Vesicomyidae (Mollusca: Bivalvia) of the genera *Vesicomya*, *Waisiuconcha*, *Isorropodon* and *Callogonia* in the eastern Atlantic and the Mediterranean

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SARSIA

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Five new species of Vesicomyidae are described and five other previously known from the eastern Atlantic and Mediterranean are revised: *Vesicomya atlantica* (E.A. Smith, 1885), N-Atlantic between the Azores and Cape Verde Basin, 1800-3225 m; *Vesicomya adamsi* (E.A. Smith, 1885), from Sierra Leone to Namibia, 4400-5124 m; *Waisiuconcha haeckeli* sp. nov., off Mauritania, 600-1200 m; *Isorropodon perplexum* Sturany, 1896, eastern Mediterranean, 1950-2500 m; *Isorropodon bigoti* sp. nov., off Congo (Brazzaville), 150 m and off Mauritania, 900-1200 m; *I. curtum* sp. nov. from off Mauritania, 900-1200 m; *I. striatum* (Thiele & Jaeckel, 1931) from the Bight of Biafra, 2492 m; *Callogonia cyrili* sp. nov., off Morocco, 1805 m; *Callogonia mauritanica* sp. nov., off Mauritania 900-1200 m; *"Vesicomya" chuni* Thiele & Jaeckel, 1931, from the Bight of Biafra, 2492 m. Detailed data on anatomy of the genus *Isorropodon* (formerly placed in the Trapezidae) are presented for the first time and it is shown to be a valid taxon belonging to the Vesicomyidae. Three other species described by Thiele & Jaeckel (1931) are briefly discussed. A parsimony analysis for all eastern Atlantic Vesicomyidae using size, hinge teeth and other shell characters supported two well-defined main groupings: *Vesicomya* and *Waisiuconcha* on the one hand, *Isorropodon* and *Callogonia* on the other, whereas the position of the remaining species could not be resolved. The possible relationships of *Vesicomya* and *Kelliella* (Kelliellidae) are briefly discussed, and it is concluded that they should be kept as separate.

Resumen

En el presente trabajo se describen cinco especies nuevas de la familia Vesicomyidae y se revisan otras cinco previamente conocidas del Atlántico oriental y del Mediterráneo: *Vesicomya atlantica* (E.A. Smith, 1885), Atlántico del Norte entre Azores y Cabo Verde, 1800-3225 m; *Vesicomya adamsi* (E.A. Smith, 1885), de Sierra Leona a Namibia, 4400-5124 m; *Waisiuconcha haeckeli* sp. nov., cuenca de Cabo Verde frente a Mauritania, 600-1200 m; *Isorropodon perplexum* Sturany, 1896, Mediterráneo oriental, 1950-2500 m; *Isorropodon bigoti* sp. nov., Congo (Brazzaville), 150 m y Mauritania, 900-1200 m; *Isorropodon curtum* sp. nov. Mauritania, 900-1200 m; *Isorropodon striatum* (Thiele & Jaeckel, 1931) de la Bahía de Biafra, 2492 m; *Callogonia cyrili* sp. nov., Marruecos, 1805 m; *Callogonia mauritanica* sp. nov., Mauritania, 900-1200 m y *"Vesicomya" chuni* Thiele & Jaeckel, 1931, de la Bahía de Biafra, 2492 m. Se aportan por primera vez datos anatómicos detallados del género *Isorropodon*, (incluido anteriormente en los Trapezidae) y se demuestra que es un taxon válido perteneciente a los Vesicomyidae. Otras tres especies descritas por Thiele & Jaeckel (1931) son comentadas. Un análisis de parsimonia usando caracteres de la charnela y otras características de la concha indica dos grupos bien definidos: *Vesicomya* y *Waisiuconcha* por una parte, *Isorropodon* y *Callogonia* por otra, mientras la posición de las restantes especies no está definida. También se comentan brevemente las posibles relaciones de *Vesicomya* y *Kelliella* (Kelliellidae), y se concluye que deben mantenerse separados.

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INTRODUCTION

The Vesicomyidae are a group of mostly infaunal bivalves which is known from soft bottoms of the deeper continental shelf to abyssal depths. Their shell size ranges from very small (4 mm, *Vesicomya atlantica* E.A. Smith, 1885) to exceptionally large (240 mm in *Calyptogena magnifica* Boss & Turner, 1980, and 270 mm in a hitherto undescribed *Calyptogena*). Most species of the family inhabit reducing sediments, predominantly of muddy consistence, and many are found in subduction areas, around hydrothermal vents (Boss & Turner 1980;

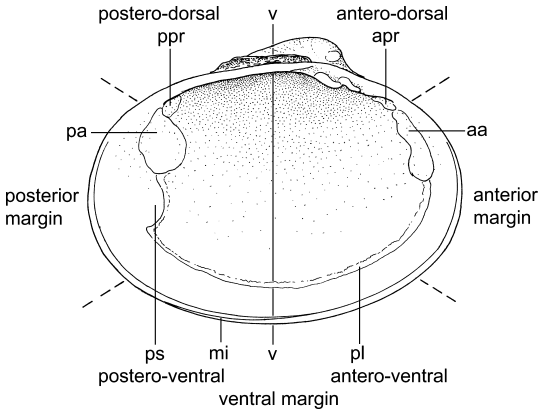


Fig. 1. Left valve of a vesicomyid to show some descriptive terms used. aa: anterior adductor muscle scar. apr: anterior pedal retractor scar. v: vertical midline. mi: marginal incision (exaggerated). pa: posterior adductor scar. pl: pallial line. ppr: posterior pedal retractor scar. ps: pallial sinus.

Tunnicliffe 1991) or in cold seep areas (Turner 1985; Okutani & Métivier 1986), but also on hydrocarbon seeps (Turner 1985). More than 70 Recent species have been described worldwide, and several genera or subgenera have been introduced, but the family has never been revised entirely and no synthetic taxonomic works on the group have been published.

From the eastern Atlantic, seven species of Vesicomyidae have been reported. Five of them had been taken by the RV *Valdivia* during the Deutsche Tiefsee-Expedition 1898-1899, viz. *Vesicomya chuni* Thiele & Jaeckel, 1931, *V. guineensis* Thiele & Jaeckel, 1931, *V. striata* Thiele & Jaeckel, 1931, *V. longa* Thiele & Jaeckel, 1931 and *V. valdiviae* Thiele & Jaeckel, 1931; these were re-evaluated and discussed in detail by Boss (1970). The two remaining species are the type species of the genus *Vesicomya*, *V. atlantica* (E.A. Smith, 1885), which was taken by the RV *Challenger* near the Azores, and *V. adamsi* (E.A. Smith, 1885), sampled by the same vessel south of Sierra Leone. The family was believed to be absent from the Mediterranean and the temperate Northeast Atlantic slope.

In the last decades, much attention has been given to large and conspicuous, vent- or seep-dwelling species of *Calyptogena* (e.g. F.R. Bernard 1974; Boss & Turner 1980; Morton 1985; Stuardo & Valdovinos 1988; Krylova & Moskalev 1996), and recently to the smaller representatives of the family (Allen 2001).

This paper describes five further species of Vesicomyidae which were recently discovered in the eastern temperate and tropical Atlantic. The genus *Isorropodon* Sturany, 1896, described from the Mediterranean and hitherto tentatively included in Trapezidae, is recognized as valid and as a member of the family Vesicomyidae, with redescription of the type species, *Isorropodon perplexum* Sturany, 1896; of this, extensive material became recently available and has been included in the study. *Vesicomya atlantica* and *V. adamsi* are also redescribed and new records given. Two of the species taken by the RV *Valdivia*, *Isorropodon striatum* (Thiele & Jaeckel, 1931) and *"Vesicomya" chuni* Thiele & Jaeckel, 1931 are included in this paper. The remaining large species mentioned above and also sampled by the RV *Valdivia* are not discussed herein but are listed in the appendix and their relationship discussed. They do not belong to the genus *Vesicomya*, under which they were described, however, their appropriate generic assignment is still uncertain and more material needs to be examined.

The family Kelliellidae Fischer, 1887, with the sole Eastern Atlantic and Mediterranean Recent representative *Kelliella miliaris* (Philippi, 1844), has been consistently placed in a separate superfamily, the Arcticoidea. *Kelliella* is nevertheless so similar to *Vesicomya* that the very grounds for generic separation may be questioned (Allen 2001). This will be briefly discussed here but will be considered more in detail in a separate publication.

MATERIAL AND METHODS

Most of the material for this study was obtained during several deep-sea expeditions as follows:

RV *Thalassa* (first of name) cruise (1971) in the Northeast Atlantic, chief scientist L. Cabioch (Station Biologique Roscoff).

RV *Jean Charcot* WALDA cruise (May-August 1971) in the southeastern Atlantic, chief scientist D. Reyss (CNEXO, now IFREMER).

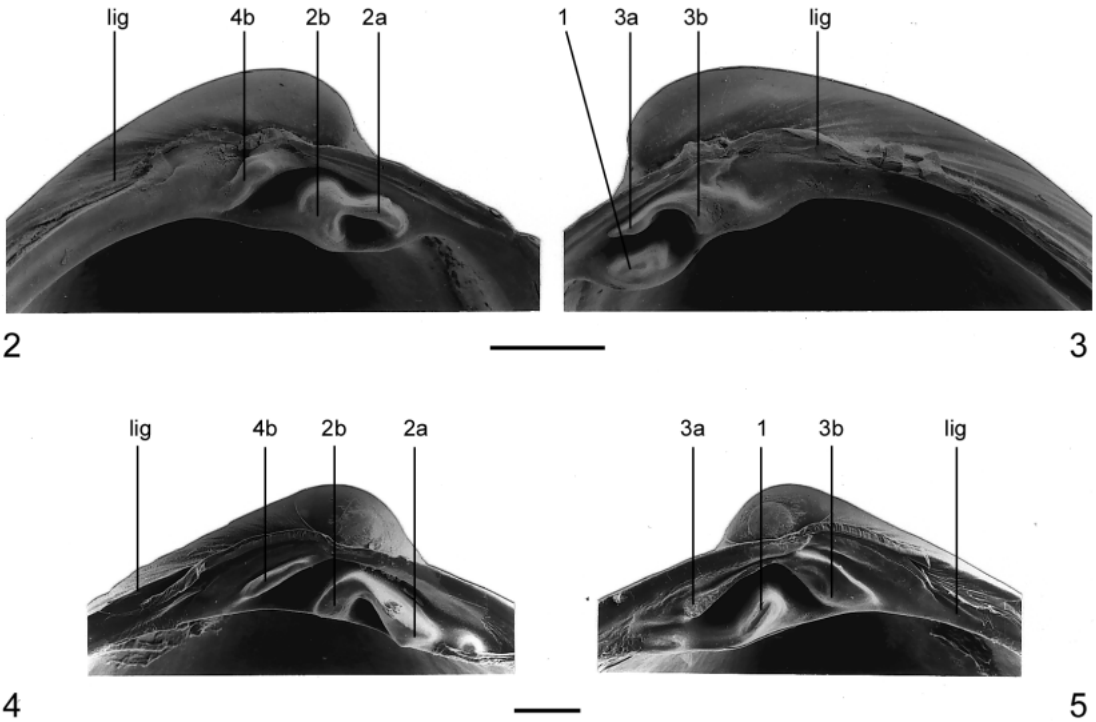
RV *Jean Charcot* BIAÇORES cruise (September-October 1971), within and around the Azores Archipelago, chief scientist J. Forest (MNHN).

RV *Ernst Haeckel* (March 1982), dredgings off Mauritania for an evaluation of fisheries potential in the NW-African upwelling area, material communicated by B. Richer de Forges.

RV *Cryos* BALGIM cruise (May-June 1984), targeted to relating benthic fauna with water masses in the Ibero-Moroccan area and Alboran Sea, chief scientist P. Bouchet (MNHN).

RV *Atalante* EUMELI cruises (January-February 1991, September 1991 and June 1992), targeted to characterize eutrophic, mesotrophic and oligotrophic areas in the deep basins between the Canaries and Cape Verde Islands, chief scientist M. Sibuet (IFREMER).

RV *Nadir* MEDINAUT cruise (December 1998) with the submersible *Nautile*, on mud volcanoes of the eastern Mediterranean, southern Turkey and southern Crete; a joint French-Dutch expedition, chief scien-



Figs 2-5. Interpretation of hinge lines in a vesicomyid, *Waisiuconcha haeckeli* sp. nov. and a venerid, *Pitar rudis* (Poli, 1795). Numbers refer to cardinal teeth as in the notation of Bernard (see Cox in Moore, 1969: N55). lig: ligament. 2-3. *Waisiuconcha haeckeli* (holotype). Scale bar: 500 µm. 4-5. *Pitar rudis* (Poli, 1795). Scale bar: 100 µm.

tists J.P. Foucher (IFREMER) and J. Woodside (Free University, Amsterdam), material communicated by M. Sibuet (IFREMER).

Besides a small lot from the NORATLANTE cruise of the RV *Jean Charcot* (1969), further material originated from commercial deep-sea trawling operations off Mauritania and was made available by F. Gubbioli (Marbella, Spain), and from environmental impact studies around oil rigs on the deeper shelf off Congo (Brazzaville), communicated by L. Bigot (La Réunion).

Most of the material consists of shells only, and these are the basis for descriptions or redescriptions. We use the terminology of Bernard (1895, 1898) for the hinge teeth (see Cox in Moore 1969:N55-N57). Vesicomyidae have very modified hinges and the homology of teeth with the generalized bivalve hinge is not straightforward. Our interpretation is based on comparison of the less modified hinges (e.g. *Waisiuconcha haeckeli*, Figs 2-3) with the hinge of a juvenile venerid (*Pitar rudis* (Poli, 1795), Figs 4-5, see also Salas & Gofas (1998), figs 102-105). We considered the small swelling posterior to cardinal 3b as the posterior edge of branch 3b in the cardinal tooth, following Horikoshi (1989:144), who has based his conclusion on an ontogenetic study. However, this structure is considered a vestigial lateral II by Okutani, Kojima & Ashi (1997). This is still debatable and could only be settled by further data on ontogenetic stages.

The gross anatomy of *Isorropodon perplexum* and *I. bigoti* was observed on preserved live-taken specimens. In addition to this, transverse serial sections were prepared from whole specimens of *I. bigoti* and examined under the microscope, allowing a more detailed anatomical description.

A parsimony analysis was performed for the northeastern Atlantic, Mediterranean and West African species of Vesicomyidae using shell characters. *Glossus humanus* (Linné, 1758) was taken as outgroup because general shell outline and hinge configuration resemble those of the genus *Vesicomya*, so that the homology of hinge and other characters can be easily established. *Kelliella miliaris* was also included in the analysis. Anatomical characters were not taken into account because data are wanting for most species of Vesicomyidae. Characters considered appropriate for coding are listed in Table 4 and were introduced in the analysis with equal weight and unordered; the matrix was run under the branch and bound search option of PAUP 3.1.1. (Swofford 1993), with zero-length branches collapsed.

ABBREVIATIONS USED IN THE TEXT

BM(NH) The Natural History Museum (formerly: British Museum (Natural History)), London, U.K.
IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MNHN Muséum National d'Histoire Naturelle, Paris, France
NHMW Naturhistorisches Museum Wien, Wien, Austria
NSMT National Science Museum Tokyo, Japan
RV Research vessel
SMNH Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Stockholm, Sweden
SMF Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt/M, Germany
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
ZMB Museum für Naturkunde der Humboldt-Universität Berlin (formerly Zoologisches Museum der H.U.), Berlin, Germany
ZMC Universitets Zoologisk Museum København, Copenhagen, Denmark
sh. shell
spm. specimen live-collected
Stn sampling station of a research vessel
v. valve

SYSTEMATICS

Family Vesicomyidae Dall & Simpson, 1901
Genus *Vesicomya* Dall, 1886

Vesicomya Dall, 1886: 272-273

Type species: *Callocardia atlantica* E.A. Smith, 1885 (by original designation). Azores to Cape Verde Basin, 2000 m.

Diagnosis: Shells very small to small, about 3 to 13 mm long, subcircular to nearly circular and very tumid to almost spherical, usually with prominent and clearly prosogyrous umbos. Surface of the valves glossy, with more or less densely spaced, fine commarginal grooves or striae, often partly obsolete, and with a very weak to well-defined lunular incision. Hinge line narrow and delicate, with three rather thin cardinals in each valve, typically arranged more or less parallel to the hinge margins. Cardinal 1 of the right valve is displaced so as to be almost parallel to the hinge margin and anterior to the fused 3a and 3b. Cardinals 2a and 2b of the left valve more or less fused, and separated from cardinal 4b which is situated posteriorly. Lateral teeth absent. Pallial line without a sinus, close to the margin of the valves, this and adductor scars usually inconspicuous. Margins outside the hinge line with one faint incision along the contact surface between the valves.

