture strong, subcancellate, initially of about 25 radial riblets, then adding secondaries and tertiaries in interspaces to reach a total of about 90 in the largest shells. Concentric ridges strong initially but these fading to leave the radial element dominating but nodulose.

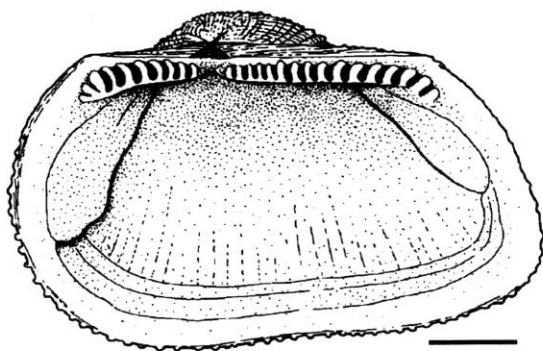


FIG. 13. — Internal view of right valve of *Arcopsis afra* (Gmelin). Angola. (Scale bar = 2 mm.)

Periostracum pale straw coloured, retained at margins only, of very weak lamellae and short bristles.

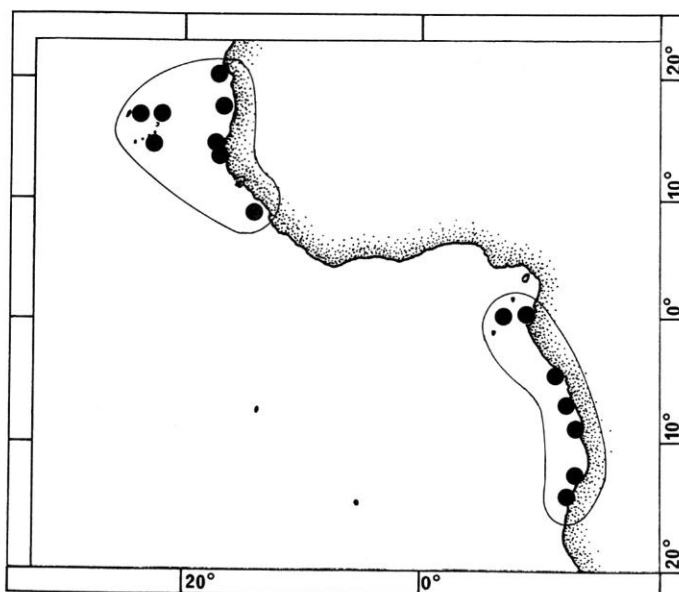
Shell white.

Adductor muscle scars equal, both with strong myophoric flanges. Posterior pedal/byssus retractor scars very small, oval. Byssus functional but of a weak narrow strap only.

SELECTED SHELL MEASUREMENTS : See figure 14.

DISTRIBUTION : Tropical West Africa from Mauritania (Cap Blanc) to Guinea and then Gabon to southern Angola (Moçâmedes), Cape Verde Islands, São Tomé. This disjunct distribution may be caused by intermittent upwelling of cold water along the north coast of the Gulf of Guinea.

