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Studies on the deep-sea Protobranchia (Bivalvia): the family Neilonellidae and the family Nuculanidae.

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CONTENTS

SYNOPSIS. The morphology and distribution of four deep-water protobranch species of the family Neilonellidae and ten deep-water protobranch species of the family Nuculanidae are described. These include four new species. The evolution of the nuculanoid siphonate form is discussed.

INTRODUCTION

This is the ninth paper in a series on the deep-sea species of Protobranchia of the Atlantic. While a few undescribed species of families reported upon in earlier papers have been found in later samples and remain to be described, this paper is the last of our major descriptive accounts of the morphologies of this exceptionally important group of deep sea bivalves.

In this paper we give an account of a number of nuculanacean species belonging to the families Neilonellidae and Nuculanidae present in our collections from the deep Atlantic. Related species already described are refered to only when essential for descriptive and comparative purposes. Unlike previous papers in this series most of the species described below are known, but only from their shell characters. This is in part due to the fact that many species come from upper-slope depths, and thus more likely to have been sampled in the past, and in part due to the fact that they are relatively large and thus less likely to have been lost due to the coarseness of nets used in earlier expeditions. Many earlier descriptions of the shell are far from adequate and new descriptions are given.

We have followed the methods and approach of earlier papers in this series (Allen and Hannah, 1989; Allen and Sanders, 1973, 1982; Allen, Sanders and Hannah, 1995; Rhind and Allen, 1992; Sanders and Allen, 1973, 1977, 1985). From stereoscopic microscope examination of shell features and whole mounts of the body stained in haemotoxylin, from dissected specimens and serial sections stained with trichome techniques, we give detailed descriptions of the shell and internal morphology of key species. Descriptions of related species are limited to points of difference and importance.

Much of the material was taken by ourselves on numerous expeditions by research vessels of the Woods Hole Oceanographic Institution. These include the 'Atlantis', 'Atlantis II', 'Chain' and 'Knorr'. Other samples were taken by JAA on the British research

vessels 'Sarsia' and 'Discovery'. In addition to these, deep-sea bivalves from a series of French expeditions using the research vessels 'La Perle', 'Cryos' and 'Jean Charcot' were kindly donated by our French colleagues. At present this material, other than the types of new species and cited specimens, is housed at the Woods Hole Oceanographic Institution and the University Marine Biological Station Millport. On completion of our studies, it is our intention to return the French collections to the Museum National d'Histoire Naturelle, Paris and our own collections to the U.S. National Museum and the Natural History Museum, London.

Museums are abbreviated as follows:- ANSP – Academy of Natural Sciences, Philadelphia; BMNH – Natural History Museum, London; MCZ – Museum of Comparative Zoology, Harvard; MNHN – Museum National d'Histoire Naturelle, Paris; SAM – South Africa Museum; USNM – United States National Museum, Washington, D.C.; ZMHU – Zoologisches Museum, Humbolt–Universitat, Berlin; ZMUC – Zoological Museum, University of Copenhagen.

Sampling gear is abbreviated as follows:-AD – anchor dredge; CP – beam trawl; CV – Blake trawl; DS – epibenthic sledge Sanders (COB); ES – epibenthic sledge (WHOI); KG – USNEL boxcorer; OS – epibenthic sledge (SMBA); WS – epibenthic sledge (IOS).

ABBREVIATIONS TO THE TEXT-FIGURES

AA	anterior adductor muscle
AN	anus
AR	anterior pedal retractor muscle
AS	anterior sense organ
BG	'byssal' gland
CG	cerebral ganglion
CM	caecum
CV	cerebro-visceral commissure
DD	digestive diverticula
DH	dorsal hood
DT	digestive ducts
FA	feeding aperture
FG	fused gill tissue
FR	faecal rod
FT	foot
GA	gill axis
GI	gill
GP	gill plate
GS	gastric sheild
HG	hind gut
HP	hinge plate
HT	hinge teeth
LI	internal ligament or resilium
LO	opisthodetic external ligament
MG	combined mid gut
MM	mantle margin
OE	oesophagus
PA	posterior adductor muscle
PE	sensory papilla
PG	pedal ganglion
PL	palp
PP	palp proboscis
PR	posterior pedal retractor muscle
PS	posterior sorting area
SE	siphonal embayment
SP	combined siphon
SR	siphonal ridge
SS	style sac
ST	sensory tentacle
SM	stomach
VG	visceral ganglion