Vesicomya atlantica (E.A. Smith, 1885)
(Figs 6-14; 98)

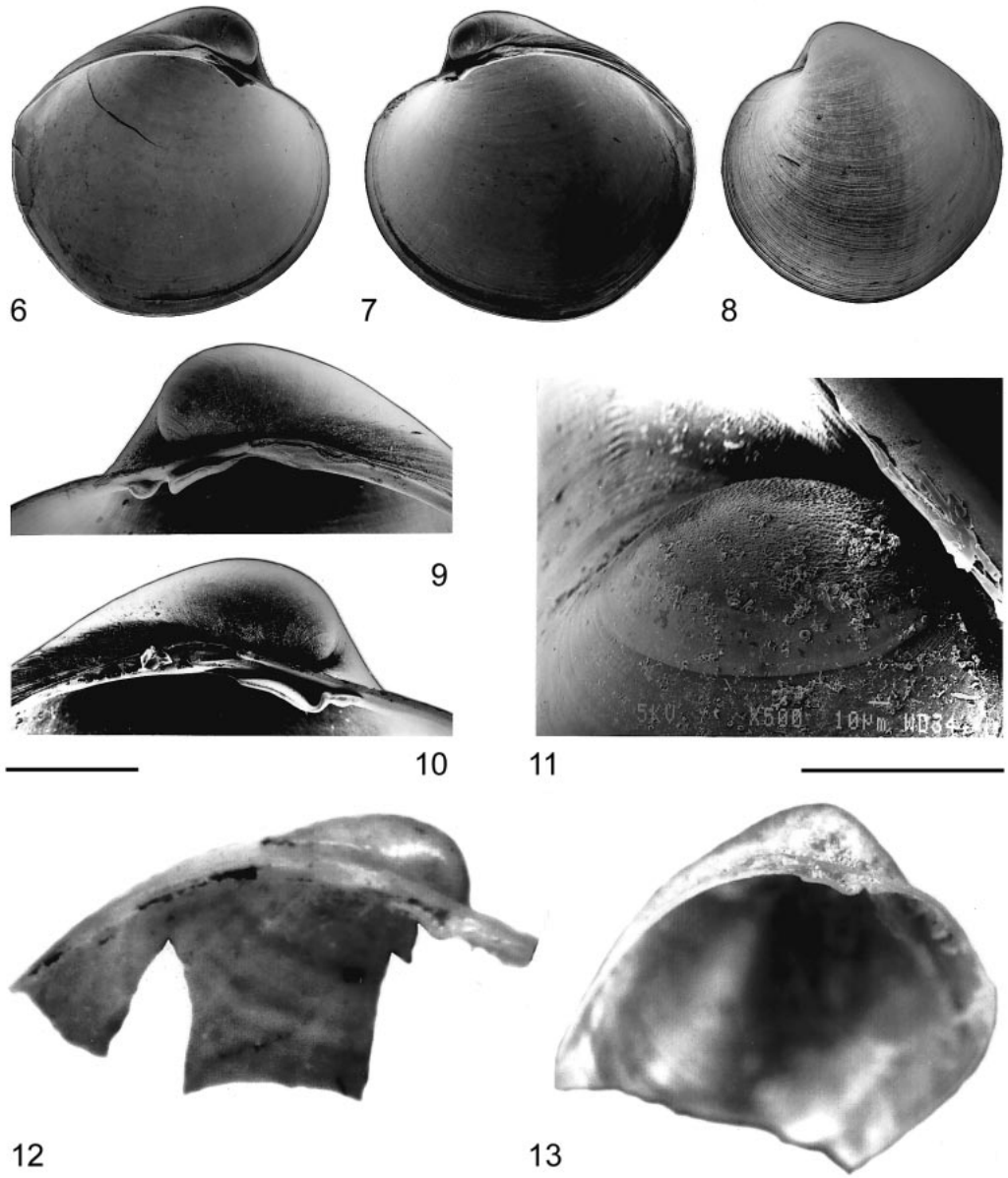
Callocardia (?) *atlantica* E.A. Smith, 1885: 157, pl. 6, fig. 8-8b

Type material: Two specimens are present in BM(NH). The first specimen was registered as holotype BMNH 1887.2.9.2712, it comes from *Challenger* Stn 73 and consists of five fragments of a left valve, one of these still glued to a tiny cardboard. The specimen (Fig. 12) is now not measurable any more and estimated at about 4 mm but is likely to be the measured and figured specimen. The second specimen (Fig. 13), from Stn 78 (37°26'N, 25°13'W, 1000 fathoms, BMNH 1887.2.9. 2713), was not recognized as type material but is also mentioned in the original description; thus both specimens are to be treated as syntypes. The specimen from Stn 78 is a single left valve with a major piece of the ventral part cut off. The length of the remaining part is 3.4 mm. To maintain the type locality, we here select the figured specimen from Stn 73 as lectotype and the specimen from Stn 78 as paralectotype.

Type locality: Off Azores, 38°30'N, 31°14'W, 1000 fathoms (*Challenger* Stn 73)

Description: Shell very small, up to 4 mm in length, slightly variable in outline, somewhat longer than high to almost as high as long, subcircular, very thin and very tumid. Anterior margin evenly rounded with a very weak indentation where the lunular incision meets the margin; ventral margin evenly convex. Posterior margin broadly rounded; postero-dorsal margin convex. Beaks prominent, strongly prosogyrous and enrolled, situated well in front of the vertical midline, not touching each other and slightly recurved away from the hinge line.

Surface of valves glossy with faint, dense and evenly spaced commarginal grooves, well visible only on the ventral half of the valves, obsolete on the earlier portion; umbonal region smooth except the protoconch; no posterior angle. Lunule broad, heart-shaped, not sunken, delimited by a very weak lunular incision. Escutcheon very long and narrow, well defined, extending over the whole postero-dorsal part, slightly sunken, delimited by a keel continuing forward between the beaks to the umbos. Surface sculpture continued on escutcheon. Perio-



Figs 6-11. *Vesicomya atlantica* (E.A. Smith, 1885). W of S. Miguel, Azores, 37°57'N, 26°08'W, 3225 m, dredged RV *Jean Charcot* BIACORES cruise, Stn DS 173A, 1. XI. 1971. 6-7. Interior of l. v. and r. v. Shell length 3.0 mm. 8. Exterior of l.v. Shell length 2.65 mm. 9-10. Close-up view of hinge line of specimen in Fig. 6-7. Scale bar: 500 µm. 11. Protoconch. Scale bar: 100 µm.

Figs 12-13. Type specimens of *Vesicomya atlantica* (E.A. Smith, 1885) in BMNH. 12. Lectotype. *Challenger* Stn 73, 38°30'N, 31°14'W, 1000 fms. 13. Paralectotype. *Challenger* Stn 78, 37°26'N, 25°13'W, 1000 fms.

stracum very thin and translucent, glossy.

Hinge line narrow, somewhat broadening under the beaks. Two visible teeth in each valve, which are quite variable, more or less parallel to the hinge line. Right valve with a short anterior tooth (1) just in front of the beaks and a longer undulate posterior tooth (assumed to be fused 3a and 3b), running from just behind the end of the anterior tooth backwards to about mid-length of the ligament. Left valve with a long, undulate tooth parallel to the antero-dorsal margin and beginning under the beak (assumed to be fused 2a and 2b) and posteriorly to it a narrow and slightly curved (4b) tooth almost parallel to

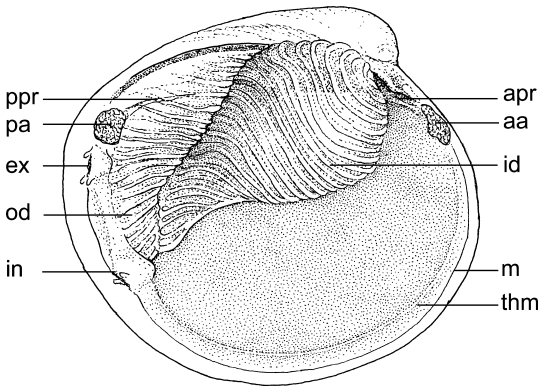


Fig. 14. *Vesicomya atlantica*. 37°58'N, 26°07'W, 3215 m, BIACORES Stn CH 171. Halfschematic view of the soft parts, right valve and right mantle lobe removed. Abbreviations: aa: anterior adductor muscle; apr: anterior pedal retractor muscle; od: outer demibranch; id: inner demibranch; ex: exhalent siphon ; in: inhalent siphon ; m: mantle edge; pa: posterior adductor muscle; ppr: posterior pedal retractor muscle; thm: thickened rim of the mantle. Shell length 2.7 mm.

the dorsal margin. Ligament external, opisthodetic, very short. Adductor muscle scars and pallial line weak or not visible. Pallial line close to the margins, without a sinus. Shell margin narrow, with a weak incision along its length, visible only under a strong lens (×30).

Protoconch rounded and convex, 165 μm in diameter, with a pitted sculpture on most of the surface, and a smooth, slightly flaring margin, about 35 μm broad.

Valves white, translucent.

Description of soft parts: Mantle very thin, attached close to the shell margin, with a smooth edge. Visceral mass very small and appressed to the dorsal part of the shell. Mantle cavity open ventrally from the anterior adductor to the base of the inhalent siphon. Siphons tiny, hardly distinct, separated by a long section of fused mantle, bearing extremely minute tentacles around the siphonal apertures. Adductor muscles very small, the posterior subcircular in section, the anterior more elongate. Foot tiny, entirely concealed by a swollen part of the inner demibranch in preserved specimens, flattened proximally and finger-like in the distal part. Ctenidia with two demibranchs on each side, occupying less than half of the available space in the shell cavity; the outer demibranch less than half the size of the inner one. Outer demibranch terminating next to the inhalent siphon and very closely appressed to the posterior mantle thickening and posterior adductor muscle.

Distribution: Northern Atlantic from the 53°55'N to the Cape Verde Basin, and West to the Azores.

Material examined: The type material; W of Ireland, 53°55'N, 17°52'W, 2456 m, dredged RV *Jean Charcot* NORATLANTE cruise, Stn 3 (E1), 2 sh., MNHN. Bay of Biscay, Banc Le Danois, 44°11'N, 4°32'W, 1925 m, THALASSA Stn X333, 8 spm. (2.5 × 2.1 mm to 2.9 × 2.6 mm, l/h 1.1 to 1.2); 44°10'N, 4°52'W, 1900 m, THALASSA Stn X334, 7 spm. (2.5 × 2.2 to 2.7 × 2.6 mm, l/h 1.0 to 1.1); 44°11'N, 5°10'W, 2000 m, THALASSA Stn X336, 3 spm. (2.4 × 2.2 to 3.0 × 2.7 mm, l/h 1.1), all dredged RV *Thalassa*, 1971, all MNHN. Azores region: W of S. Miguel, 37°57'N, 26°08'W, 3225 m, dredged RV *Jean Charcot* BIACORES cruise, Stn DS 126, 3360 m, 9 spm. (2.6 × 2.5 to 3.8 × 3.5 mm); Stn CH171, 3125 m, 8 spm. (2.6 × 2.5 to 3.8 × 3.5 mm); Stn DS 173A, 3225 m, 40 spm. (2.0 × 1.8 to 3.7 × 3.5 mm, l/h 1.0 to 1.05), all MNHN. Cape Verde Basin (West of Mauritania), 18°37'N, 21°03'W, 3125 m, dredged RV *Atalante* EUMELI 2 cruise, Stn CP 09, 2 spm. (3.5 × 3.2 to 3.7 × 3.3 mm); 18°34'N, 21°02'W, 3139 m, Stn KG 13, 1 sh. (2.3 × 2.1 mm); 18°33'N, 21°03'W, 3136 m, Stn KG 14, 1 spm. (3.7 × 3.4 mm) and 4 v.; 18°27'N, 21°02'W, 3118 m, Stn KG18, 1 sh. (4.1 × 3.8 mm, l/h 1.1), all MNHN.

Biotope: Muddy bottom in 1800-3225 m. In the material from EUMELI, the species was found in samples from the mesotrophic and eutrophic zones.

Remarks: Although the type material of *V. atlantica* is now in fragments, the hinges of both type specimens are still preserved (Figs 12, 13) and coincide with those in the newly collected material treated in this paper. In the paralectotype, a weak lunular incision, another character of *V. atlantica* is still visible, as well as the long and narrow escutcheon. This supports that the studied material represents *V. atlantica*.

There is a marked resemblance between the shells of this species and *Kelliella miliaris*, currently placed in a different family (Kelliellidae) and superfamily (Arcticoidea). Shell characters, including the unusual grooves of the ventral margin, are similar, and this could lead to question the generic separation. The main differences regard the morphology of the hinge, where the anteriorly displaced cardinal 1 of *Vesicomya* cannot be recognized in *Kelliella miliaris*; the left valve of *K. miliaris* has a short, protruding cardinal situated just under the beak, for which there is no straightforward hypothesis of homology with the teeth of *Vesicomya*. *Kelliella* has a single, very wide exhalent siphon and a large functional foot (Clausen 1958, and our observations), reaching outside the valves when extended. In *V. atlantica*, there are two clearly separated inhalent and exhalent apertures, and small tentacles around these; the foot is tiny and permanently concealed by the gills. On these grounds,

we conclude that *Kelliella* and *Vesicomya* must be maintained as separate genera, at least until a more general picture of the phylogeny of these groups emerges, using anatomical and molecular characters.

The species figured by Allen (2001:204, fig. 5) as *Kelliella nitida* Verrill, 1885 is the same as our Fig. 14, and both taxa are likely to be synonyms. The species illustrated by Allen (2001:206, fig. 6) as *Kelliella atlantica* (Smith, 1885) is a very different species, possibly *Vesicomya adamsi*, whereas that figured on the same page (Allen 2001:206, fig. 7) is probably what is called *V. atlantica* herein, and that figured for anatomy (Allen 2001:207, figs 8-9) differs in having a functional foot and is deemed a different species.

Vesicomya adamsi (E.A. Smith, 1885)
(Figs 15-22; 76-77; 99)

Callocardia (?) *adamsii* E.A. Smith, 1885: 155-156, pl. 6, fig. 7-7b

Type material: Holotype BMNH 87.2.9.2707, a complete shell (12.6 × 11.5 × 9.0 mm).

Type locality: S of Sierra Leone, 3°10'N, 14°51'W, 2450 fms (*Challenger* Stn 348).

Description: Shell up to 13.7 mm long, slightly longer than high, high-triangular, cordiform, somewhat variable in outline and length/height ratio, thin and very tumid. Anterior margin evenly rounded, with a small indentation where the lunular incision meets the anterior margin; ventral margin well convex. Posterior margin rounded-tapering. Beaks prominent, strongly prosogyrous and enrolled, well in front of the vertical midline, not touching each other and slightly twisted away from the hinge line.

Surface glossy, with strong, dense, regular and evenly spaced commarginal grooves, occasionally a few growth lines; no posterior angle. Lunule very broad, heart-shaped, not sunken and well delimited by a strong lunular incision. Escutcheon very long, stretching over the whole postero-dorsal partly, rather narrow, well defined, slightly sunken, delimited by a rounded keel, continuing forward between the beaks to the umbos. Commarginal grooves continuing on lunula and escutcheon more dense and somewhat irregular. Only vestiges of the periostracum may occasionally be seen, mostly on the escutcheon.

Hinge line rather strong, broadening under the beaks and the ligament. Two variable teeth in each valve, more or less parallel to the hinge line. Right valve with a short anterior tooth (1) below the beaks and a longer undulate posterior tooth (assumed to be fused 3a and 3b), running from behind the end of the anterior tooth and sometimes above it and continuing backwards to nearly mid-length of the ligament. Left valve with a rather long and strong undulate tooth parallel to the antero-dorsal margin and beginning under the beak (assumed to be fused 2a and 2b) and a rather thick and slightly inclined posterior tooth (4b). Ligament external, opisthodetic, very short. Adductor muscle scars and pallial line very weak or not visible. Pallial line without a sinus, situated close to the margins. Shell margin rather narrow, with a weak longitudinal incision on the surface which touches the other valve, visible only under a strong lens.

Protoconch rounded and convex, about 200 µm in diameter, rather smooth, with a slightly flaring margin, not sharply delimited, about 35 µm broad.

Valves entirely white.

Distribution: Known from the tropical eastern Atlantic from off Sierra Leone (Smith 1885) and Romanche Deep (Odhner 1960) to off Namibia, between 4400 and 5300 m.

Material examined: Namibia: 18°52.1'S, 7°23.1'E, 5124 m, trawled RV *Jean Charcot*, WALDA, Stn CY 02, 50 spm. (9.2 × 8.5 × 6.9 to 13.7 × 12.7 × 10.8 mm), l/h 1.05 to 1.2), live-collected but soft parts decayed, all MNHN.

Biotope: muddy bottom.

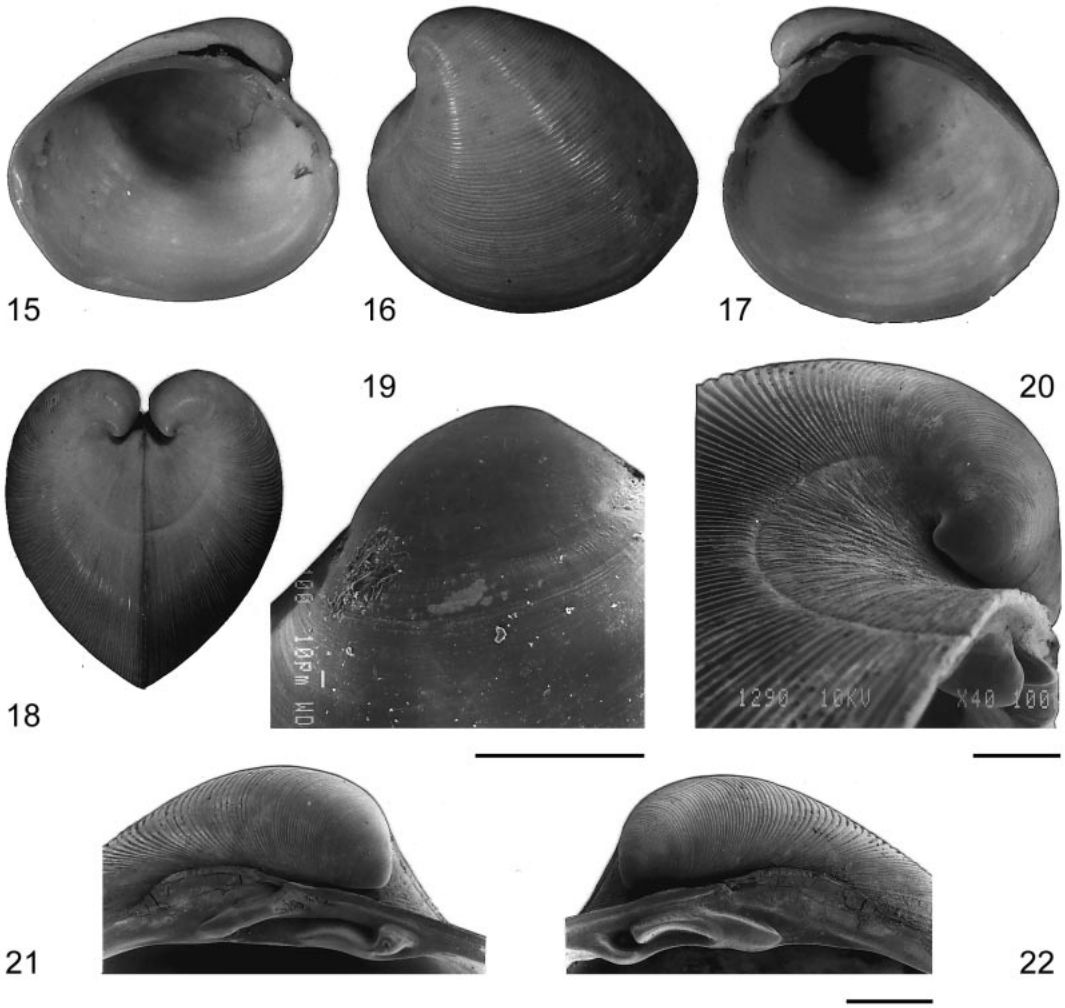
Remarks: This species with its strongly protruding and prosogyrous enrolled umbos recalls a tiny *Glossus* or *Meiocardia*, however, *Vesicomya* is distinguished from them by having a hinge without laterals, smaller umbos, a fine commarginal sculpture (*Glossus* has smooth surface, *Meiocardia* coarse commarginal ribs), a more circular shell outline and by the presence of lunule and escutcheon.