MATERIAL EXAMINED : **Cape Verde Islands** : No precise locality, 1 sh. + 2 v., coll. DE CESSAC; 1 sh. + 3 v., coll. Exp. "Talisman", 1881; Ponta do Sol, Santo Antão, 1 v., coll. NICKLÈS, 24.V.1950; off S. Tiago, 15°16,5' N/23°47,5' W, 40-45 m, 1 v., dredged RV. "Calypso"; Ilha do Sal, many v.; all MNHN. **Mauritania** : Off Port-Etienne (now Nouadhibou), 20°20' N/16°22' W, 10 m, many v., leg. MARCHE-MARCHAD, 8.V.1965; off Nouakchott, 18°00' N/16°06' W, 15 m, 1 sh.; off Nouakchott, 17°36' N/16°06' W, 10 m, 1 v., both dredged R/V "N'Diogo", leg. RICHER DE FORGES (ORSTOM), 1981; all MNHN. **Senegal** : Cap Vert, 12 spm. + 3 v., coll. MAUNY, 1964; Cap Rouge, many sh. + many v., coll. GRUVEL, 1912; Rufisque, 2 sh. coll. DAUTZENBERG, 1906; Gorée, 1 sh., coll. JOUSSEAUME; Ouaran, 50 km S of Dakar, 7 spm., leg. BOUCHET, 2.VIII.1973; l'Anse Bernard, Dakar, 6-8 m, 1 v.; S of Gorée, 30-40 m, 1 v.; off Dakar, 16-25 m, 1 v.; off Dakar, 10 m, 1 spm.; off Gorée 78 m, 1 v., all leg. MARCHE-MARCHAD, 1954-56; M'Bour, on beach, 1 v., leg. VON COSEL, 22.III.1988; all MNHN. **Guinea** : No precise locality, 1 sh. + 6 v., leg. MARCHE-MARCHAD, 1.VI.1953, coll. Staadt, MNHN. **São Tomé** : Praia Mouro Peixe, 0-2 m, 12 spm., leg. S. GOFAS, XI.1983, MNHN. **Gabon** : Cap Esterias, 1-1.5 m, 5 spm., leg. VON COSEL, XII.1985. MNHN. **R. P. Congo** : Pointe-Noire, Plage Mondaine, 2 v., leg. VON COSEL, XI/XII.1985, MNHN. **Angola** : Ambrizete, Zaire province, on beach, 1 spm. + 3 v.; Praia Etambar, Corimba, Luanda province, 0-2 m, many spm., 10-20 m, 1 sh.; Baía do Mussulo, Luanda province, 0-1 m, many sh.; Futungo-Ilha do Destierre, Baía do Mussulo, 0-1 m, 7 spm.; Cacucaco, Bengo province, intertidal, 1 spm.; Praia Santiago, Bengo province, 1-2 m, 1 spm.; Baía de Santa Maria, Benguela province, 0-2 m, 14 spm.; Caota, Benguela province, 0-2 m, 1 spm.; Baía do Limagem, Benguela province, 0-2 m, 1 spm.; São Nicolau, Moçâmedes province, intertidal, many spm.; Baía das Pipas, Moçâmedes province, intertidal, 2 spm.; Baía da Lucira, Moçâmedes province, intertidal, 11 spm.; Lucira, Praia do Cesar, Moçâmedes



MAP 5. — Distribution of *Arcopsis afra*.

province, intertidal, 3 spm.; Lucira, Santa Marta. Moçâmedes province, 40 m, 1 v.; Praia das Conchas, Moçâmedes province, intertidal, 2 spm.; all leg. S. GOFAS, XII.1981; all MNHN.

BIOTOPE : This species lives byssally attached to the undersides of rocks and stones, from the low water mark to about 40 m. It should be noted that the vast majority of records of this species are from the intertidal zone.

REMARKS

The only other Atlantic species of *Arcopsis* is *A. adamsi* Dall, 1886 from the Caribbean. In general form it is identical to *A. afra* but the sculpture is more dense with about twice as many riblets at any equivalent size.

Confusion with *Striarca lactea* is common with many museum specimens being incorrectly labelled. Although the overall shape is similar, the sculpture of *A. afra* is coarse and the ligament remains very small (fig. 15).