Family Neilonellidae Schileyko 1989

Shell usually robust, inflated, moderately large, not particularly elongate, more or less ovate, shell posteriorly extended to some degree and may be acutely rounded or carinate, usually marked concentric sculpture; umbo prominant, anterior to midline; hinge teeth taxodont, continuous or interrupted below the umbo; ligament external, sometimes with an internal component; siphons present; hind gut either a single loop or a series of loops and coils to the left and right of the body.

The family comprises four genera, *Neilonella, Pseudotindaria, Neilo* and *Protonucula* (Allen and Hannah, 1986). By reason of their external ligament, the neilonellids in the past have been included in the family Malletiidae, however this family was shown to be an assemblage of unrelated taxa and is now much restricted (Sanders and Allen, 1985). The robust, ovate, concentically ridged shells of the neilonellids are in marked contrast to the thin, translucent, elongate shells, lacking any marked concentric sculpture, of the malletiids.

Genus *NEILONELLA* Dall 1881

TYPE SPECIES. *Leda (Neilonella) corpulenta* Dall 1881; OD.

Shell moderately robust, relatively wide, strong concentric sculpture, anterior margin rounded, posterior margin slightly attenuate and may be acutely rounded, not carinate; umbo prominant, anterior to the midline; hinge plate moderately strong, many chevron teeth, small gap between anterior and posterior series; external ligament opisthodetic, inserting in an external gutter in each valve, with minute internal resilifer, siphonal embayment shallow; hind gut single loop to the right of the body.

Genus *PSEUDOTINDARIA* Sanders and Allen 1977

TYPE SPECIES. *Pseudotindaria erebus* (Clarke 1959); OD.

Shell robust, relatively wide, anteriorly and posteriorly rounded, not carinate, strong concentric sculpture; hinge plate strong with numerous chevron teeth continuous below umbo; ligament external, anterior part short, posterior part elongate; hind gut with complex series of loops and coils to the right and left of the body.

Genus *NEILO* Adams 1854

TYPE SPECIES. *Neilo cumingii* Adams 1854; by monotypy.

Shell robust, relatively wide, moderately elongate and posteriorly extended, postero-dorsal margin straight or slightly concave, carinate, posteriorly truncate or slightly rostrate, postero-ventral margin may be somewhat sinuous, two rounded radial ridges from umbo to posterior margin, concentric sculpture; hinge plate well-developed; numerous chevron teeth, anterior and posterior series separate and may differ in size (anterior larger); ligament external.

Genus *PROTONUCULA* Cotton 1930

TYPE SPECIES. *Protonucula verconis* Cotton 1930; OD.

Shell relatively fragile, oval, compressed, glossy, concentric sculpture; umbo prominent; hinge plate narrow, chevron teeth squat, broad, continuous; ligament relatively small, external, amphidetic.

Neilonella salicensis (Seguenza 1877)

TYPE SPECIMEN. Whereabouts unknown.

TYPE LOCALITY. Upper Pliocene fossil, southern Italy.

CITED SPECIMENS. BMNH 1995051.