Genus *Waisiuconcha* Beets, 1942

Waisiuconcha Beets, 1942: 315-316, fig. 147-151

Type species: *Waisiuconcha alberdinae* Beets, 1942 (by original designation). Buton Island, Indonesia, most probably Upper Oligocene (Fig. 80). – Two Recent species described from Japan: *Waisiuconcha katsuae* (Kuroda, 1952), and *W. surugensis* Habe, 1976 (Fig. 81) (see also Higo & al. 1999); a third Japanese species cited by these authors in the genus *Waisiuconcha*, *W. nakaii* (Okutani, 1962) may be, according to the original drawing (Okutani 1962, pl. 4 , fig 1 a), a species of *Isorropodon*.

Diagnosis: Shells very small to small, 4 to 23 mm long, thick, oval-veneriform to subcircular, inflated to very inflated, with rounded or rounded-tapering posterior margin. Umbos prominent, prosogyrous and well in front



Figs 15-22. *Vesicomya adamsi* (E.A. Smith, 1885). W of Namibia, 18°52.1'S, 7°23.1'E, 5124 m, trawled RV *Jean Charcot*, WALDA cruise, Stn CY 02. 15. Interior of l.v. Shell length 13.2 mm. 16. Exterior of l.v. Shell length 13.0 mm. 17. Interior of r.v. Shell length 13.4 mm. 18. Same specimen, anterior view. 19. Protoconch. Scale bar: 100 µm. 20. Close-up view of lunular incision. Scale bar: 500 µm. 21-22. Hinge plate of both valves. Scale bar: 100 µm.

of the vertical midline. Surface with fine to well-developed commarginal striae or grooves, lunular incision well defined. Hinge line strong and broad, with three cardinals in each valve (Figs 2-3). Cardinal 1 in the right valve rather strong and situated beneath cardinal 3a; cardinal 3b partly overlapping with 3a and more or less fused with it. Cardinals 2a and 2b of the left valve fused and widely separated from cardinal 4b which is situated posteriorly. Lateral teeth absent. Margins outside the hinge line with one or two shallow grooves (see fig. 32) along the contact surface between the valves (which is rather broad due to shell thickness). Pallial line situated in a considerable distance from the margin, no pallial sinus.

Remarks: The genus *Waisiuconcha* is close to *Vesicomya* but more variable in outline. The main distinguishing feature is the conspicuously broader hinge line with strong teeth, with on the left valve the peculiar triangular middle (2b) tooth (fused to the anterior 2a), and on the right valve the more or less markedly curved 3a cardinal above the cardinal 1 which is not displaced as far forward as in *Vesicomya*. In fact, the hinge of *Waisiuconcha* is less modified than that of other Vesicomyidae, and a comparison with the hinge dentition of very young Veneridae (e.g. *Pitar rudis* (Poli, 1795), Figs 4-5) show that main difference is the presence of tiny anterior laterals in *Pitar*.

Waisiuconcha is further distinguished from *Vesicomya* by the pallial line being more distant from the margin, and the thicker valve margins with more than one groove along it, whereas *Vesicomya* has only one such incision. A comparable sculpture, slightly oblique, is known from the venerid genus *Transennella*. Dall, 1883. All other distinctive characters of *Vesicomya*, e.g. generally tumid valves, broad, heartshaped lunule not sunken and delimited by an incision, sculpture of commarginal grooves, long and rather narrow escutcheon are also present in *Waisiuconcha* and, as well as the incisions on the margin. This indicates the close relationship of the two genera.

Waisiuconcha haeckeli sp. nov.
(Figs 2-3; 23-32; 78-79; 104)

Type material: holotype MNHN, off Mauritania, 19°27'N, 17°06'W, 800-825 m, RV *Ernst Haeckel*, Stn CH262, 1982, leg. B. Richer de Forges, a complete shell (3.6 × 3.15 mm, l/h 1.1), live-collected and dried. Paratypes, same locality, 1 juv. sh. (2.4 × 2.2 mm), 10 single v., (3.3 × 3.2 to 4.0 × 3.8 mm, l/h 1.0 to 1.1), partly eroded on the umbos or slightly chipped.

Type locality: Cape Verde Basin, off Mauritania, 19°27'N, 17°06'W, 800-825 m,

Description: Shell very small, to 4 mm long, slightly variable in outline, juveniles somewhat longer than high, adults almost as high as long, subcircular-veneriform, rather thick and solid, tumid. Antero-dorsal margin in the lunular area straight, anterior margin rounded. Very weak indentation where the lunular incision meets the margin; ventral margin convex. Posterior margin rounded, postero-dorsal margin convex, with a weakly marked angle to the posterior margin. Beaks prominent, strongly prosogyrous, slightly enrolled, well in front of the vertical midline, hardly or not touching each other and twisted away from the hinge line.

Surface with widely spaced and slightly variable commarginal grooves, which are well visible only on the anterior and ventral part of the valves, less pronounced to obsolete on the earlier part and posteriorly; umbos smooth; no posterior angle. Lunule short, broader than long, heart-shaped, not sunken, delimited by a well marked lunular incision. Escutcheon very long, stretching over the whole postero-dorsal part, rather narrow, well defined, slightly sunken, on right valve slightly broader than on left valve, delimited by a rounded keel. Sculpture continued and more dense on lunule and escutcheon. Periostracum very thin and translucent, glossy.

Hinge line strong, broad, broader under the beaks. Two teeth in each valve, which are variable in shape. Cardinal 1 in the right valve rather strong, parallel to the ventral margin and situated beneath the beaks and beneath cardinal 3a. Cardinal 3a strongly curved, running from above the anterior end of cardinal 1 backwards to beneath the end of the ligament. Cardinal 3b partly overlapping with 3a and more or less fused with it. Left valve with cardinals 2a and 2b more or less fused, and a very conspicuous and deep socket to accommodate cardinal 1. Cardinal 4b rather thin, quite distant from the fused 2a-2b, running from above 2a backwards to beneath the posterior end of the ligament, subparallel to the hinge margin or slightly inclined. Ligament opisthodetic. Adductor muscle scars and pallial line very weakly marked or not at all. Pallial line rather distant from the margins, without a sinus. Valve margin broad, with two to three incisions, very weak but clearly visible, nearly parallel to the edges but running into them at some point.

Protoconch rounded and convex, small, about 160 µm in diameter, with a pitted sculpture on the upper portion, the remaining surface being smooth..

Valves entirely white.

Distribution: Known only from the Cape Verde Basin, off Mauritania.

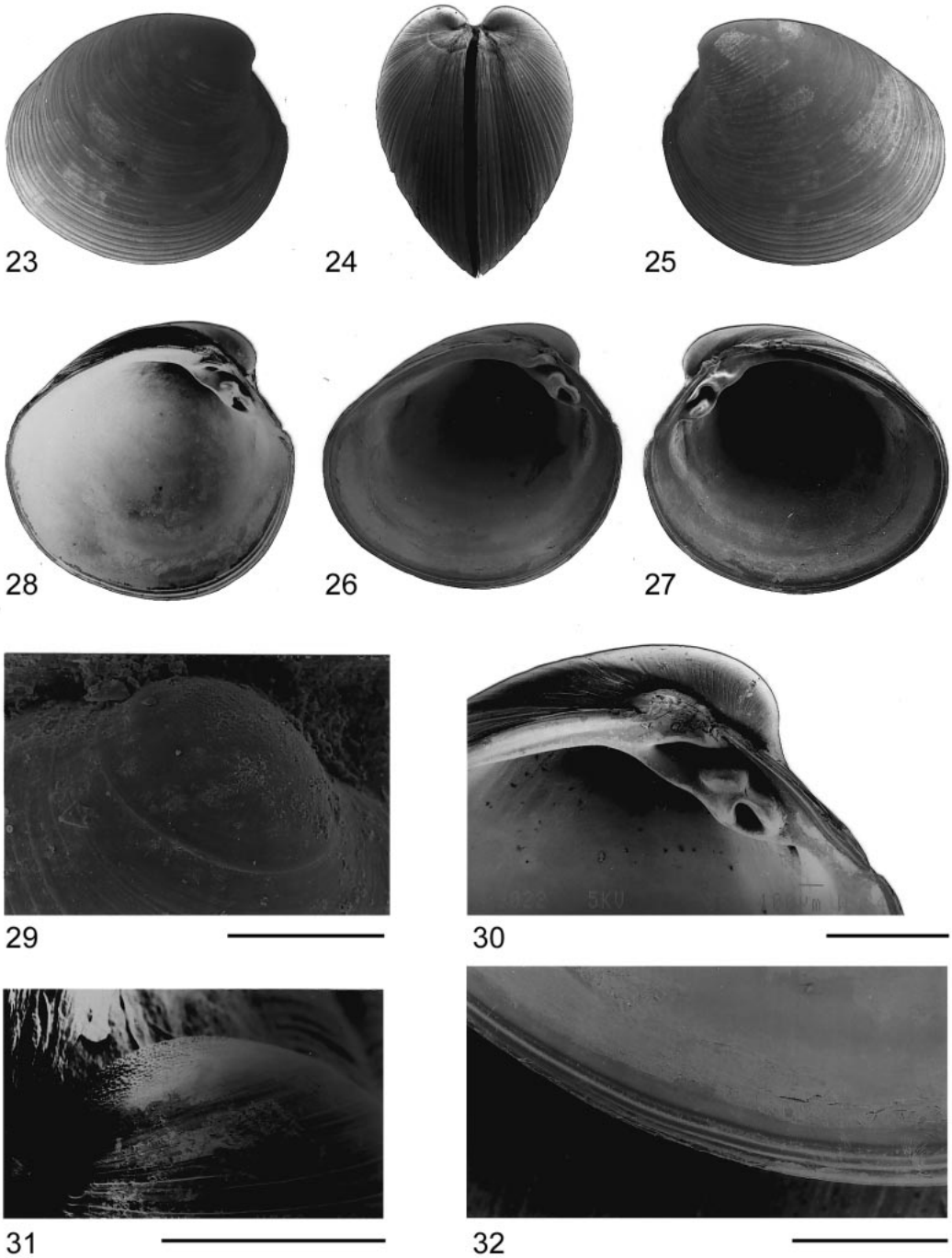
Material examined: The type material; Mauritania: 18°46'N, 16°51'W, 606-610 m, RV *Ernst Haeckel* Stn CH268, 1982, 5 v. (2.7 × 2.45 to 3.6 × 3.5 mm, l/h 1.0 to 1.1), leg. Richer de Forges, MNHN; off Mauritania (no precision), 900-1200 m, in the residue of commercial trawlers, 5 dried spm. (2.8 × 2.7 to 3.5 × 3.2 mm, l/h 1.0 to 1.1), communicated by F. Gubbioli, MNHN.

Biotope: Most probably in muddy sediments, 600-1200 m.

Derivatio nominis: The species is named after the RV *Ernst Haeckel* of the former German Democratic Republic, with which part of the material and the holotype were collected.

Remarks: This species somewhat resembles *Vesicomya atlantica*, but is immediately distinguished by its thicker and slightly less tumid shell, the umbos placed more forward, the posterior part not so high, the less modified hinge dentition and by having more than one groove in the shell margin. The type species of *Waisiuconcha*, *W. alberdinae*, is more oval-veneriform. Juvenile specimens of *W. haeckeli* are less tumid than adults and thus resemble more *W. alberdinae*. This is the first record of *Waisiuconcha* outside the Indo-Pacific.

A single shell of probably another species of *Waisiuconcha* was found among the material taken off Mauritania (900-1200 m), communicated by F. Gubbioli. The



Figs 23-32. *Waisiuconcha haeckeli* sp. nov. 23-27. Holotype MNHN, off Mauritania, 19°27'N, 17°06'W, 800-825 m, RV *Ernst Haeckel*, Stn CH262, 1982, leg. B. Richer de Forges. 23. Exterior of r.v.; 24. Anterior view; 25. Exterior of l.v.; 26. Interior of l.v.; 27. Interior of r.v. Shell length 3.6 mm. 28. Off Mauritania (no precision), 900-1200 m, in the residue of commercial trawlers, interior of l.v. Shell length 3.4 mm. 29. Protoconch of holotype. Scale bar: 100 µm. 30. Hinge line of l.v., specimen from the residue of commercial trawlers. Scale bar: 500 µm. 31. Lateral view of protoconch to show granuled surface, same origin. Scale bar: 100 µm. 32. Inner view of ventral margin to show the longitudinal incisions in the margin, l.v. of holotype. Scale bar: 500 µm.

shell is short-oval and measures 6.2 × 4.7 mm; it has the typical hinge configuration of this species group and also fine, longitudinal, slightly inclined grooves on the ventral valve margin, like in *Transennella*. The exterior has rather strong irregular commarginal striae. More material will be needed before a new species can be ascertained and described.

Genus *Isorropodon* Sturany, 1896

Isorropodon Sturany, 1896: 17

Type species: *Isorropodon perplexum* Sturany, 1896 (by monotypy). North of Alexandria, Egypt, eastern Mediterranean.

Diagnosis: Shells small to medium-sized, oval-oblong, rather thin, inflated, with prosogyrous umbos situated well in front of the vertical midline. Lunular incision indistinct or missing. Pallial sinus very small, marked by an extremely shallow inflexion of the pallial line only. Hinge line rather narrow, with three cardinals in each valve which are more or less parallel to the hinge margin. Valve margins smooth.

Remarks: *Isorropodon* is distinguished from *Vesicomya* by the much larger and more oval to oval-oblong shell, the poorly developed to missing lunular incision and the smooth valve margins without an incision. *Vesicomya* is smaller, the shells are very tumid to nearly spherical, the general hinge teeth configuration however is the same in both.

Sturany (1896) did not formally incorporate the genus *Isorropodon* in a family, but compared it with *Cypricardia* [= *Coralliophaga*] *lithophagella* (Payraudeau, 1826), which is currently held in the Trapezidae. Following this, Keen in Moore (1969) placed *Isorropodon* in the Trapezidae with a question mark. Examination of the type material of *I. perplexum* revealed the hinge morphology is that of Vesicomyidae, and thus that *Isorropodon* should correctly be placed into this family. The Trapezidae also have a somewhat similarly modified hinge, but differ in having posterior laterals.

Isorropodon perplexum Sturany, 1896
(Figs 33-48; 82-83; 100)

Isorropodon perplexum Sturany, 1896: 17-18, pl. 1 figs 24-27
Vesicomya sp., Corselli & Basso, 1966: 235-236, fig. 6

Type material: 9 syntypes in NHMW, single v. (2 r.v., 7 l.v., 2 large fragments: 10.9 × 7.8 mm ; 8.4 × 5.9 mm ; 7.9 × 5.4 mm ; 7.6 × 5.5 mm; 7.5 × 5.8 mm ; 7.3 × 5.3 mm; 6.0 × 4.4 mm ; 5.1 × 3.7 mm ; 4.5 × 3.5 mm ; l/h 1.3 to 1.5), one v. fresh, the others postmortal greyish brown.

Type locality: North of Alexandria, Egypt, 32°30'N, 29°08'E, 2420 m.

Description: Shell small, up to 12 mm long (exceptionally up to 15 mm), thin, very variable in outline, tumidity and length/height ratio, from oblong-oval to high-oblong, tumid to very tumid. Anterior margin evenly rounded to somewhat truncate, ventral margin convex, in some specimens less so on the anterior part. Posterior margin more or less broadly convex. Beaks prosogyrous, well in front of the vertical midline.

Surface dull, with strong to very strong, dense, irregular commarginal growth lines, occasionally a few broad, shallow growth waves or stages on the postero-ventral part of the valve; no posterior angle. Lunule obsolete, a slight delimitation, however, is visible on a few valves. Escutcheon long, very narrow, weak but well defined. Periostracum glossy and translucent, becoming more dull with a pale straw colour towards the margin of large specimens.

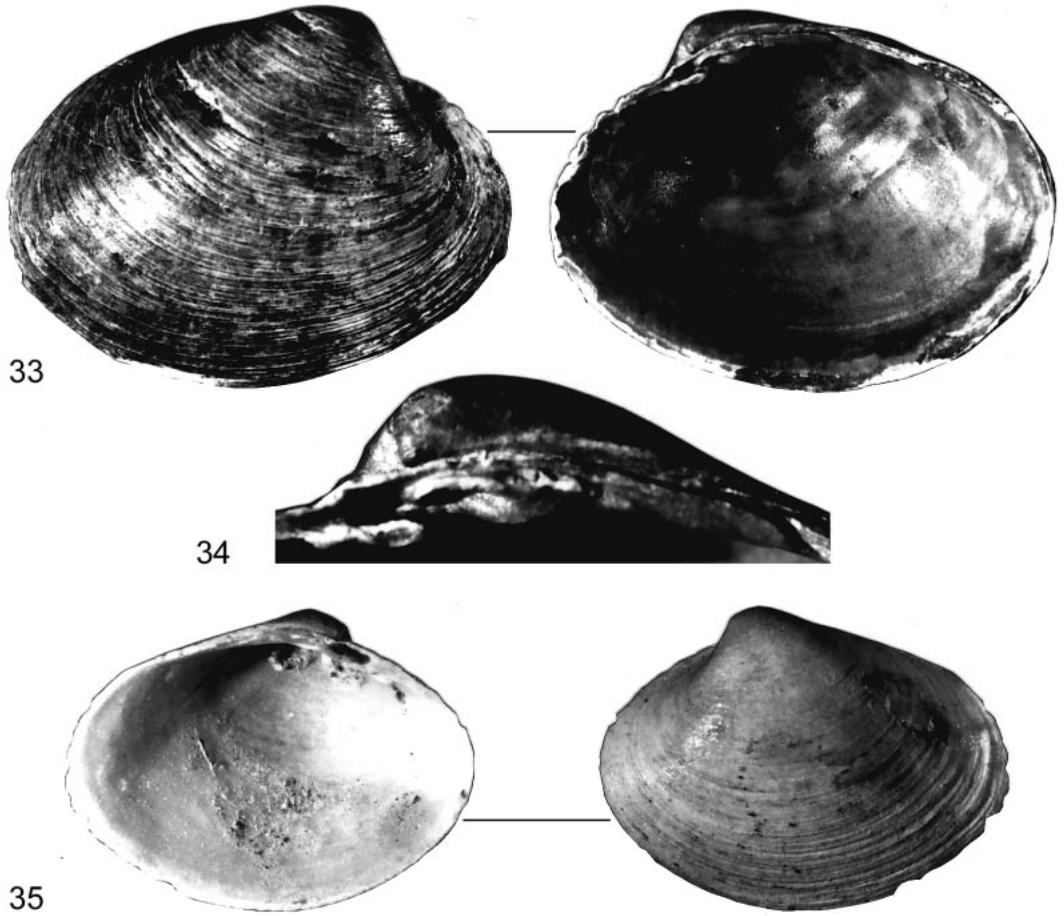
Hinge line variable from narrow and delicate to frequently rather broad with strong teeth, slightly broadening under the beaks, with teeth very variable in shape. Right valve with a short anterior tooth (1) just in front of the beaks, parallel to the margin and a longer undulate posterior tooth (assumed to be fused 3a and 3b), running from just above the end of the anterior tooth backwards to nearly mid-length of the ligament. Left valve with a rather long and strong undulate linear tooth parallel to the dorsal margin and under the umbo (assumed to be fused 2a and 2b) and a thin laminar posterior cardinal tooth (4b) which is slightly inclined. Ligament opisthodetic, rather short. Posterior pallial line slightly deflected inwards so as to be nearly straight, but not forming a real sinus. Inside frequently with very faint radial vermiculations.