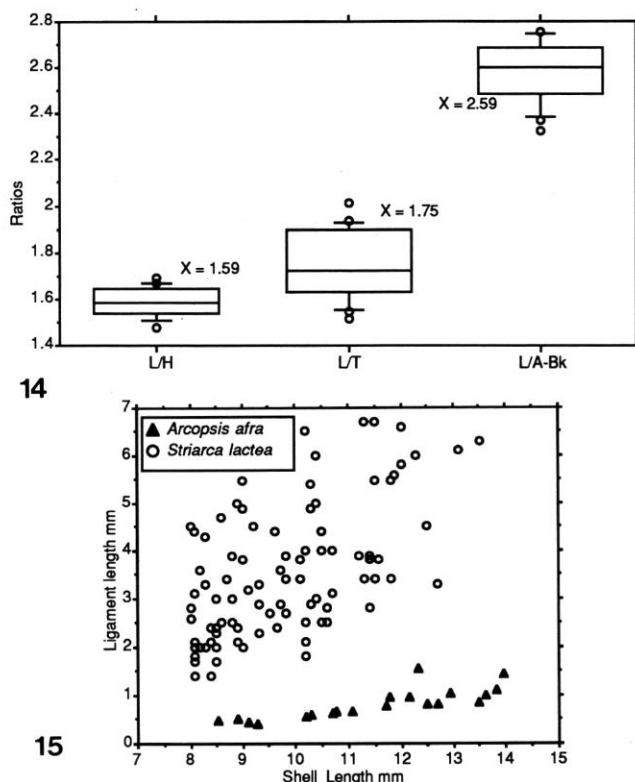


FIG. 14-15. — 14 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Arcopsis afra* (n = 20). 15 : Graphs of Ligament Length plotted against Shell Length for *Arcopsis afra* and *Striarca lactea* from West Africa.

ZOOGEOGRAPHICAL REMARKS ON THE WEST AFRICAN ARCOIDEA

The West African tropical marine fauna is derived primarily from the Tethyan fauna which spread into the southern Atlantic as it appeared during the Late Cretaceous. This combined with the supposed trans Atlantic migration of larval forms to and from the Caribbean and West Africa frequently led to the conclusion that there is a close relationship between these regions. In table 1 we list the West African shallow water Arcoidea along with related taxa from the Mediterranean, Caribbean, Panamic and Indo-Pacific provinces. Species common to West Africa and another province are scored as 3, species in the same subgenus as 2, species in the same genus as 1 and where the genus is not represented as 0. From these scores a total score is calculated by adding 1, 2 and 3 scores and a higher than

TABLE 1. — A list of the recent West African shallow water Arcoidea with their counterparts in the Mediterranean, Caribbean, Indo-Pacific and Panamic provinces. 3 = those taxa common at the species level or sibling species; 2 = those taxa common at a subgeneric level; 1 = those taxa common at a generic level; 0 = no taxa considered to be common at generic level. E denotes an endemic genus.

West African Species	Mediterranean		Caribbean		Indo-Pacific		Panamic	
<i>Arca noae</i>	<i>Arca noae</i>	3	<i>Arca zebra</i>	2	<i>Arca navicularis</i>	2	<i>Arca pacifica</i>	2
<i>A. bouvieri</i>	<i>Arca noae</i>	2	<i>Arca zebra</i>	2	<i>Arca navicularis</i>	2	<i>Arca pacifica</i>	2
<i>A. a. turbatrix</i>		1	<i>Arca imbricata</i>	2	<i>Arca avellana</i>	3	<i>Arca mutabilis</i>	2
Subtotal score: <i>Arca</i>		6		6		7		6
<i>Acar cf. plicata</i>	<i>Acar pulchella</i>	1	<i>Acar domingensis</i>	2	<i>Acar plicata</i>	3	<i>Acar gradata</i>	2
<i>Barbatia complanata</i>		1	<i>Barbatia candida</i>	3	<i>Barbatia foliata</i>	2	<i>Barbatia reeveana</i>	2
<i>B. gabonensis</i>	<i>Barbatia barbata</i>	2		1	<i>Barbatia sculpturata</i>	2		1
<i>B. ionthados</i>		1		1	<i>Barbatia tenella</i>	3		1
<i>B. legumen</i>		1		1	<i>Barbatia obliquata</i>	2		1
<i>B. allocostata</i>		1		1	<i>Barbatia bistrigata</i>	3		1
Subtotal score: <i>Barbatia</i>		6		7		10		6
<i>Anadara polii</i>	<i>Anadara polii</i>	3		1		1		1
<i>A. corbuloides</i>	<i>A. corbuloides</i>	3	<i>Anadara baughmani</i>	2		1	<i>Anadara mazatlanica</i>	2
<i>A. eborensis</i>		1		1		1	<i>A. Esmerarca reinharti</i>	3
<i>A. subglobosa</i>		1		1		1		1
<i>A. senegalensis</i>		1	<i>A. Cunearca chemnitzii</i>	2	<i>A. Cunearca pilula</i>	2	<i>A. Cunearca emeralda</i>	2
<i>A. camerunensis</i>		1		2	<i>A. Cunearca pilula</i>	2	<i>A. Cunearca nux</i>	3
<i>A. geissei</i>		1	<i>Anadara floridana</i>	2		1	<i>Anadara formosa</i>	2
<i>Senilia senilis</i> E		0		0		0		0
Subtotal score: <i>Anadarinae</i>		11		11		9		14
<i>Sheldonella minutalis</i>		0	<i>Sheldonella bisulcata</i>	3	<i>Sheldonella lateralis</i>	2	<i>Sheldonella delgada</i>	2
<i>Stenocista gambiensis</i> E		0		0		0		0
<i>Noetiella congoensis</i>		0		0	<i>Noetiella vivianae</i>	3		0
<i>Arcopsis afra</i>		0	<i>Arcopsis adamsi</i>	3		1	<i>Arcopsis solida</i>	3
<i>Striarca lactea</i>	<i>Striarca lactea</i>	3		0	<i>Striarca symmetrica</i> agg.	3		0
Subtotal Score: <i>Noetidae</i>		3		6		9		5
Total Number of taxa/ category	4 2 11 5		3 7 7 4		6 8 6 2		2 10 7 4	
Total common taxa above genus Total Score	6 27		10 30		14 40		12 32	