Leda pusio var.*latior* Jeffreys 1876a, p.190, nom. nud.; 1876b, p.430.
Leda pusio Jeffreys 1879, p.578, in part.
Leda pusio var.*salicensis* Seguenza 1877, p.1178, pl.4, fig.20.
Yoldia sericea var.*striolata* Verrill 1884, p.226; 1885, p.576.
Leda salicensis Locard 1898, p.348, pl.14. figs 22–25.
Neilonella subovata Verrill and Bush 1897, p.57, figs 7, 8, 22; type locality: Georges Bank to Cape Hatteras, 125–1731fms; syntype: USNM 34826 (examined by HLS).
Tindaria (Neilonella) guineensis Thiele 1931, in Theile and Jaeckel 1931, p.50, pl.3, fig.70; type locality; Gulf of Guinea, 710–2492m; type: ZMHU (not seen).
Neilonella guineensis Knudsen 1970, p.59, text-fig.39, pl.5, fig.3, pl.6, figs 8–10.
Neilonella schepmani Prashad 1932, p.27, pl.1, figs 50, 51; type locality; Banda Sea, Siboga sta.221, 2798m; ZMHU (not seen).
Pseudoneilonella salicensis Laghi 1986, p.191, text fig.1, pl.5, figs 1–7.
Pseudoneilonella latior Laghi 1986, p.192, text fig.1, pl.7, figs 7a-c.
Pseudoneilonella salicensis atlantica Laghi 1986 p.192, text fig.1, pl.6, figs 1–7.
Pseudoneilonella montanaroe Laghi 1986, p.193, text fig.1, pl.9, figs 4–8; type locality: off Portugal, Porcupine Expedition, 400m, USNM No. 199739 (not seen).
Neilonella striolata (Brugnone) Warén 1989, p.252, figs 3a, 16a–d.

Warén (1989) gives a lengthy and detailed discussion of much of the nomenclatoral history of this species although, the history is even more complex than he reports. Warén (1989) synonymized *N. salicensis* with an earlier described species *N. striolata* (Brugnone, 1876). The type of *N. striolata* is lost but from the original description and figure by Brugnone (1876) and those of Seguenza (1877) (who synonymized it with *Yoldia abyssicola* Torrell) and later authorities (e.g. Jeffreys, 1879; Locard, 1898) it is clear that the posterior part of the shell of *N. striolata* is significantly different in form to that of *N. salicensis*. Whereas the posterior shell margin of *N. salicensis* is acutely rounded that of *N. striolata* is sub-rostrate with the posterior limit of the shell more ventral in position and the distal postero-dorsal margin more steeply angled (Figs 1,2 & 4).

The brief description of *N. guineensis* by Theile in Theile and Jaeckel(1931) was enlarged upon by Knudsen (1970) who compared specimens from the Galathea Expedition with those of the Valdivia and Siboga Expeditions. From our examination of the Galathea material from 02°17'S 08°10'E (2770m) and our own specimens from 02°32'S 08°18'E (2514m) we conclude that *N.guineensis* and *N. salicensis* are the same species. Knudsen (1970) also synonymized *N. schepmani* with *N. guineensis*. Although *N. schepmani* is from the Banda Sea (Prashad, 1932) which might cast doubt on this synonymy, it must be remembered that *N. salicensis* is a very widespread species and we believe that it is comparable to

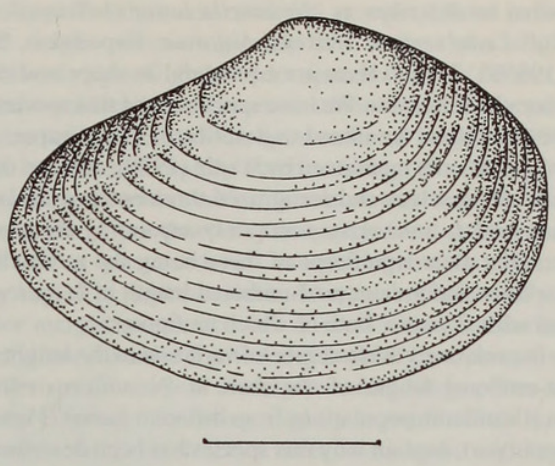

Fig. 1. '*Yoldia abyssicola*' Torell. Right valve, redrawn from Seguenza (1877), synonymized with *Leda producta* Monterosato and *Yoldia striolata* Brugnone. Scale = 1mm.