Protoconch round and convex, about 160 µm in diameter, slightly corrugated on the upper portion, smooth towards the edge.

Valves entirely white when fresh.

Description of the soft parts: Mantle very thin, with three folds, attached to the shell by both the pallial muscle and small but strong dorsal foot retractors. Mantle cavity open ventrally from the anterior adductor to the base of the inhalent siphon. Siphons separate, short and with papillae around the siphonal apertures.

Anterior adductor muscle in cross-section somewhat bean-shaped, posterior adductor muscle suboval in shape, larger than the anterior one. Foot sturdy and strongly rugose, rather large and elongate, curved, with a blunt



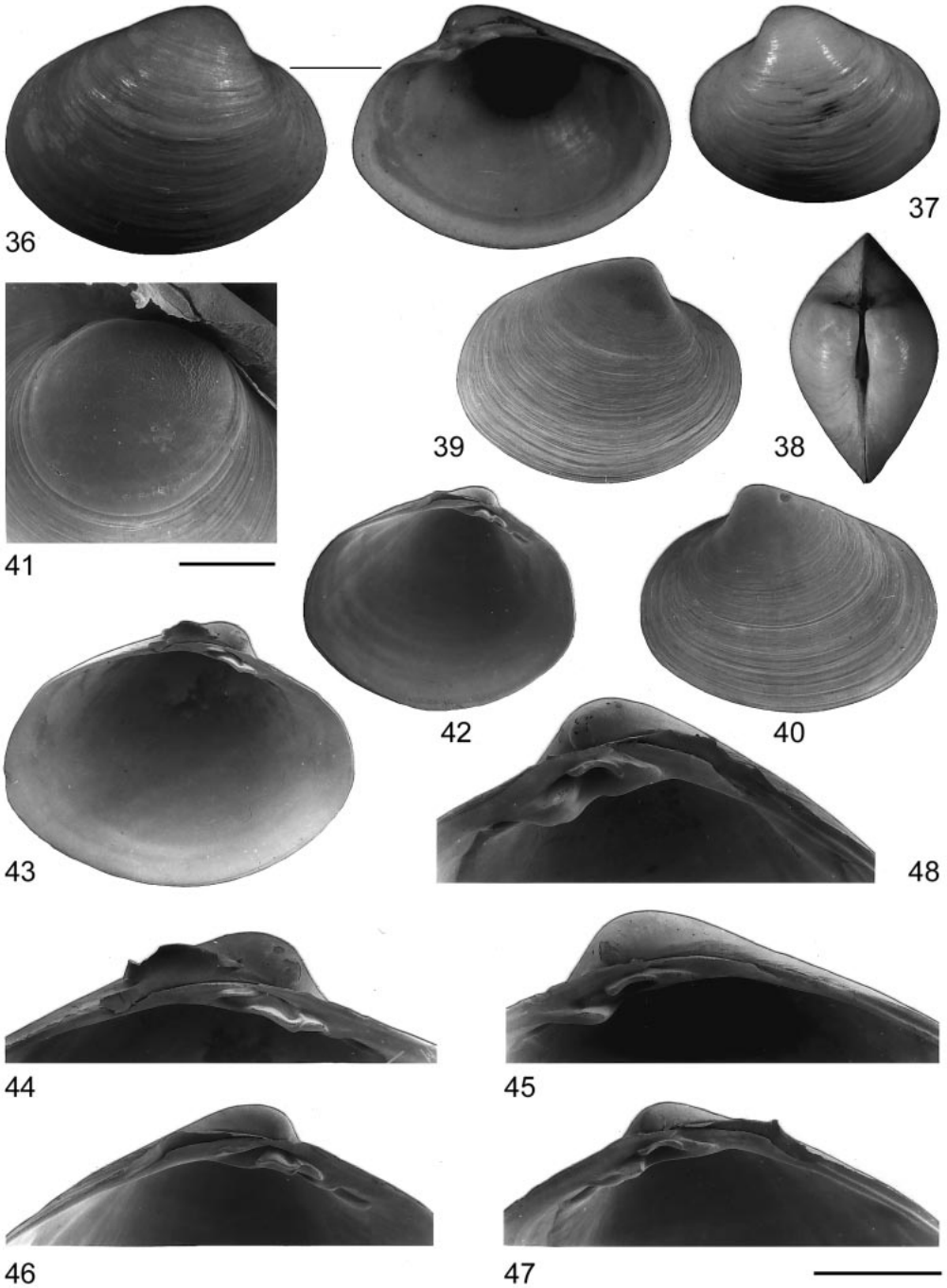
Figs 33-35. *Isorropodon perplexum* Sturany, 1896. Syntypes NHMW. North of Alexandria, Egypt, 32°30'N, 29°08'E, 2420 m. 33. Exterior and interior of r.v. Shell length 7.9 mm. 34. Close-up view of hinge of r.v. 35. Interior and exterior of l.v. Shell length 5.1 mm.

distal end which is directed forward and upward when retracted. Proximal part of the foot with anteriorly a well-defined semicircular lobe and posteriorly two lateral keels, terminating in a pointed posterior heel. Ventral midline of the foot with an axial keel extending from below the heel to the anterior end.

Ctenidia with only one very large and thick demibranch on each side which corresponds to the inner demibranch in other eulamellibranchate bivalves; outer demibranch absent. Gills occupying a large part of the available space in the shell cavity, entirely covering the visceral mass and protruding into the swollen part of the shell beneath the umbos.

Distribution: Eastern Mediterranean, known from off the Nile Delta, the Napoli and Milano mud volcanoes south of Crete (empty valves only) and the Amsterdam and Kazan mud volcanoes south of Turkey. It is an important component of the deep-water fauna in the eastern Mediterranean, representing roughly 1/4 of the bivalve shells collected by the MEDINAUT cruise.

Material examined: The type material. Olympe zone, off Southern Crete, Napoli mud volcano, 33°43.5'N, 24°41'E, 1945m, MEDINAUT dive MN1, 40 v (3.5 × 2.8 to 9.9 × 7.4 mm) 3 sh. (4.5 × 3.6; 4.9 × 4.1; 5.8 × 4.5 mm); Milano mud volcano, 33°44'N, 24°47'E, 1955 m, MEDINAUT dive MN3, 3 v. (10.2 × 7.8 to 11.0 × 9.5 mm); same site, dive MN5, 9 v. (5.8 × 4.8 to 9.8 × 7.8 mm); Anaximandre zone, off South Turkey, Amsterdam mud volcano, 35°20'N, 30°16.5'E, 2030 m, MEDINAUT dive MN8, ca. 1100 v., (max. 12.2 × 9.3 mm, l/h 1.2 to 1.4), 52 sh. (2.8 × 2.4 to 10.1 × 7.8 mm), 6 spm. (2.5 × 2.0, 3.0 × 2.5, 3.0 × 2.5, 4.4 × 3.8, 4.8 × 3.8, 7.6 × 6.2 mm); same site,



Figs 36-47. *Isorropodon perplexum* Sturany, 1896. Fresh specimens from the MEDINAUT cruise, 1998. 36. Amsterdam mud volcano, S of Turkey, 35°20'N, 30°16.5'E, 2030 m dive MN8. external and internal view of l.v. Shell length 10.3 mm. 37-38. Same locality, another sh., external and dorsal view. Shell length 8.3 mm. 39. Napoli mud volcano, S of Crete, 33°43.5'N, 24°41'E, 1945 m dive MN1, external view. Shell length 4.8 mm. 40. Same locality. Shell length 6 mm. 41. Same locality. Protoconch. Scale bar: 100 µm. 42. Same locality. inner view of l.v. Shell length 4.5 mm. 43. Same locality, inner view of l.v. Shell length 5.8 mm. 44-45. Close-up view of hinge line of specimen of fig. 42. Scale bar: 100 µm. 46-47. Close-up view of hinge line of specimen of fig. 41. Scale bar: 100 µm.

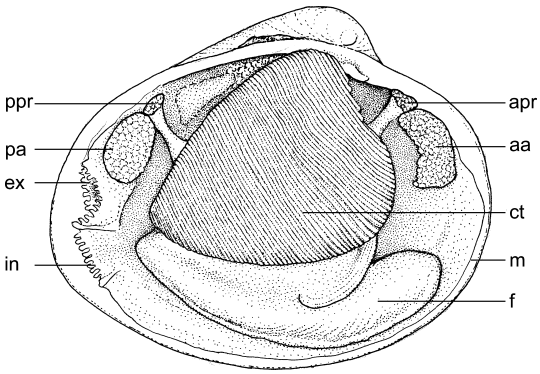


Fig. 48. *Isorropodon perplexum*. Kazan mud volcano, S of Turkey, 35°26'N, 30°33.5'E, 1700 m dive MN10, MEDINAUT cruise. Halfschematic view of the soft parts, right valve and right mantle lobe removed. Abbreviations: aa: anterior adductor muscle; apr: anterior pedal retractor muscle; ct: ctenidium; ex: exhalent siphon; f: foot; in: inhalent siphon (sectioned); m: mantle edge; pa: posterior adductor muscle; ppr: posterior pedal retractor muscle. Shell length 7.3 mm.

dive MN14, 5 spm. (3.4 × 2.6 to 4.9 × 3.7 mm); Faulty Ridge, 35°27'N, 30°25'E, 1538 m, MEDINAUT dive MN9, 46 v. (3.2 × 2.6 to 12.3 × 8.8 mm); Kazan mud volcano, 35°26'N, 30°33.5'E, 1700 m MEDINAUT dive MN10, 52 v. (4.4 × 3.8 to 11.8 × 9.9 mm), 2 sh. (6.8 × 5.8, 11.0 × 8.9 mm), 1 spm. (7.3 × 6.0 mm); same site, MEDINAUT dive MN12, 24 v. (2.9 × 2.5 mm to 15.5 × 11.5 mm), all leg. M. Sibuet, Nov.-Dec. 1998. MNHN.

Biotope: Muddy bottom in cold seep areas, from 1950 to 2500 m.

Remarks: For a long time the whereabouts of the Sturany collection were unknown, and *I. perplexum* was only known from Sturany's description and figures. The collection was refound only recently in the NHMW, and this and the newly collected material allowed a complete redescription.

The *Vesicomya* sp. reported by Corselli & Basso (1996) in 1950 m from the Napoli Dome is, judging from the figure, a juvenile *I. perplexum*. This species is the first representative of the family to be recorded in the Mediterranean.

Isorropodon bigoti sp. nov.
(Figs 49-58; 84-85)

Type material: Holotype MNHN, "N'Kossa" oilfield, off Pointe-Noire, 5°53.5'S, 11°38.84'E, 150 m, 1 spm. in alcohol (17.4 × 12.4 × 9.9 mm, l/h 1.4). Paratypes: same locality, MNHN, 6 sh. (10.6 × 8.4 × 6.0, 13.4 × 9.1 × 7.1, 13.6 × 9.5 × 7.3, 15.6 × 11.3 × 8.5, 16.3 × 11.8 × 9.1, 18.1 × 12.7 × 10.0 mm), 1 v. (21.0 × 14.4 mm), l/h 1.4 to 1.5); IRSNB, 1 sh. (14.6 × 10.5 × 7.7, l/h 1.4); Natal Museum, 1 sh. (14.2 × 9.9 × 7.5, l/h 1.4); NHMW, 2 sh. 13.2 × 9.5 × 7.4, 17.2 × 12.2 × 9.7 mm, l/h 1.4); SMF, 2 sh. (14.1 × 9.6 × 7.0, 16.1 × 11.2 × 8.5 mm, l/h 1.4 and 1.5); USNM, 2 sh. (11.8 × 9.0 × 6.2, 16.2 × 10.7 × 8.7 mm, l/h 1.3 and 1.5); ZMC, 1 sh. (15.0 × 10.4 × 7.9 mm, l/h 1.4).

Type locality: "N'Kossa" oilfield, off Pointe-Noire, Congo (Brazzaville), West Africa.

Description: Shell small, up to 21 mm long, oblong-ovate, variable in outline and length/height ratio, thin and very tumid. Anterior margin evenly rounded, frequently appearing rounded-truncate. Ventral margin convex, in larger specimens less so on the anterior part, so that the highest part is well behind the beaks. Posterior margin broadly convex. Beaks prosogyrous, well in front of the vertical midline, in large adult specimens near the end of the first third.

Surface with faint, irregular growth lines and weak to well developed, rather narrow to broad and very irregular growth waves, which may occasionally be wrinkly and which are often reflected on the interior; no posterior angle. No lunule but faint lunular incision occasionally visible. Escutcheon long and very narrow and weak but well defined, with rounded delimitations. Periostracum glossy, transparent and almost colourless.

Hinge line narrow and delicate, slightly broadening only under the beaks. Right valve with a narrow anterior tooth (1) parallel to the margin and a longer undulate posterior tooth (assumed to be fused 3a and 3b) running from above the end of the anterior tooth backwards to beneath the anterior part of the ligament. A deep horizontal socket between the teeth. Left valve with a rather long and strong undulate linear tooth parallel to the dorsal margin and situated under the umbo (assumed to be fused 2a and 2b) and above it a thin laminar posterior cardinal (4b) parallel to the dorsal margin. Teeth may be partly resorbed (dissolved) in very large old specimens. Ligament opisthodetic, rather short. Posterior pallial line slightly deflected inwards so as to be nearly straight, but not forming a real sinus. Fine, irregular radial vermiculations may be visible on the interior of the valves.

Protoconch round and convex, 170 to 180 µm in diameter.

Valves entirely white.

Description of soft parts (based partly on serial sections): Mantle very thin, thickened in the distal region because of the presence of a vascular sinus parallel to the mantle margin. Inner surface of the distal mantle region glandu-

lar. Mantle attached to the shell by both the pallial muscle and small, but strong dorsal muscles, which correspond to the foot retractors. There are three mantle folds: the outer fold, the middle fold with more or less numerous papillae, particularly in the anterior region; and the very large, vascularized inner fold with papillae on its inner surface in the anterior and posterior regions.

Mantle with a vascularized region behind and below the anterior adductor muscle and another vascularized area in the distal region and parallel to the mantle edge. Mantle cavity open ventrally from the anterior adductor to the base of the inhalent siphon, where there is a rather delicate membrane, easily broken on the preserved specimens. Siphons separate, short and with papillae around the siphonal apertures; these slightly more developed on the more protruding inhalent siphon.

Anterior adductor muscle in cross-section elliptical, somewhat bean-shaped; posterior adductor muscle suboval in shape and larger than the anterior one. Foot muscular and strongly rugose, rather large and elongate, curved, tapering at its distal end which is directed forward and upward and reaches the ventral edge of the gills. Proximal part of the foot with two lateral keels and a posterior heel. Ventral midline of the foot with a short proximal furrow between the lateral keels, then with another keel extending from below the here to the anterior end.

Ctenidia with only one very large and thick demibranch on each side which corresponds to the inner demibranch in other eulamellibranchiate bivalves; outer demibranch absent. Demibranch consisting of a descending lamella and an ascending lamella; the latter being shorter (about a half) than the former. Gills occupying most of the available space in the shell cavity, in length entirely covering the visceral mass from the posterior side of the anterior adductor muscle to the anterior side of the pericardial cavity and posterior adductor muscle, in height covering from the dorsal side of the visceral mass to the upper part of the foot.

Ventral margin of each demibranch with a well-developed food groove. Filaments with interfilamentar junctions, consisting of tightly packed groups of cilia. Interlamellar space of both demibranchs with a few very delicate interlamellar septa. Within the interlamellar space numerous blood cells, causing dark red colour of the gills (also visible in the preserved specimens).

Mouth behind and dorsal to the anterior adductor muscle. Labial palps very small and hardly visible. Oesophagus tubular; digestive diverticula not well developed; stomach small and suboval in shape. Midgut short and resembling the style sac, extending from the stomach to ventrally, posteriorly curved upward, connecting with a thin intestine, which passes through the visceral mass to the pericardial cavity. The stomach of the studied specimens was filled with microorganisms and fine particles of detritus.

Pericard large, elongate and located postero-dorsally with respect to the visceral mass. Ventricle with thick muscular walls, subconical in form, and cream in the preserved specimens. Kidneys lateral to the ventricle, reaching from the sides of the latter to the posterior adductor muscle. In the examined specimens gonads well developed, almost filling the visceral cavity from the stomach level and between the digestive diverticula to the pericard. The sexes are separate.

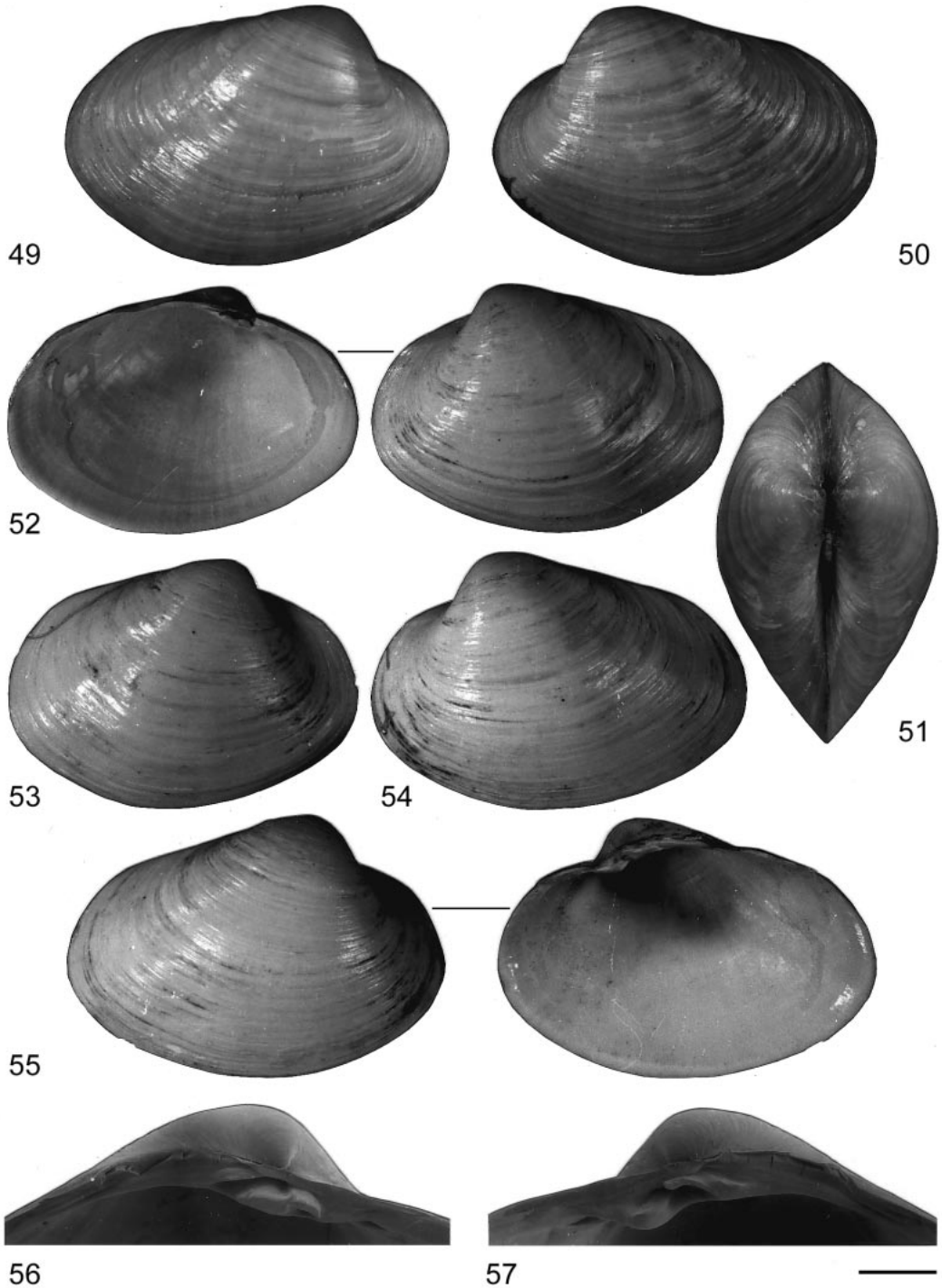
Distribution: Known from off the Congo (Brazzaville) Republic and from off Mauritania.