generic score by adding only the 2 and 3 scores. In both instances the greatest affinity is with the Indo-Pacific province.

The level of endemism is small with only two genera restricted totally to West Africa, namely *Senilia* and *Stenocista*.

We conclude that there are no species in common between the Caribbean and West Africa but that there are four between West Africa and the Mediterranean. Despite the number of species in common with the Mediterranean the overall affinity is the least and this must be due to the different climatic conditions now prevailing and the drying of the Mediterranean during the Tertiary. A better comparison would be with the Miocene/Pliocene faunas of the region.

By looking at the subtotal scores for different higher taxa it can be seen that there is variation in the patterns observed. Most noticeable is the paucity of species of *Barbatia* in the Caribbean/Panamic region. This suggests that the *Barbatia* radiation is primarily of Indo-Pacific origin and may have occurred after the closing of the Mediterranean. The presence of so many species of *Barbatia* in West Africa could have resulted from subsequent migration around the Cape during periods of raised sea temperatures in the Pleistocene. The opposite trend is indicated by the Anadarinae which appear to have closest affinity with the Panamic province. The Panamic diversity of Anadarinae is much higher than that of the Caribbean despite the repeated submersion of the Panamanian isthmus. The Panamic-Pacific and tropical West African provinces have a similar composition of habitat types in that there is a good diversity of soft bottoms with relatively turbid water and a paucity of coral reef biotopes with clear water. Many of the Anadarinae prefer soft sediment-turbid water regimes and this may explain the similarity in diversity of species in the Panamic and West African regions. We postulate that when the Panamanian isthmus was open there may have been a greater diversity in the Caribbean and this may be another case where comparison with the Tertiary faunas would be more conclusive. However compared with the Indo-Pacific the similarity is less as there are only a few species in that region which could be assigned to the subgenera *Cunearca* and *Larkinia*, and *Caloosarca* and *Rasia* seem to be genuinely absent. Interestingly the thin shelled, subspherical forms belonging to subgenus *Scapharca* which are diverse in the Indo-Pacific are totally absent from West Africa.

The West African Noetidae show strong generic affinity with the Indo-Pacific but where there are species in the Caribbean they are very similar. OLIVER (1987a,b) has shown that during the Tertiary period the Noetidae were more diverse in the Mediterranean with *Sheldonella*, *Noetiella* and *Arcopsis* present along with *Striarca*.