Ledella sublevis, which also has a widespread distribution in the Atlantic and extends into the southwest Pacific (Allen and Hannah, 1989).

Further compexity in the synonymy of *N. salicensis* concerns so-called varieties of '*Leda pusio* Philippi' a species that has recently been investigated by Laghi (1986).

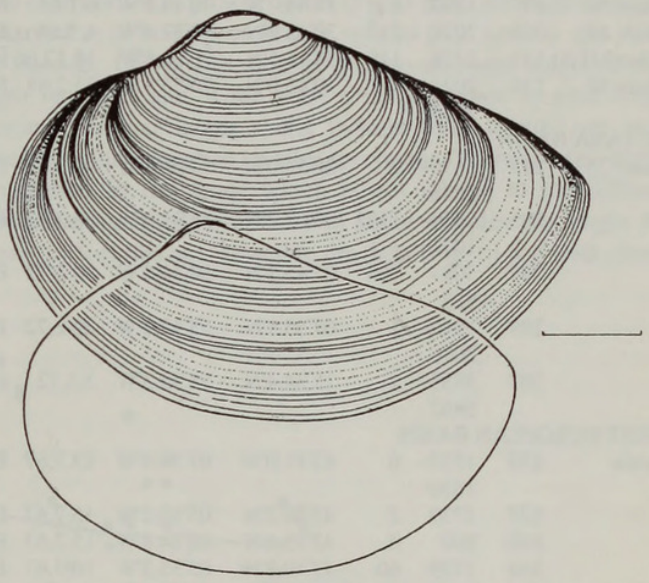

Fig. 2. *Neilonella salicensis*. **a**, view of shell, from Atlantis II station 73 in the North America Basin, drawn from the left side; **b**, outline of shell from Biogas VI station DS 86 in the West European Basin to show difference in shape. Scale = 1mm.

L. pusio is rostrate and not a neillonellid, but a ledellid, possibly synonymous with *L.acuminata* (Jeffreys 1870)(Laghi, 1986). Jeffreys (1879) reporting on *Leda pusio* taken by the 'Lightning' and 'Porcupine' Expeditions, refers to what he thought was a variety of this species which he had previously named *L. pusio* var.*latior* (Jeffreys,1876) and which he changed to *L. pusio* var.*salicensis* of Seguenza (1877). Laghi (1986) proposed a new genus *Pseudoneilonella* to accommodate this latter and raised to species level a number of the records of Jeffreys (1876, 1879). Since then, Warén (1989) has synonymized these with *Neilonella salicensis* and this we confirm.

Jeffreys (1879) also listed a further variety which he called *semistriata* and which is now regarded as a separate species (Warén, 1989). In his detailed analysis Warén (1989, figs 17E & F) also

figures what he describes as '*Neilonella latior* (Jeffreys)?, young syntype of *Leda sericea* Jeffreys, *Valorous* Expedition, Stn 12, USNM 199595' These valves are equilateral in shape and differ in outline from *N. salicensis*. We have specimens of this species in our collections and these we intend to describe in a later paper.

Locard (1898), not mentioned by Warén (1989), came to the same conclusion as ourselves and recognized three entities, *Leda pusio, L. striolata* and *L. salicensis,* accurately separating them on shell characters, the most significant of these being the more elongate, triangular form and greater post-umbonal length of *L. salicensis* as compared with *L. pusio,* both of which he figures.