Material examined: The type material. Numerous associated specimens (85 v., 10 sh. 35 spm. in alcohol and dry) from the type locality, all MNHN. Mauritania (provisional identification): continental shelf, 900-1200 m (no precision, most probably off Nouakchott), in the residue of commercial trawler, 2 sh., leg. F. Gubbioli, May 1992, MNHN.

Biotope: In the type locality, the species was collected in mud with very fine sand in a depth of 150-250 m under or close to an oil drilling platform. These depths are unusually shallow for vesicomyids but may be explained by a high concentration in organic matter in the vicinity of the mouth of the Congo river. The Mauritanian specimens were taken much deeper; the character of that locality is not known but probably was a soft muddy bottom in a reducing zone.

Derivatio nominis: The species is named after Lionel Bigot, who collected the type lot and who was so kind to entrust it to us, together with other interesting mollusc species from the same samples.

Remarks: This new species is very close to *Isorropodon perplexum* in general outline. The variability in the outline is comparable but in *I. perplexum* even very small specimens are occasionally more elongate whereas in *I. bigoti* juveniles are generally shorter and more regularly oval than fully grown specimens. The new species is distinguished by its larger size (commonly 15-20 mm instead of 7-12 mm), the much less visible and more spaced growth lines and the more conspicuous wavy pattern of growth stages. There is no difference in the hinge configuration which is just as variable. Both species share the form of the pallial inflexion, too shallow to be called a sinus. The geographic isolation between this and *I. perplexum* is likely to be total, as the latter was not recorded from the Western Mediterranean nor from the Ibero-Moroccan Gulf. The larvae in the family have a



Figs 49-57. *Isorropodon bigoti* sp. nov. "N'Kossa" oilfield, off Pointe-Noire, Congo (Brazzaville), 5°53.5'S, 11°38.84'E, 150 m. 49-51. Holotype MNHN. 49. Exterior of r. v.; 50. Exterior of l. v.; 51. Dorsal view. Shell length 17.4 mm. 52-53. Paratype MNHN. 52. Interior and exterior of l.v.; 53. Exterior of r.v. Shell length 13.4 mm. 54-55. Paratype MNHN. 54. Exterior of l.v.; 55. Interior and exterior of r.v. Shell length 18.1 mm. 56-57. Paratype MNHN. Hinge lines. 56. Close-up view of hinge line of l.v. Scale bar: 1 mm. 57. Close-up view of hinge line of r.v. Scale bar: 1 mm.

limited capacity for dispersal (Lutz 1988), and even a stepwise dispersal would be unlikely in this context.

The two specimens from Mauritania are provisionally included in *I. bigoti*, in fact, there are no substantial differences to specimens from the Congo of the same size. For a more clear judgement of these, additional material will be necessary.

I. striatum (Thiele & Jaeckel, 1931) is also very close in outline and tumidity, hinge configuration and sculpture, however, it is much larger (other differences, see under that species). *Kelliella elongata* Allen, 2001, described from 481 m deep in the Angola basin, and of which the type material (holotype and two paratypes BMNH 1998180) could be examined by the first author after finishing the ms of this paper, is in fact an *Isorropodon*. It is much smaller (holotype: 1.95 mm long, larger paratype: 2.13 mm long), and the shells (figures, see Allen 2001:214, figs 17-18) differ in having a more pronounced umbo, shorter outline, and a slightly more distinct lunule. The anatomical illustration (Allen 2001:215, fig. 19) represents a specimen from the Argentina basin, and differs radically from *I. bigoti* by having delicate gill filaments, through which the visceral mass can be seen, instead of a very solid and opaque demibranch.

Within the family Vesicomyidae, internal anatomy was hitherto known only for some species of the genus *Calyptogena*. Thiele & Jaeckel (1931) gave a short description of the animal in their original description of *Vesicomya striata* (here assigned to the genus *Isorropodon*) but without any figure. For *Isorropodon bigoti*, a more detailed anatomical study was possible thanks to the large number of preserved specimens which could be sectioned.

The most important difference between *Isorropodon* and *Calyptogena* spp. are the ctenidia, which in the former have one demibranch only, whereas in all known *Calyptogena* spp. two demibranchs are present, the outer demibranch being less developed than the inner one. Thiele & Jaeckel (1931) also mention a single demibranch on each side for *I. striatum* (see below). Nevertheless, in the type species of *Vesicomya*:, two demibranchs are present. The remaining "inner" demibranch of *I. bigoti* is very large and thick (filled with blood cells); if compared to the figures of the different species of *Calyptogena* (see references above), it is comparatively very much thicker.

In contrast to all studied *Calyptogena* species, the foot of *I. bigoti* is more elongate and has a different and uncharacteristic shape: it resembles that of *Kelliella miliaris* (Philippi, 1844), which also is elongate, with a well-developed posterior keel, and which is situated in a similar position inside the mantle cavity. However, the foot of *Kelliella abyssicola* has two lateral keels (Clausen 1958).

The vascularized area behind and below the anterior adductor muscle of the mantle of *I. bigoti* and the dark red colour of the mantle edges in the preserved animal are characters also observed in *Calyptogena magnifica* (Boss & Turner 1980) and *C. (E.) extenta* (Krylova & Moskalev 1996), whereas Stuardo & Valdovinos (1988) do not mention them in their description of *C. australis.* However, in the figure (Stuardo & Valdovinos 1988: fig.1), a pallial vessel parallel to the mantle edge is seen.

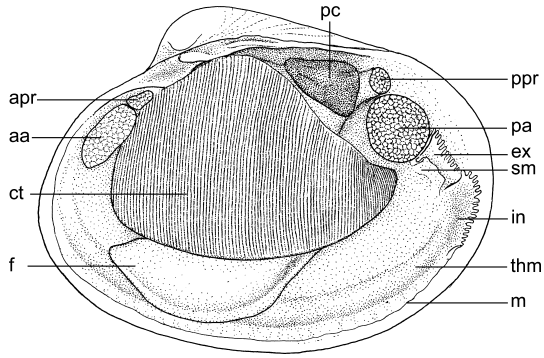


Fig. 58. *Isorropodon bigoti* sp. nov. Halfschematic view of the soft parts, left valve and left mantle lobe removed. Abbreviations: aa: anterior adductor muscle; apr: anterior pedal retractor muscle; ct: ctenidium; ex: exhalent siphon (sectioned); f: foot; in: inhalent siphon (sectioned); m: mantle edge; pa: posterior adductor muscle; pc: pericardial cavity; ppr: posterior pedal retractor muscle; sm: siphonal membrane of exhalent siphon; thm: thickened rim of the mantle. Shell length 13.5 mm.

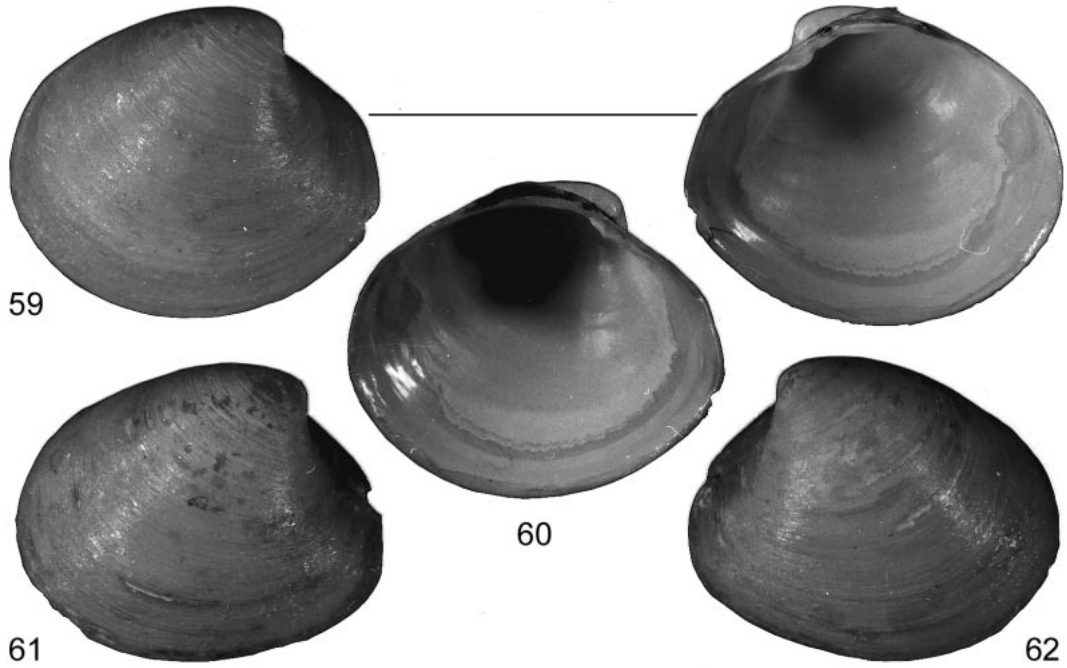
The digestive system of *I. bigoti* is similar to *Calyptogena* spp. It is shorter because of the lower length/height ratio of *I. bigoti*. Gonad types or sexes were not mentioned in the studies of *Calyptogena* spp. (Boss & Turner 1980; Stuardo & Valdovinos 1988; Krylova & Moskalev 1996) therefore a comparison between them and *I. bigoti* is not possible.

Isorropodon curtum sp. nov.
(Figs 59-62; 86-87)

Type material: Holotype MNHN, off Mauritania (no precision), taken by commercial trawlers in 900-1200 m, a complete shell (11.2 × 9.5 mm), leg. F. Gubbioli, V. 1992. Paratype: same locality, 1 sh. (11.3 × 9.2 mm), MNHN.

Type locality: Mauritania, West Africa.

Description: Shell small, to 11.3 mm long, oval, thin and tumid, length/height ratio 1.2. Anterior margin rounded, but appearing more or less rounded-truncate. Ventral margin convex, occasionally less so on the anterior part. Posterior margin broadly convex. Beaks prosogyrous,



Figs 59-62. *Isorropodon curtum* sp. nov. off Mauritania (no precision), taken by commercial trawlers in 900-1200 m. 59-60. Holotype MNHN, 59. Interior and exterior of r.v.; 60. Interior of l.v. Shell length 11.2 mm. 61-62. Paratype MNHN, 61. Exterior of r.v.; 62. Exterior of l.v. Shell length 11.3 mm.

well in front of the vertical midline, at the end of the first fourth of the valve length.

Surface with very fine and densely spaced commarginal striae and irregular fine growth lines which may be slightly lamellar near the margins; no posterior angle. There are also faint and narrow growth waves. Lunule not sunken but delimited by a fine but sharp incision; escutcheon narrow and ill-defined with rounded delimitations. Periostracum somewhat dull, iridescent, transparent and almost colourless.

Hinge line well arched, delicate, very narrow posteriorly to the beaks. Two teeth visible in each valve, beneath the umbos. Right valve with a short anterior tooth (1) parallel to the margin and a longer undulate posterior tooth (assumed to be fused 3a and 3b), running from above the anterior tooth backwards, not reaching the anterior end of the ligament. Deep horizontal depression between the teeth. Left valve with a rather long and strong undulate linear tooth parallel to the dorsal margin and situated under the umbo (assumed to be fused 2a and 2b) and above it a thin laminar posterior cardinal (4b) slightly inclined, almost parallel to the dorsal margin. Ligament opisthodetic, rather short. Posterior pallial line very slightly deflected inwards just under the posterior adductor scar, but not forming a sinus.

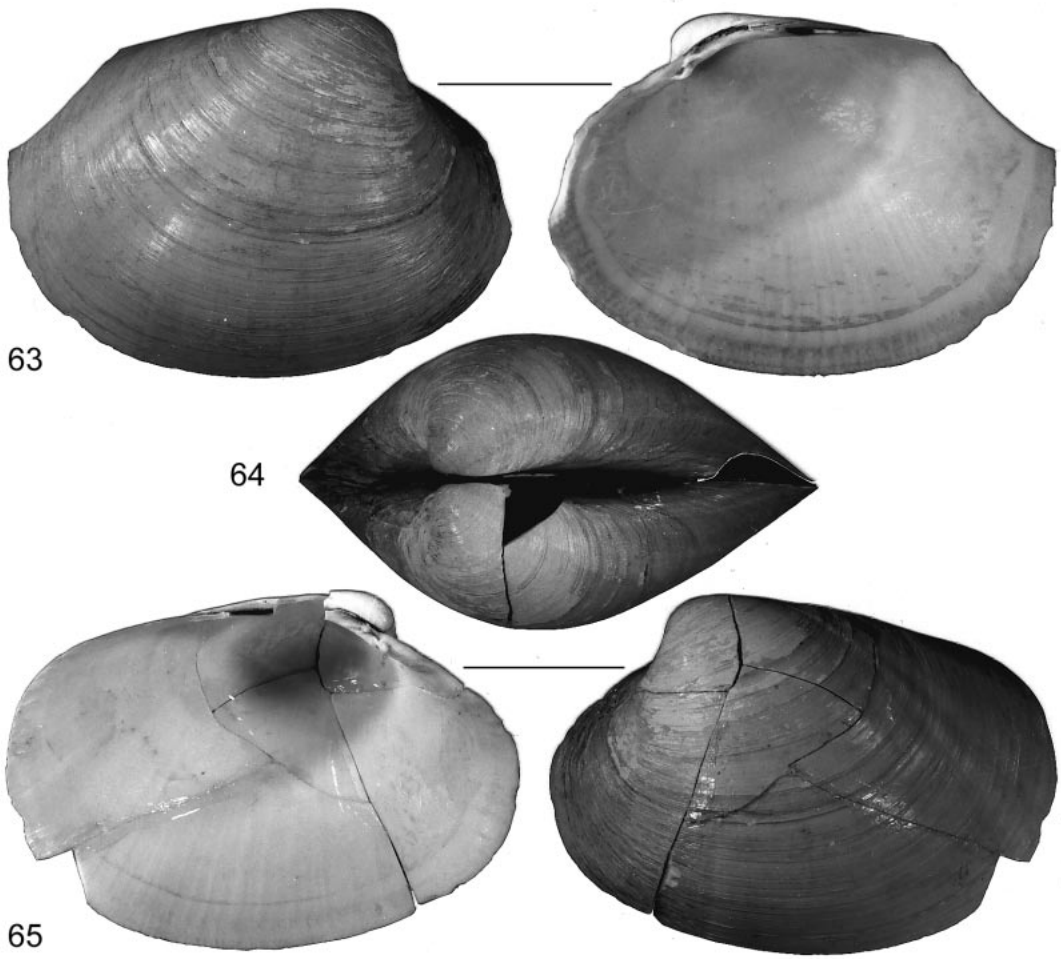
Valves entirely white.

Distribution: Known only from off Mauritania.

Material examined: The type material only.

Biotope: Not known but most probably muddy bottom.

Remarks: This species was contained in a mixed lot with *I. bigoti* and *Callogonia mauritanica* sp. nov. (see below). It is most close to *I. perplexum*, however, it does not fall into its variability, and there are slight constant differences: the posterior half of the valve is broader with the centre of tumidity being situated more towards posterior, the anterior part of the ventral margin is less convex, the valves are less tumid and the umbos are less prominent. The hinge line is narrower and the hinge teeth are finer than in most specimens of *I. perplexum*. The pallial line in *I. curtum* is not truncated posteriorly but only slightly further apart from the edge of the shell, and the ligament is longer. The shell of *I. perplexum* is slightly longer and has a narrower, rounded or rounded-truncated anterior margin. From *I. bigoti*, the new species is distinguished by its considerably shorter shell, the more forward placed umbos, the more arched hinge line and the different surface sculpture consisting of fine commarginal striae, whereas *I. bigoti* is smooth. All three species share the absence of a pallial sinus and have the



Figs 63-65. *Isorropodon striatum* (Thiele & Jaeckel, 1931), Holotype ZMB. Shell length 47 mm. 63. Exterior and interior of r.v. 64. Dorsal view. 65. Interior and exterior of l.v.

same general hinge configuration. Although we have received the specimens of *I. curtum* without the soft parts and therefore were not able to examine the gills, the common shell characters lead us, at least provisionally to consider the species congeneric.

Isorropodon striatum (Thiele & Jaeckel, 1931)
(Figs 63-65; 101)

Vesicomya striata Thiele & Jaeckel, 1931:230 (72), pl. 4, fig. 104.
Vesicomya (Vesicomya) striata Thiele & Jaeckel, 1931 – Boss, 1970:73-74, figs 11, 23, 26.

Type material: Holotype ZMB Berlin, a complete shell (47.0 × 34.0 × 26.4 mm); one valve broken (soft parts separated from the shell and not seen).

Type locality: Niger Delta, Bight of Biafra, W of Campo, Cameroon (2.0°N, 8°4.3'E), 2492 m.

Description: Shell 47 mm long, oblong-ovate, rather thin-shelled and very tumid. Anterior margin rounded, ventral margin evenly convex, posterior margin broadly convex. Beaks prosogyrous, well in front of the vertical midline, near the end of the first third.