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PLATE I

1. — *Stenocista gambiensis* (Reeve) : Gambia (no details), MNHN, 28 mm.
- 2A-B. — *Stenocista gambiensis* (Reeve) : Guinea, 9°42' N/13°50,2' W, 3 m, MNHN. 19.5 mm.
3. — *Stenocista gambiensis* (Reeve) : Senegal, Cap Skirring, 3-5 m, MNHN. 12 mm.
- 4A-B. — *Noetiella congoensis* Thiele & Jaeckel : R. P. Congo, Pointe-Noire, off plage ORSTOM, 5-7 m, MNHN. 12.2 mm. 4B, periostracum and surface deposit removed.
- 5A-B. — *Sheldonella minutalis* n. sp. : Holotype. Angola, Cabo Ledo, Luanda province, 10-40 m, MNHN. 6.7 mm.
- 6A-B. — *Striarca lactea epetrima* n. ssp. : Holotype. Angola, Baia do Limagem, Benguela province, 0-2 m, MNHN. 9.5 mm.
- 7A-B. — *Striarca lactea scoliosa* n. ssp. : Holotype. Nigeria, 06°02' N/04°6' E, 100 m, MNHN. 9.7 mm.
- 8A-C. — *Striarca lactea lactea* (Linné) : France, Guéthary, Gulf of Gascony, MNHN. 11.3 mm.
- 9A-B. — *Striarca lactea*, intermediate form : Mauritania, 18°19' N/16°34' W, 210 mm, MNHN. 13.6 mm.
- 10A-C. — *Arcopsis afra* (Gmelin) : Angola, Praia Etambar, Corimba, Luanda province, 0-2 m, MNHN. 12.5 mm.