Surface with very fine, close-set, irregular growth lines and numerous slightly stronger growth stages, which both are wrinkly on the anterior slope and which are not reflected on the interior. No posterior angle but posterior slope with a few very broad and shallow radial waves, only visible under oblique light and reflected on the interior. Lunule very short and broad, ill-defined and delimited by a very weak lunular incision. Anterior slope below the lunule with a few very broad and faint waves.

Escutcheon very narrow and weak, well-defined just behind the beaks, more posteriorly with rounded delimitations. Periostracum rather dull, thin and pale straw-coloured.

Hinge teeth very small and hinge line very narrow for the shell size, slightly broadening only under the beaks. Two visible teeth in each valve. Right valve with a narrow anterior tooth (1) parallel to the margin and a longer undulate posterior tooth (assumed to be fused 3a and 3b) running from above the middle of the anterior tooth backwards to beneath the anterior part of the ligament. Deep horizontal depression between the teeth. Left valve with a rather long undulate tooth parallel to the dorsal margin and situated under the umbo (assumed to be fused 2a and 2b) and above it posterior cardinal (4b) descending obliquely from the dorsal margin. Teeth in the left valve partly resorbed (dissolved). Ligament opisthodetic, rather short. Posterior pallial line without pallial sinus. Interior with faint, shallow, irregular radial waves or "vermiculations" (Boss 1970).

Valves entirely white.

Soft parts: We give here an English translation of Thiele & Jaeckel's original description of the soft parts (1931: 72 [230]): "The animal of *Vesicomya striata* has a thin and wholly smooth mantle edge which only at the posterior end is fused with that of the opposite side for a short distance and which bears there on the suture a row of very small papillae; an exhalent hole is not separated but slightly apparent. The foot is tapering and somewhat compressed, ventrally keeled, without a byssus; behind its base, there is a conspicuous flat, weakly concave surface which is tapering towards posterior. The gill appears on each side as a very thick fold which ventrally is turned over towards the interior; the surface shows very fine, transverse lamellae. The mouth palpi are small and rather short."

Distribution: Known only from the Niger Delta, Bight of Biafra.

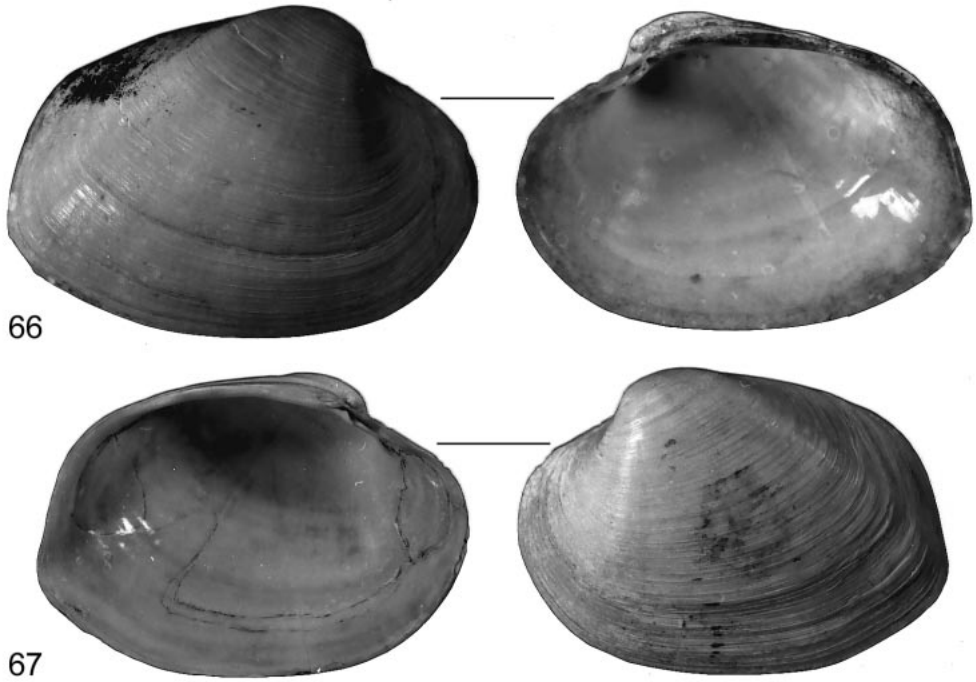
Biotope: Soft muddy bottom, in 2492 m

Remarks: This species differs from the three preceding species by its much larger size (47 mm) and the straw-coloured periostracum (characterized "light brownish" by Boss 1970). The oval-oblong outline approaches it to *I. bigoti*, however, its anterior margin is evenly rounded and the posterior margin more rounded-truncated; the surface sculpture consists of fine commarginal striae ("very fine, poorly developed, closely set lirations", Boss 1970), whereas in *I. bigoti*, the surface has moderately broad waves only. A "weakly incised lunular line" is well visible in *I. striata* but more or less obsolete in *I. bigoti*. The radial so-called "vermiculations" on the inside are also present in specimens of *I. perplexum* and *I. bigoti*. The short description of the soft parts points out that the ctenidia have only one demibranch, typical for *Isorropodon*, and also the foot seems to be close to that of *I. bigoti*.

V. guineensis Thiele & Jaeckel, 1931 (see Thiele & Jaeckel 1931:229, pl. 9(4), fig. 102; Boss 1970:71-72, figs 5, 6, 18, 19) was taken by the RV *Valdivia* together with *Isorropodon striatum* in the same dredge haul, and Boss (1970) presumes it possibly being conspecific. It is distinguished from *Isorropodon perplexum, I. curtum* and *I. bigoti* by its considerably larger size (60 mm). In general outline, it resembles *I. curtum* but is longer; it has

Table 1. Comparison of some features in *Isorropodon*.

	I. perplexum	*I. bigoti*	*I. curtum*	*I. striatum*
maximum shell size	12 mm	21 mm	11 mm	47 mm
shell outline	high-oblong to oblong-oval	oblong-oval	high-oblong (veneriform)	oblong-oval
tumidity	moderately to very tumid	very tumid	moderately tumid	very tumid
surface	very strong growth lines	weaker growth lines	fine growth lines and striae	very fine, close-set growth lines
lunular incision	obsolete, sometimes slightly visible	obsolete, sometimes slightly visible	fine and well marked	visible but very weak
pallial sinus	slight indentation in pallial line	slight indentation in pallial line	almost absent	slight indentation in pallial line
hinge plate	narrow to moderately narrow	narrow	narrow	narrow



Figs 66-67. *Callogonia leeana* (Dall, 1889), Syntypes USNM, East of Tobago, 11°40'N, 58°33'W, 880 fms. 66. Syntype 1. interior and exterior of r.v. Shell length 33.6 mm. 67. Syntype 2. interior and exterior of l.v. Shell length 29.4 mm.

also a slightly rounded-truncated anterior margin and an arched hinge line. Judging from the outlines of the specimens figured by Boss (1970) and from own observations we doubt that *I. striatum* and *"V." guineensis* are conspecific, but more and fresh material of both species will be necessary for a final decision. Boss (1970) places *V. guineensis* in *Vesicomya* (s. str.); he mentions as a difference the "distinctly developed" lunular incision in *Vesicomya* (s.l.) *ticaonica* Dall, 1908 (Philippines) and *V*. (s.l.) *cordata* Boss, 1968 (off Golfo de Uraba, Colombia). The descriptions and figures given by Boss (1970), however, suggest more similarities of the Niger Delta species with the genus *Isorropodon*.

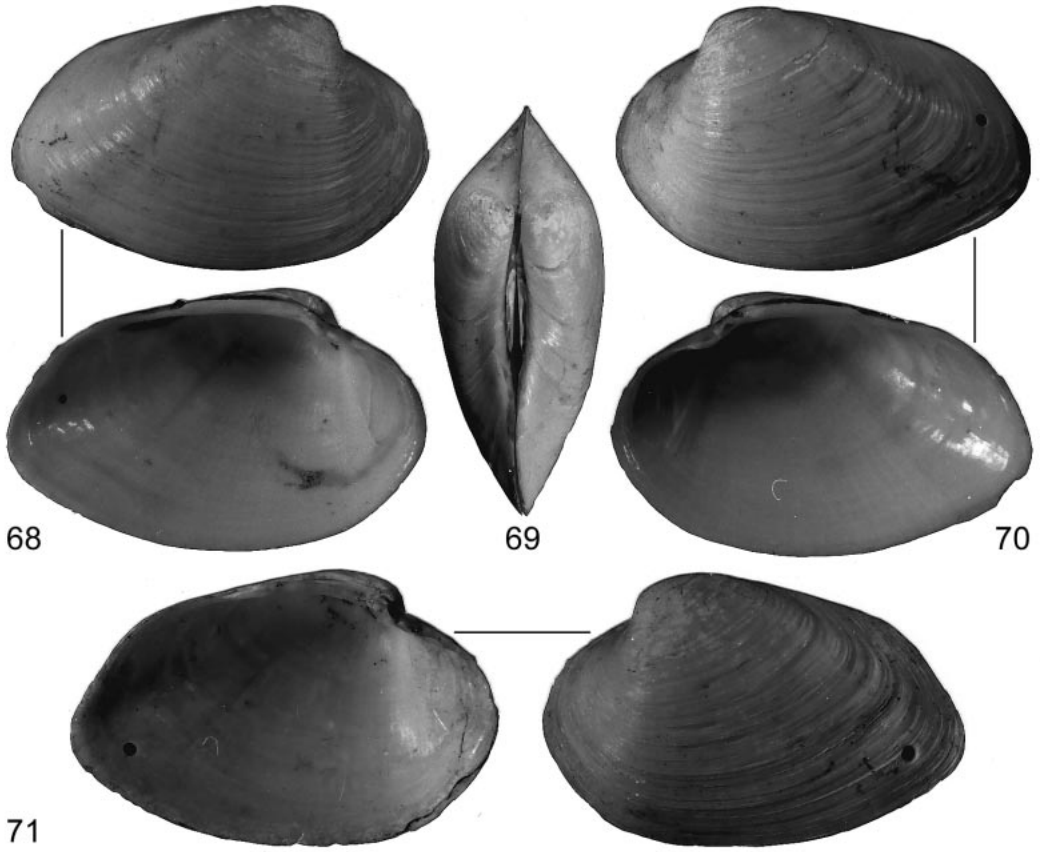
Genus *Callogonia* Dall, 1889

Callogonia Dall, 1889:440 (figured: Dall 1890, pl. 10, figs 6, 7, 8, 9)

Type species: *Callocardia (Callogonia) leeana* Dall, 1889 (by monotypy). Caribbean, East of Tobago, 11°40'N, 58°33'W, 880 fms. (Fig. 66-67; 90-91; 102).

Diagnosis: Shells rather small to medium-sized, oval-trapezoidal to oval-oblong, moderately inflated, with prosogyrous umbo situated well in front of the vertical midline. Posterior angle rounded but well developed, separating the posterior area from the rest of the valve and ending in a rounded posterior end of the ventral margin. No lunule or lunular incision. Hinge with three cardinals in each valve which are more or less parallel to the hinge margin. Lateral teeth absent. Pallial line with a well developed sinus, irregularly triangular in shape. Inner termination of sinus pointing towards the dorsal margin more or less posterior to the umbo, ending with a small but often sharp prolongation of the pallial line.

Remarks: The genus *Callogonia* differs from *Isorropodon* by the presence of an obliquely truncate posterior area, which is lacking in *Isorropodon*. The shells of *Callogonia* are less tumid, they are of different outline which in most species is more rectangular-oval. The principal distinctive character is the moderately deep but conspicuous, more or less triangular, obliquely upwards pointing pallial sinus. It typically bears a prolongation of the pallial line on the tip which in some species is a continuation of the dorsal limb. The hinge of *Callogonia* is comparatively stronger, the teeth configuration is the same as in *Isorropodon*.



Figs 68-71. *Callogonia cyrili* sp. nov. W of Straits of Gibraltar, 35°26'N, 08°00'W, 1805 m, trawled RV *Cryos*, BALGIM cruise, Stn CP65. 68-69. Holotype MNHN, 68. Exterior and interior of r.v.; 69. Dorsal view; 70. Exterior and interior of l.v. Shell length 26 mm. 71. Paratype MNHN. Interior and exterior of l.v. Shell length 26 mm.

Callogonia cyrili sp. nov.
(Figs 68-71; 92-93; 103)

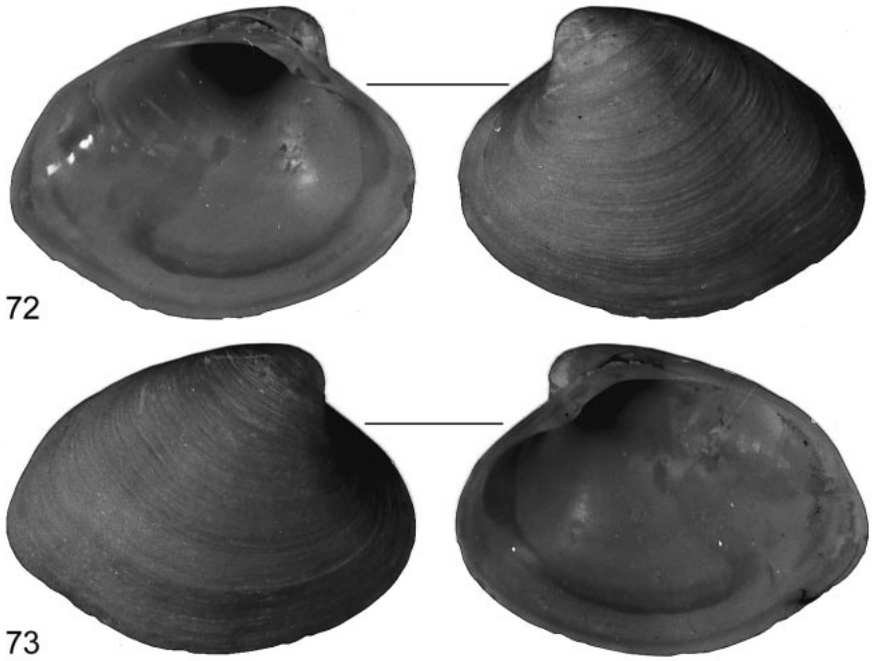
Type material: Holotype MNHN a complete sh. (26.0 × 16.6 × 10.6 mm, l/h 1.6), trawled RV *Cryos*, BALGIM cruise, Stn CP65, 35°26'N, 08°00'W, 1805 m, leg. Bouchet & Warén, 4. VI. 1984; Paratypes: same locality, 5 left v., 3 MNHN (26.0 × 17.0; 24.1 × 16.0; 18.5 × 12.1 mm, all l/h 1.5) 1 USNM (22.1 × 14.1 mm, l/h 1.6), 1 SMNH (20.9 × 13.8 mm, l/h 1.5).

Type locality: off Morocco, 35°26'N, 08°00'W.

Description: Shell to 26 mm long, oblong-oval, little variable in outline and length/height ratio, thin and moderately tumid. Anterior margin broadly and evenly rounded. Ventral margin evenly convex, only in the very posterior part often less convex or straight. Posterior margin obliquely truncate with rounded corners. Beaks prosogyrous, well in front of the vertical midline, in fully grown specimens near the end of the first fourth.

Surface with fine, dense, irregular commarginal growth lines, some coarser growth lines and stages and a few ill-defined, shallow, more or less broad commarginal waves. Lunule absent, escutcheon long and rather narrow, with rounded delimitations. Posterior angle rounded but well marked and posterior area well set-off from the rest of the shell. Periostracum very thin and colourless, somewhat glossy.

Hinge line rather narrow but strong, in each valve with two teeth beneath the umbos or the antero-dorsal margin just in front of them. Right valve with an anterior, strong and laminar tooth (1) parallel to the antero-dorsal margin and situated just in front of the umbo, and a slightly longer, stronger undulate posterior tooth (assumed to be fused 3a and 3b) running from behind the anterior tooth backwards to beneath the anterior part of the ligament. Left valve anteriorly with a long, strong and undulate



Figs 72-73. *Callogonia mauritanica* sp. nov. off Mauritania (no precision), taken by commercial trawlers in 900-1200 m. Holotype MNHN. Shell length 7.6 mm. 72. Interior and exterior of l.v.; 73. Exterior and interior of r.v.

linear tooth parallel to the dorsal margin (assumed to be fused 2a and 2b) and situated under the umbo and in front of it; posteriorly to it a slightly inclined, short and laminar posterior tooth (4b) present but mostly partly or completely dissolved. Ligament external, opisthodetic, long, on a well developed, rather strong nymphal plate. Pallial sinus rather short but well marked, nearly triangular, acute and pointing obliquely upwards to the dorsal margin well behind the umbos; pallial line prolonged on the anterior side of the sinus extremity.

Valves entirely white.

Distribution: Known only from the type locality off northern Atlantic Morocco.

Material examined: The type material only.

Biotope: Muddy bottom with most probably reducing sediment.

Derivatio nominis: It is our pleasure to dedicate this species to Cyril Dolin, an ardent paleontologist who skilfully restored one of the specimens used in this study and who on other occasions assisted the first author in restorations of deep sea specimens heavily broken during sampling by manipulator.

Remarks: The new species is very close to the Caribbean *Callogonia leeana* (Figs 66-67), however, it is clearly distinguished by its smaller size and the more tapering and somewhat narrower posterior part of the valves. The posterior truncated margin is more inclined in *C. cyrili*. Both species have in common the narrow hinge line, the rather small hinge teeth and the form of the pallial sinus (see drawings).

Callogonia mauritanica sp. nov.
(Figs 72-73; 94-95)

Type material: Holotype MNHN, off Mauritania (no precision), taken by commercial trawlers in 900-1200 m, a complete shell, leg. F. Gubbioli, V. 1992. The specimen was contained in a mixed lot with *Isorropodon bigoti* sp. nov. and *I. curtum* sp. nov.

Type locality: Mauritania, West Africa.

Description: Shell very small for the genus, 7.6 mm long and 6.0 mm high (l/h ratio: 1.3), oval, rather thin and moderately tumid. Anterior margin evenly rounded but not too broad. Ventral margin convex, in the posterior part straight. Posterior margin obliquely truncate with rounded corners. Beaks prosogyrous, well in front of the

vertical midline, at the end of the first fourth of shell length.

Surface with dense, rather coarse, irregular commarginal growth lines and also some fine irregular striae. Lunule absent, escutcheon long and rather broad, with rounded delimitations. Posterior angle broadly rounded but posterior area nevertheless demarcated from the rest of the shell. Periostracum very thin and colourless.