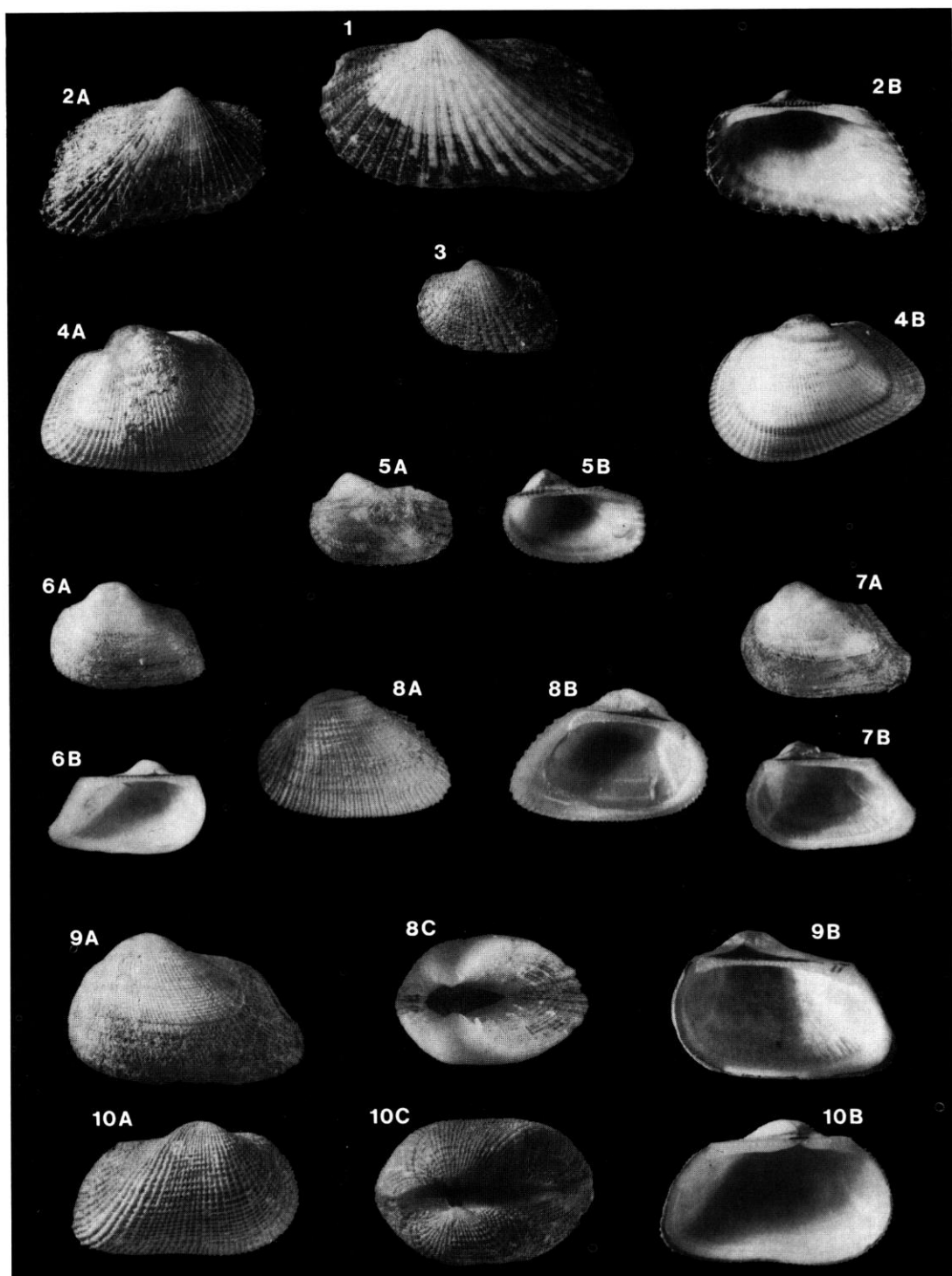


PLATE I

PLATE II

Scanning electron micrographs of the shells of recent species of *Sheldonella*. (Scale bar = 2 mm.)

1. — *Sheldonella minutalis* n. sp. : Guinea, 9°18' N/13°41,5' W, 20 m. MNHN.
2. — *Sheldonella minutalis* n. sp. : Angola, Ambrizete, Zaire province, MNHN.
3. — *Sheldonella bisulcata* (Lamarck) : Brazil, NMWZ.
4. — *Sheldonella lateralis* (Reeve) : South Africa, Natal, NMWZ.

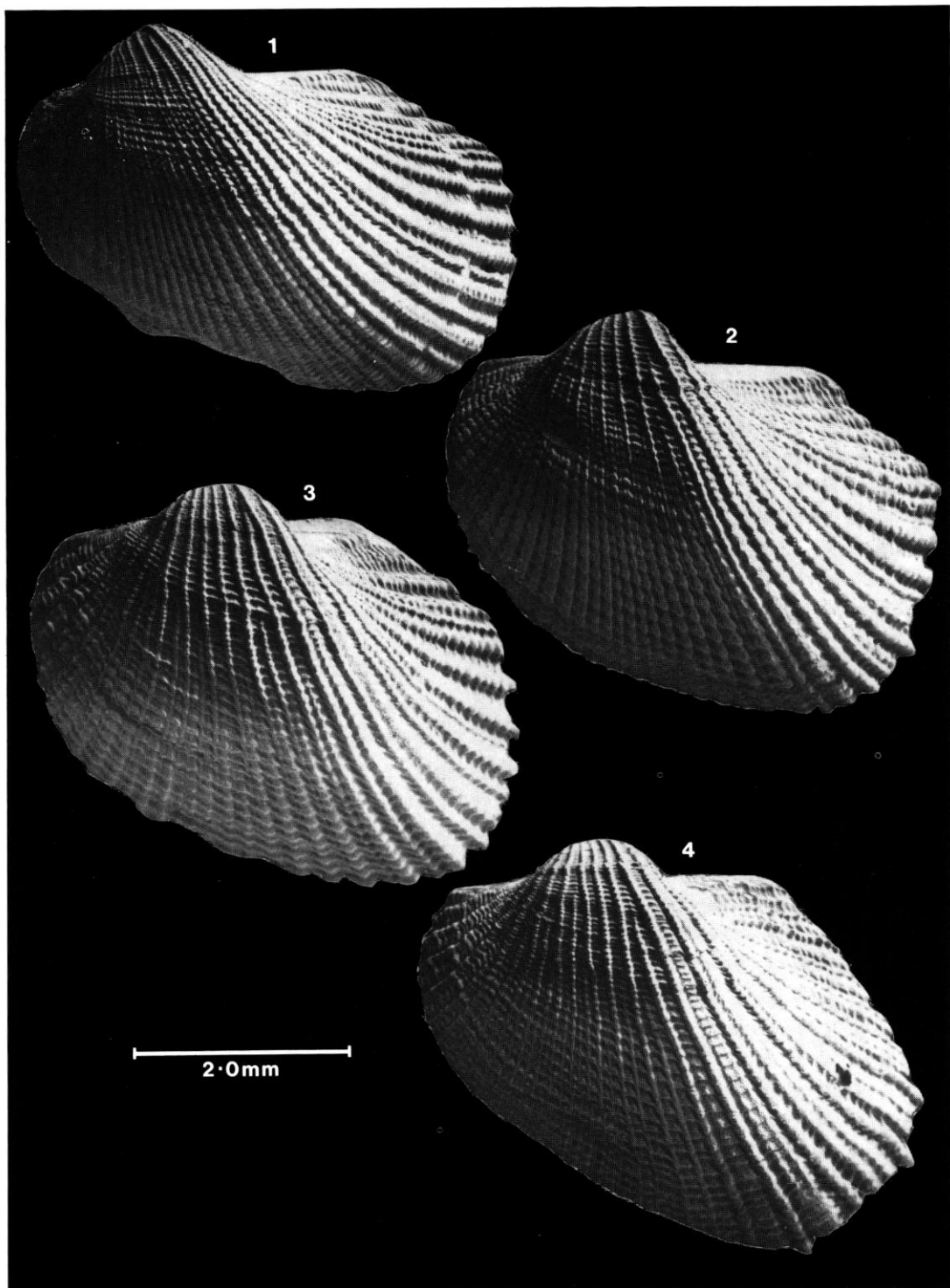
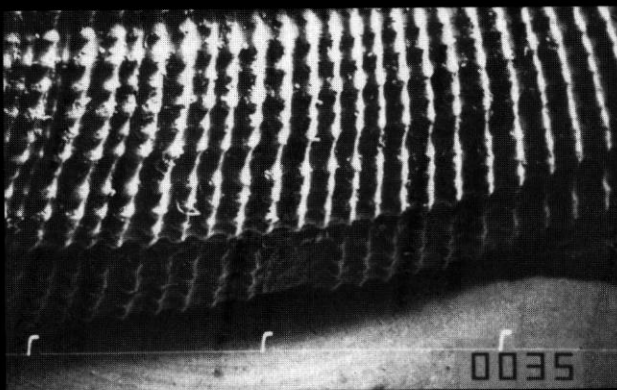


PLATE II

PLATE III

Scanning electron micrographs of the median ventral area of the shells of : A, *Striarca lactea* (L.) from Banyuls, France and B, *Striarca lactea epetrima* n. ssp. from Angola. (Scale bar intervals = 2 mm.)

A



B

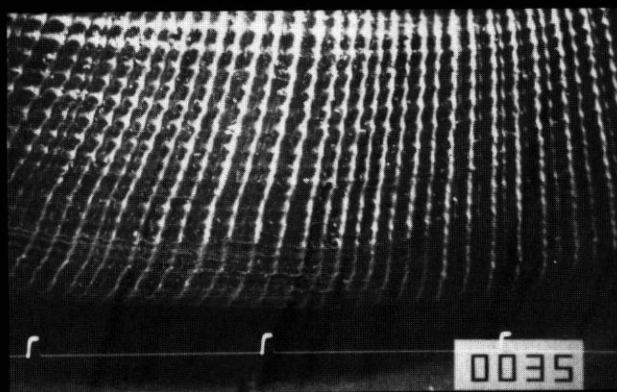


PLATE III