Hinge line strong and quite broad under the beaks, in each valve with two teeth beneath the umbos or the antero-dorsal margin just in front of them. Right valve with an anterior, rather short, strong and laminar tooth (1) parallel to the antero-dorsal margin and situated beneath the umbos, and a slightly longer and stronger, arched posterior tooth (assumed to be fused 3a and 3b), running from above the posterior end of the anterior tooth and continuing below and behind the umbo. Left valve anteriorly with a long, strong and irregular linear tooth parallel to the dorsal margin and situated under the umbo (assumed to be fused 2a and 2b) and posteriorly to it a slightly inclined, rather long and somewhat arched posterior tooth (4b) beginning above the anterior tooth. Ligament external, opisthodetic, quite short, on a well developed nymphal plate. Pallial sinus triangular and pointing obliquely upwards to a point situated somewhat behind the umbos. There is an irregular prolongation of the pallial line impression at the tip of the sinus.

Valves entirely white.

Distribution: Known only from the type locality.

Material examined: The holotype only.

Biotope: Probably mud, in 900-1200 m.

Remarks: This species is distinguished from *Callogonia leeana* and *C. cyrili* by its much smaller size and the shorter and more oval valves which remind one of a small *Pitar*. The posterior part is still more tapering than in *C. cyrili*. The hinge line in *C. leeana* and *cyrili* is almost equally broad over its whole length, whereas in *C. mauritanica* it is much broader under the umbos, becoming gradually narrower towards the posterior end. The hinge teeth are also stronger than in the other two species but their general configuration is the same as in the other *Callogonia*.

"Vesicomya" chuni Thiele & Jaeckel, 1931
(Figs 74-75, 96-97; 107)

Vesicomya (Callogonia) chuni Thiele & Jaeckel, 1931: 228-229 (71-72), pl. 4, fig. 103.
Vesicomya (Callogonia) chuni Thiele & Jaeckel, 1931 – Boss, 1970:68-69, figs 1, 2, 21, 24.

Type material: Lectotype ZMB Berlin, a left valve (92.5 × 55.5 mm), selected by Boss (1970); paralectotype, a right valve (95.9 × 62.4 mm), ZMB.

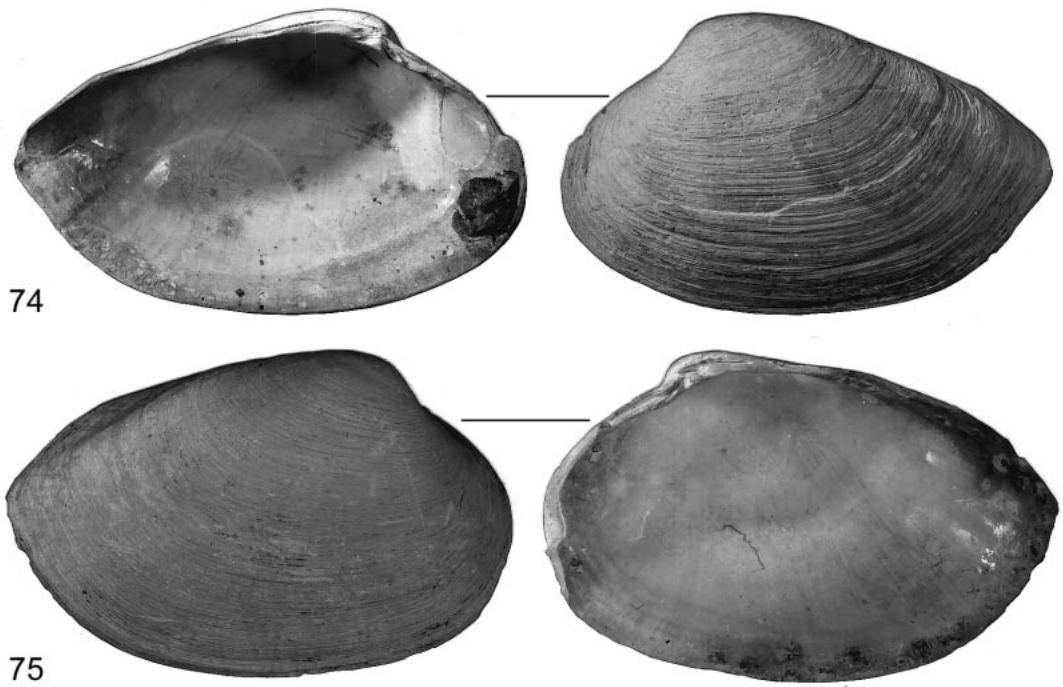
Type locality: W of Campo, Cameroon, 2°00'N, 8°4.3'E, 2492 m.

Description: Shell to 96 mm long, oblong-oval, variable in outline rather thick and moderately tumid. Anterior margin broadly rounded. Ventral margin convex, but less so in the anterior two thirds. Posterior margin broadly tapering, ending in a slightly rounded corner close to the horizontal midline, appearing almost somewhat rostrate. Beaks prosogyrous, well in front of the vertical midline, in fully grown specimens near the end of the first fourth or just behind it.

Surface with fine, dense, irregular commarginal growth lines and numerous coarser growth waves and stages, in the studied specimens already partly eroded. Lunule ab-

Table 2. Comparison of some features in *Callogonia* and *"Vesicomya" chuni.*

	C. leeana	*C. cyrili*	*C. mauritanica*	*"Vesicomya" chuni*
maximum shell size	34 mm	26 mm	7.6 mm	96 mm
shell outline	oval-trapezoidal, postero-ventral corner	oval-oblong, postero-ventral corner	oval-veneriform, postero-ventral corner	oval-oblong, postero-dorsal corner
surface	many fine and some coarser growth lines	many fine and some coarser growth lines	coarse growth lines	fine growth lines and coarser growth waves
posterior angle	well marked, rounded	well marked, rounded	broadly rounded	two rounded posterior angles
pallial sinus	well marked	well marked	well marked, large	well marked but small
hinge plate	narrow	narrow	moderately narrow	narrow
hinge teeth	all teeth more or less in a line	all teeth more or less in a line	all teeth more or less in a line	anterior card. under the middle c. with depression between



Figs 74-75. *"Vesicomya" chuni* Thiele & Jaeckel, 1931. 74. Lectotype ZMB. Shell length 92.5 mm. 75. Paralectotype ZMB. Shell length 95.9 mm.

sent, escutcheon missing. In place of it and parallel to the postero-dorsal margin a sulcus with a rounded delimitation which can be characterized as a second posterior angle (see also Boss 1970). Posterior angle closely below this ridge rounded but well marked and ending in the posterior "rostrum". Posterior area narrow and well set-off from the rest of the shell. Periostracum not seen.

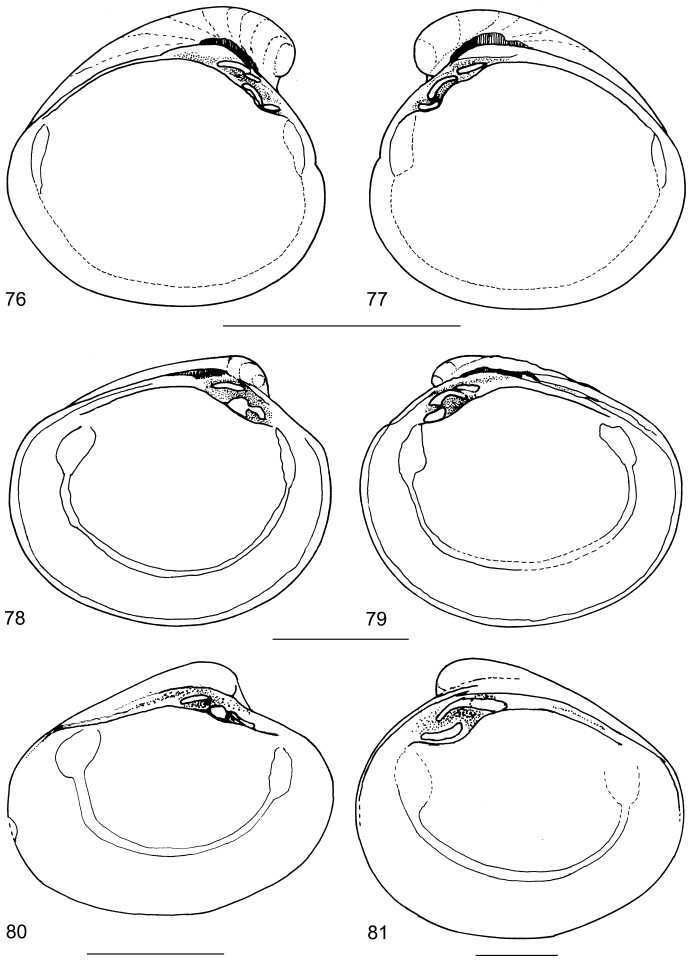
Hinge line rather narrow but strong. Right valve with a lower anterior, strong and laminar tooth (1), which starts almost parallel to the antero-dorsal margin, then curves upwards and ends directly under the beaks, and a longer and stronger posterior tooth (assumed to be fused 3a and 3b). It starts above the anterior tooth parallel to it, ascends towards the umbo and then descends backwards to beneath the anterior part of the ligament. Left valve anteriorly with a long, strong and somewhat irregular linear tooth almost parallel to the dorsal margin (assumed to be fused 2a and 2b) and situated under the umbo and in front of it; posteriorly to it a well inclined, shorter and laminar posterior tooth (4b) present, in the lectotype broken off and only the basis visible. Ligament external, opisthodetic, rather short, on a narrow but strong nymphal plate. Pallial sinus short but well marked, nearly triangular, more or less acute and pointing obliquely upwards to the dorsal margin just behind the umbos; no well-marked prolongation of the pallial line on the anterior side of the sinus extremity. Inside of the valves with very faint, irregularly sized and spaced vermiculations or waves and a weak rib running from the umbonal cavity to the lower tip of the anterior adductor scar.

Valves entirely white.

Distribution: Niger Delta, Bight of Biafra (Cameroon, 2°00'N, 8°4.3'E, 2492 m) to Ghana (4°58'N, 3°48'E, 2268-2332 m).

Biotope: Muddy bottom, known from 2268 to 2492 m.

Remarks: We include this species in the paper because Thiele & Jaeckel (1931) placed it into the "section" *Callogonia* on the grounds of its "moderately" deep pallial sinus, which was confirmed by Boss (1970), and superficially, the *Valdivia* specimens resemble this genus. However, there is a fundamental difference between *Callogonia* and *"Vesicomya" chuni* in the hinge teeth configuration: in the right valve of *"V." chuni*, the anterior part of the fused cardinals 3a-3b is stretching forward above the greater part of cardinal 1 and bent over it with a deep depression separating them (see Fig. 107), whereas in *Callogonia* the anterior part of cardinals 3a-3b starts directly at or just above the end of the cardinal 1 which is much more displaced forwards. Also the pal-



Figs 76-97. Halfschematic drawings of the interior of Vesicomyidae to show muscle impressions and pallial line.

76-77. *Vesicomya adamsi* (E.A. Smith, 1885). l.v. and r.v., off Namibia, 18°52.1'S, 7°23.1'E, 5124 m, WALDA, Stn CY 02. Scale bar: 10 mm.

78-79. *Waisiuconcha haeckeli* sp. nov. Juvenile specimen, l.v. and r.v., off Mauritania, 19°27'N, 17°06'W, 800-825 m, RV *Ernst Haeckel*, Stn CH262. Scale bar: 1 mm.

80. *Waisiuconcha alberdinae* Beets, 1942. Holotype, Mining Institute Delft. Buton Island, Indonesia, most probably Upper Oligocene. Type species of the genus. Drawn from the figure in Beets (1942: pl. 30 fig. 147). Scale bar: 10 mm.

81. *Waisiuconcha surugensis* Habe, 1976. Holotype NSMT. Suruga Bay, Japan, 35°03'N, 138°45.6'E, 290-480 m. Drawn from the figure in Habe (1976: 45, pl. 1, fig. 1). Scale bar: 1 mm.

lial sinus is different, it is comparatively smaller and slightly less acute than in *Callogonia* and the prolongation of the pallial line is very short or absent. Moreover, the shell outline differs: the posterior corner is not postero-ventral but situated at the end of a taper in or just above the horizontal midline, the posterior angle is short, the posterior area is divided by a second angle and a shallow sulcus between them. These differences justify a separation as a distinct genus. A second species, obviously belonging to the same group is *Vesicomya (Callogonia) angulata* (Dall, 1896) from the Gulf of Panama (2320-3050 m) (see Dall 1908). A third, still unnamed species with the same combination of characters and thus also belonging to this group has recently been collected on the Barbados accretionary Prism, a region of cold seeps (for more details, see Cosel & Olu (1998) with references) and will be described elsewhere.

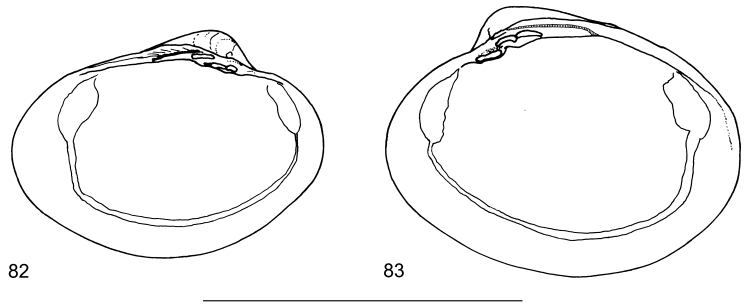
DISCUSSION

The systematics of Vesicomyidae are still far from settled (see Boss 1968). The family has been placed classically in Glossoidea (Newell 1965; Keen in Moore 1969; Vokes 1980) but Taylor, Kennedy & Hall (1973), based on shell microstructure of *Calyptogena ponderosa* Boss, 1968, indicated a closer relationship with the Arcticoidea. Following this criterion, Slack-Smith (1998) placed the Vesicomyidae in the Arcticoidea. Another view is expressed by Scarlato & Starobogatov (1979) who include it in the Veneroidea.

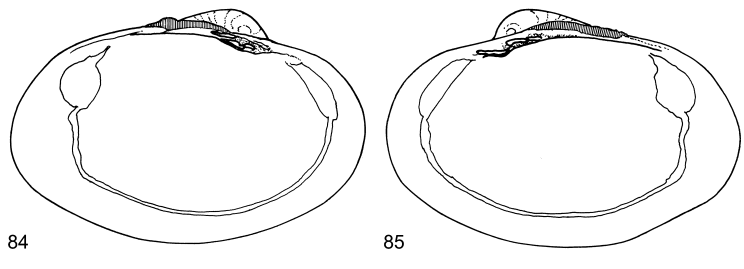
At the generic and subgeneric level, there is no agreement as how many genera are to be considered in the family. Okutani (1962) considers *Calyptogena* and *Akebiconcha* to be included in the family Arcticidae whereas *Vesicomya* was placed in the family Vesicomyi-

82. *Isorropodon perplexum* Sturany, 1896. Syntype NHMW.

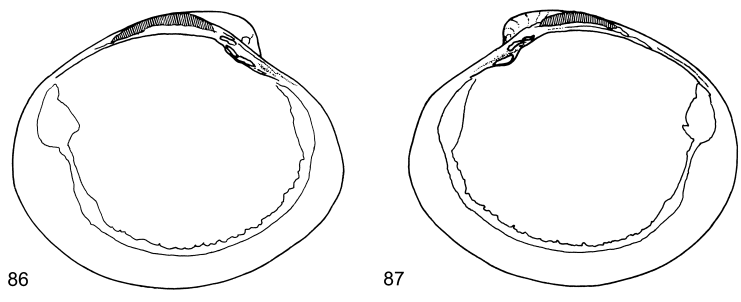
83. *Isorropodon perplexum* Sturany, 1896. Syntype NHMW. Scale bar: 10 mm.



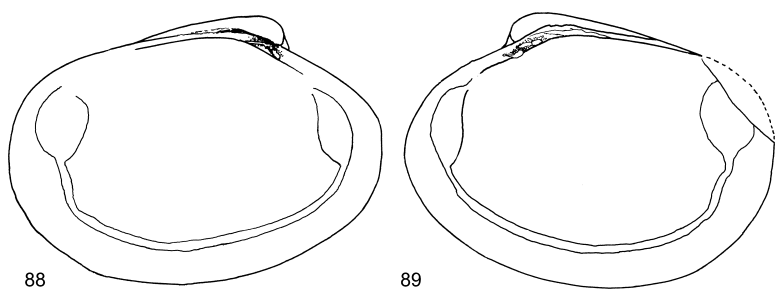
84-85. *Isorropodon bigoti* sp. nov. "N'Kossa" oilfield, off Pointe-Noire, 5°53.5'S, 11°38.84'E, 150 m. Scale bar: 10 mm.



86-87. *Isorropodon curtum* sp. nov. Off Mauritania (no precision), taken by commercial trawlers in 900-1200 m. Scale bar: 10 mm.



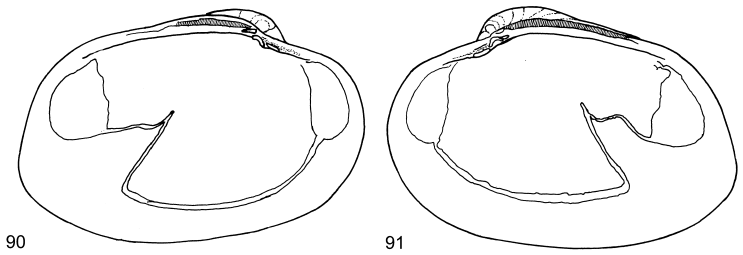
88-89. *Isorropodon striatum* (Thiele & Jaeckel, 1931). Holotype ZMB. Scale bar: 10 mm.



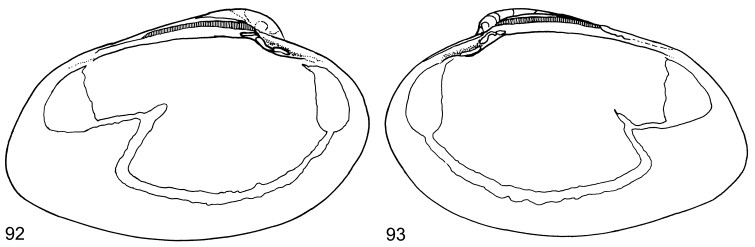
dae. The current arrangement is mostly based on few shell characters, such as outline, size, hinge dentition and presence or absence of a pallial sinus and its shape, but other features, e.g. presence or absence of a defined lunula or lunular incision, presence of a posterior angle and presence or absence of fine marginal grooves on the valve margins were not considered. Species have been assigned, often tentatively, to various genera or subgenera, and initially some were also placed in other families.

There is much variation in the hinge teeth configuration which reaches from radially arranged cardinals like in Veneridae and *Arctica* to somewhat irregular cardinal teeth more or less parallel to the hinge line, as in *Glossus*.

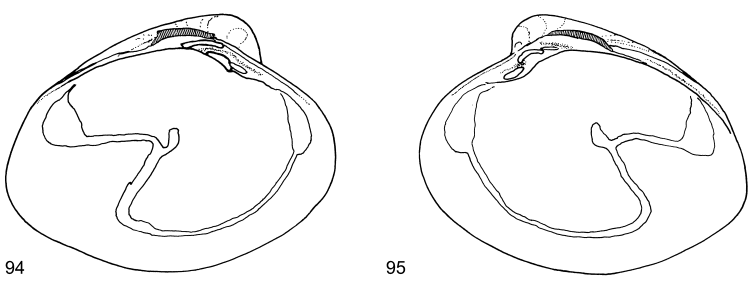
Presence or absence and size of the pallial sinus is another informative character. The smaller species such as *Vesicomya atlantica*, and also some larger species do not have a sinus, and this may be related to the mode of life near the sediment surface. Among larger species, the



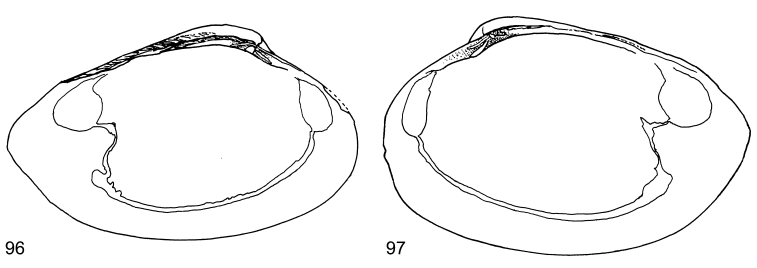
90-91.*Callogonia leeana* (Dall, 1889). Syntypes USNM. Scale bar: 10 mm.



92-93. *Callogonia cyrili* sp. nov. Holotype MNHN, W Straits of Gibraltar, 35°26'N, 08°00'W, 1805 m. Scale bar: 10 mm. Note the slightly smaller pallial sinus in the r.v.



94-95. *Callogonia mauritanica* sp. nov. Off Mauritania (no precision), taken by commercial trawlers in 900-1200 m. Scale bar: 5 mm.



96. *"Vesicomya" chuni* Thiele & Jaeckel, 1931. Lectotype ZMB. Scale bar: 10 mm.

97. *"Vesicomya" chuni* Thiele & Jaeckel, 1931. Paralectotype ZMB. Scale bar: 10 mm.

shape and depth of the sinus displays considerable variation which we consider of taxonomical significance.

Within the Vesicomyidae, the range of body size is unusually large. For this reason, size ranges were considered as another useful character. We have attempted to explore additional characters for the parsimony analysis and included features of the outline and sculpture of the shell.

The search for a most parsimonious reconstruction gave 35 equiparsimonious trees of 24 steps, with a consistency index (CI) of 0.792. A 50 % majority rule consensus (Fig. 108) and a strict consensus were constructed, and differ only in that the branch uniting the *Isorropodon* species appears unresolved with respect to *Callogonia*. This reconstruction may represent a hypothesis of relationships if the uniquely derived character states outnumber convergent ones, which in this case is debatable. The reconstruction supports two groupings.

The branch including *Vesicomya* spp., *Kelliella* and *Waisiuconcha* is the most consistent. It is supported by characters 5 (marginal incisions), 7 (commarginal sculpture) and 9 (small size). The most unusual and thus possibly truly synapomorphic character is the presence of marginal incisions. The grouping of the two *Vesicomya*

species is further supported by characters 3 (posterior angle) and 8 (hinge), whereas *Waisiuconcha* appears autapomorphic for having more than one groove on the inner part of the ventral margin. The clustering of *Waisiuconcha* with *Kelliella* is supported by sharing a less enrolled umbo, a character which is very liable to convergence and may be given little confidence. On these grounds, we will take a conservative position and maintain *Waisiuconcha*, *Vesicomya* and *Kelliella* as three separate, although possibly related, genera.

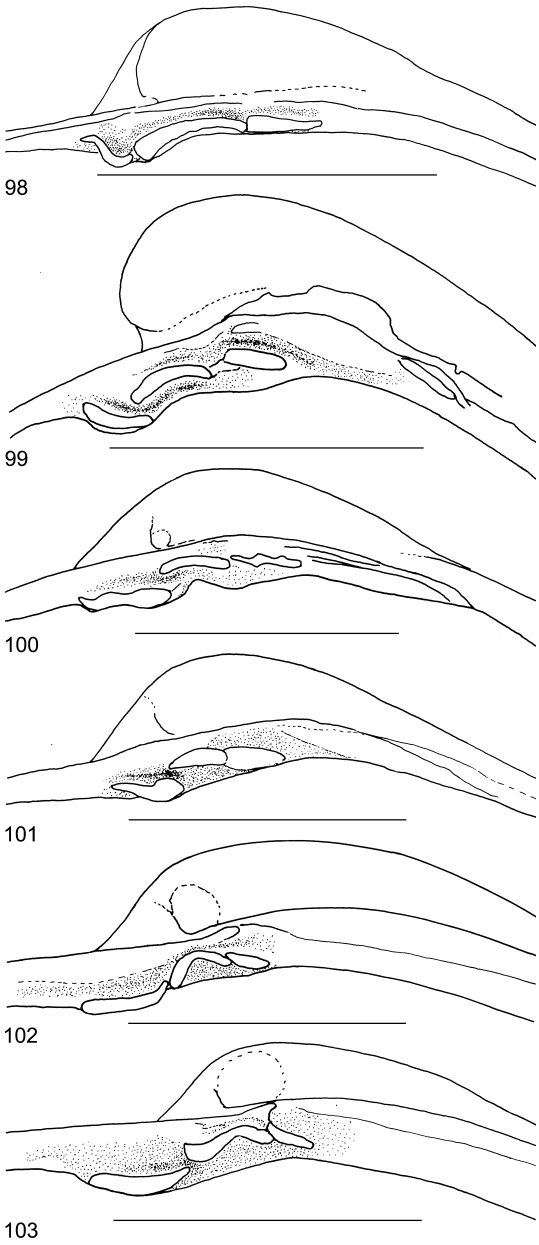
The question of the relationship between Vesicomyidae and Kelliellidae remains to be investigated. The resemblance between *Kelliella* and the two *Vesicomya* species *V. adamsii* and *V. atlantica* was already pointed out by Smith (1885) and Dall (1886) and later by Bernard (1974). The five species assigned to *Kelliella* by Knudsen (1970) should be correctly placed in *Vesicomya* according to the characters of siphonal apertures, gills and hinge. Knudsen did not mention the foot and this may reflect the peculiar configuration in *Vesicomya* where it is concealed by the gills. Foot shape is nevertheless similar in *Isorropodon bigoti* and *Kelliella miliaris* so that the relationships are not settled.

Another grouping brings together the three species of *Isorropodon* and *Callogonia leeana*. This is supported by characters which are liable to convergence: size and outline, but also by the hinge configuration with all teeth more or less aligned. In *Callogonia*, character 1 (sinus) and 3 (posterior angle) are apomorphic and identical among the three species studied. There is no uniquely

Table 3. Comparison of characters in some genera of Vesicomyidae.

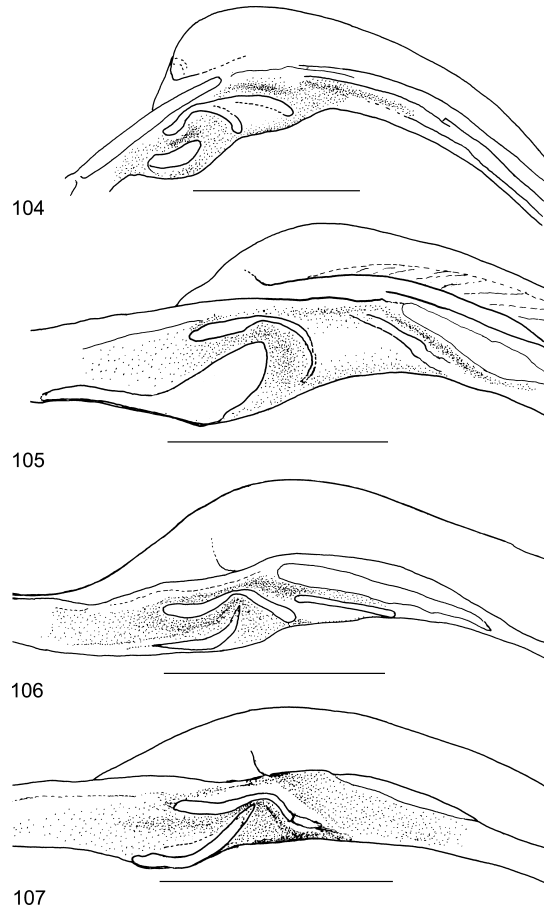
	Vesicomya	*Waisiuconcha*	*Isorropodon*	*Callogonia*	*Calyptogena**
shell size	3-10 mm	4-23 mm	8-47 mm	7-34 mm	50-270 mm
shell outline	subcircular	subcircular veneriform	oblong to oval-oblong	veneriform to oval-trapezoid	oblong to very elongate
tumidity	very inflated	moderately to very inflated	moderately to very inflated	moderately inflated	in general not very tumid
surface	commarginal grooves	commarginal grooves	irregular grooves and growth lines	irregular grooves and growth lines	irregular growth lines and ridges
posterior angle	absent	absent	absent	well defined rounded	not marked
lunular incision	well defined	well defined	ill defined to obsolete	absent	absent
position of pallial line	close to margin	distant from margin	close to margin	moderately close to margin	moderately close to margin, often inclined
pallial sinus	absent	absent	weak indentation	well developed	entirely absent or small sinus present
hinge plate	narrow	rather broad to broad	narrow	narrow	narrow to rather broad
hinge teeth	all teeth more or less in a line	ant. cardinal under middle c. with depression between	all teeth more or less in a line	all teeth more or less in a line	In general arrangement more like in veneroids
incisions in ventral margins	1	1-2	none	none	none
ctenidia	2 demibranchs	?	1 demibranch	?	2 demibranchs

*In the genus *Calyptogena*, several subgenera have been described, which, at least in part, may eventually become full genera.



Figs 98-103. Halfschematic drawings of the hinge line of the r.v. of Vesicomyidae: *Vesicomya*-like dentition.

98. *Vesicomya atlantica* (E.A. Smith, 1885) 18°33'N, 21°03'W, 3136 m, EUMELI 2 Stn KG14. Scale bar: 1 mm. 99. *Vesicomya adamsi* (E.A. Smith, 1885). WALDA cruise Stn CY02. Scale bar: 5 mm. 100. *Isorropodon perplexum* Sturany, 1896. Syntype NHMW. Scale bar: 5 mm. 101. *Isorropodon striatum* Thiele & Jaeckel, 1931. Holotype ZMB, Scale bar: 10 mm. 102. *Callogonia leeana* (Dall, 1889). Syntype USNM. Scale: 5 mm. 103. *Callogonia cyrili* sp. nov. Holotype. Scale bar: 5 mm.



Figs 104-107. Halfschematic drawings of the hinge line of the r.v. of Vesicomyidae: more veneroid dentition.

104. *Waisiuconcha haeckeli* sp. nov. Mauritania, 900-1200 m. Scale bar: 1 mm. 105. *"Vesicomya" valdiviae* Thiele & Jaeckel, 1931. Lectotype ZMB. Scale bar: 10 mm. 106. *"Vesicomya" longa* Thiele & Jaeckel, 1931. Holotype ZMB. Scale bar: 10 mm. 107. *"Vesicomya" chuni* Thiele & Jaeckel, 1931. Holotype ZMB. Scale bar: 10 mm.

shared shell character for *Isorropodon*, but the four *Isorropodon* species cluster together in 69 % of the equiparsimonious trees based on shell characters. This grouping is very strongly supported by the absence of the outer demibranch, ascertained in *I. perplexum*, *I. bigoti* and *I. striatum* and reasonably generalizable to *I. curtum* thus justifying holding *Isorropodon* as a valid taxon. The presence of two demibranchs in the type species *Vesicomya atlantica* and the outgroup proves that the existence of only one demibranch is derived.

In the consensus tree, the position of *"Vesicomya" valdiviae* (Fig. 105), *"Vesicomya" guineensis*, *"Vesico-*

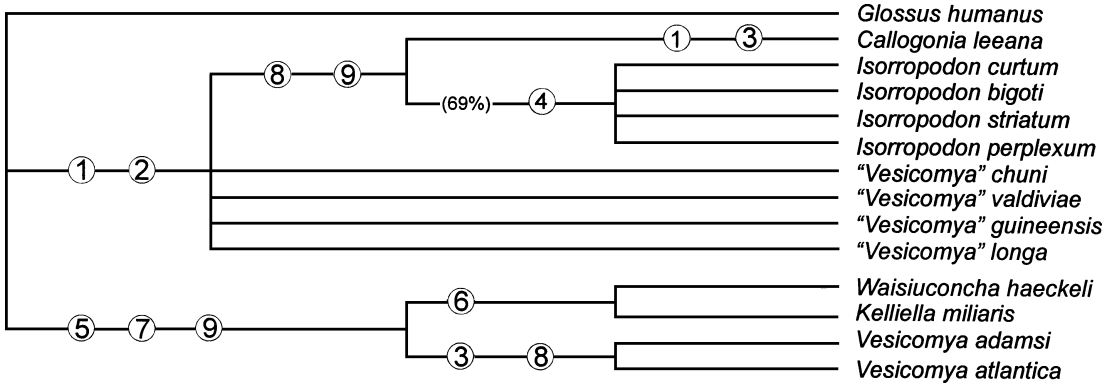


Fig. 108. Most parsimonious reconstruction obtained under PAUP using character matrix presented in Table 5. The numbers show changes in character states: 1, pallial sinus; 2, outline; 3, posterior angle; 4, lunular incision; 5, marginal incision; 6, umbo; 7, surface sculpture; 8, hinge dentition; 9, shell size.

mya" longa (Fig. 106) and *"Vesicomya" chuni* (Fig. 107), is unresolved, as could be expected with the small number of characters considered. All these *"Vesicomya"* s.l. are ill-defined, they share mainly the hinge configuration of the right valve with a curved central cardinal, under which is placed the anterior cardinal. Among these, *"Vesicomya" chuni* is particular in having two posterior angles, and a well defined sinus whereas the other three *"Vesicomya"* have one or no posterior angle and hardly any sinus. The taxonomic status of these species needs a revision and some may need the assignment to new genera. The parsimony analysis was repeated excluding these species, and this did not change the topology of the two branches previously discussed.

Table 4. Matrix of characters used for parsimony analysis of eastern Atlantic Vesicomyidae.
1. Pallial sinus: absent: 0; indentation in pallial line: 1; short but well defined: 2; present with prolongation: 3.
2. Outline: circular to rounded-triangular: 0; oblong: 1; oval to elongate-oval: 2.
3. Posterior angle (a discontinuity in the shell profile running from the umbo to the posterior end of the ventral margin): absent: 0; present and mostly rounded: 1; two angles: 2.
4. Lunular incision: absent: 0; more or less faintly marked: 1; well marked: 2.
5. Fine longitudinal incisions on margin: absent: 0, one only (or only on r.v.): 1; more than one: 2.
6. Umbo: not enrolled: 0; slightly enrolled: 1; markedly enrolled: 2.
7. Surface sculpture: with regular concentric grooves: 1; with irregular growth lines: 0.
8. Cardinal teeth in r.v.: all teeth more or less in a line, anterior and middle cardinal almost touching or joined: 0; cardinal 1 situated under cardinal 3a-b which forms a strongly curved "roof" above it; separated by deep depression between them: 1; cardinal 1 and cardinal 3 more or less parallel and separated by a deep depression, but cardinal 3 not bent: 2. Cardinals consisting of a small rounded bulge under the umbo and a long anterior lamellar tooth: 3
9. Size: under 10 mm: 0; 10-50 mm: 1; more than 50 mm: 2.

Characters	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Glossus humanus	0	0	0	0	0	2	0	2	2
Callogonia spp.	3	1	1	0	0	0	0	0	1
Isorropodon curtum	1	1	0	1	0	0	0	0	1
I. bigoti	1	1	0	1	0	0	0	0	1
I. striatum	1	1	0	1	0	0	0	0	1
I. perplexum	1	1	0	1	0	0	0	0	1
"Vesicomya" chuni	2	2	2	0	0	0	0	1	2
"Vesicomya" valdiviae	1	2	0	0	0	0	0	1	2
"Vesicomya" guineensis	1	2	0	1	0	0	0	1	2
"Vesicomya" longa	1	2	0	2	0	0	0	1	2
Waisiuconcha haeckeli	0	0	0	2	2	1	1	1	0
Vesicomya adamsi	0	0	1	2	1	2	1	0	1
V. atlantica	0	0	1	2	1	2	1	0	0
Kelliella miliaris	0	0	0	2	1	1	1	3	0

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Appendix. List of Eastern Atlantic Vesicomyidae.

Vesicomya adamsi (E.A. Smith, 1885). Off Sierra Leone and Namibia, 4400-5200 m.

Vesicomya atlantica (E.A. Smith, 1885). W of Ireland and Bay of Biscay to off Mauritania, (18°30'N), 1800-3225 m (Type species of the genus *Vesicomya*).

Waisiuconcha haeckeli Cosel & Salas sp. nov. Off Mauritania, 800-1200 m.

Isorropodon bigoti Cosel & Salas sp. nov. 60 km off Pointe-Noire, 150-300 m; Mauritania, 900-1200 m.

Isorropodon curtum Cosel & Salas sp. nov. Mauritania, 900-1200 m.

Isorropodon elongatum (Allen, 2001). Angola basin (22°57'S, 13°05'E), 481 m; Sierra Leone Basin (10°36'N, 17°39.0'W), 1976 m. Also in the North America and Argentine Basins, 478-5100 m (Allen, 2001)

Isorropodon perplexum Sturany, 1896. Eastern Mediterranean, 1950-2500m.

Isorropodon striatum (Thiele & Jaeckel, 1931). W of Campo, Cameroon, 2492 m.

Callogonia cyrili Cosel & Salas sp. nov. Ibero-Moroccan Gulf, 1805 m.

Callogonia mauritanica Cosel & Salas sp. nov. Mauritania, 900-1200 m.

"Vesicomya" chuni Thiele & Jaeckel, 1931. Ghana (Accra) to Cameroon, 2268-2492 m.

"Vesicomya" guineensis Thiele & Jaeckel, 1931. Niger Delta, Bight of Biafra, W of Campo, Cameroon (2.0°N, 8°4.3'E), 2492 m.

"Vesicomya" longa Thiele & Jaeckel, 1931. Off Rio de Oro (24°35.3'N, 17°4.7'W), 140 miles (230 km) W of Morro Garnet, 2500 m; Niger Delta, Bight of Biafra, W of Campo, Cameroon (2.0°N, 8°4.3'E), 2492 m; between Gabon and São Tomé (1°42'N, 7°51'W) 2550 m.

"Vesicomya" valdiviae Thiele & Jaeckel, 1931. Off Rio de Oro (24°35.3'N, 17°4.7'W), 140 miles (230 km) W of Morro Garnet, 2500 m.

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