There is a relatively wide degree of variation in the height, length and post-umbonal length of the shell in *N. salicensis* and this variation is similar in populations from different basins (Figs 4 & 5). This may, in part, explain why this species has been described anew so many times.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
NORTH AMERICA BASIN							
AtlantisII	62	2496	13	39°26.0'N	70°33.0'W	21.8.64	ES
12	64	2886	2	38°46.0'N	70°06.0'W	21.8.64	ES
	73	1330–1470	495	39°46.5'N	70°43.3'W	25.8.64	ES
Chain 50	87	1102	6	39°48.7'N	70°40.8'W	6.7.65	ES
Chain 58	103	2022	217	39°43.6'N	70°37.4'W	4.5.66	ES
AtlantisII 30	131	2178	119	39°38.5'N	70°36.5'W	18.12.66	ES
Chain 88	210	2024–2064	48	39°43.0'N	70°55.5'W	23.2.69	ES
GUYANA BASIN							
Knorr 25	293	1456–1518	2	08°58.0'N	54°04.3'W	27.2.72	ES
	295	1000–1022	1575	08°04.2'N	54°21.3'W	28.2.72	ES
	297	508–523	194	07°45.3'N	54°24.0'W	28.2.72	ES
	299	1942–2076	1	07°55.1'N	55°42.0'W	29.2.72	ES
	307	3835–3862	2	12°34.4'N	58°59.3'W	3.3.72	ES
WEST EUROPEAN BASIN							
Sarsia	S33	1537–1830	6	43°41.0'N	03°36.0'W	13.7.67	ES
	S37	1739	2	43°39.2'N	03°30.2'W	15.7.67	ES
	S40	860	4	43°35.6'N	03°24.8'W	15.7.67	ES
	S44	1739	60	43°40.8'N	03°35.2'W	16.7.67	ES
	S50	2379	16	43°46.7'N	03°38.0'W	18.7.67	ES
	S65	1922	2	46°15.0'N	04°50.0'W	25.7.67	ES
Chain 106	313	1491–1500	432	51°32.2'N	12°35.9'W	17.8.72	ES
	316	2173–2209	583	50°58.7'N	13°01.6'W	18.8.72	ES
La Perle	DS11	2205	1	47°35.5'N	08°33.7'W	8.8.72	DS
Biogas I							
J.Charcot	DS25	2096	9	44°08.2'N	04°15.0'W	1.11.72	DS
Polygas							
J.Charcot	DS32	2138	2	47°32.2'N	08°05.3'W	19.4.73	DS
Biogas II							
BiogasIII	DS38	2138	2	47°32.2'N	08°35.8'W	25.8.73	DS
	DS49	1845	70	44°05.9'N	04°15.6'W	31.8.73	DS
Biogas IV	DS52	2006	16	44°06.3'N	04°22.4'W	18.2.74	DS
	DS63	2126	5	47°32.8'N	08°35.0'W	26.2.74	DS
Cryos	CP07	2170	5	44°09.8'N	04°16.4'W	21.6.74	CP
Biogas V							
J.Charcot	DS77	4240	1	47°31.8'N	09°34.6'W	24.10.74	DS
Biogas VI	DS80	4720	4	46°29.5'N	10°29.5'W	26.10.74	DS
	DS82	4462	1	44°25.4'N	04°50.8'W	29.10.74	DS
	DS86	1950	198	44°04.8'N	04°18.7'W	31.10.74	DS
	DS87	1913	173	44°05.2'N	04°19.4'W	1.11.74	DS
	DS88	1894	31	44°05.2'N	04°15.7'W	1.11.74	DS
Incal	DS01	2091	98	57°59.2'N	10°41.3'W	15.7.76	DS
	DS02	2081	91	57°58.2'N	10°48.5'W	16.7.76	DS
	CP01	2068	19	57°57.7'N	10°55.0'W	16.7.76	CP
	DS05	2503	3	56°28.1'N	11°11.7'W	18.7.76	DS
	OS01	2634	4	50°14.4'N	13°10.9'W	30.7.76	OS
	WS02	2498	1	50°19.3'N	12°55.8'W	30.7.76	WS
	CP10	4823	2	48°25.5'N	15°10.7'W	31.7.76	CP
	WS03	4829	1	48°19.2'N	15°23.3'W	1.8.76	WS
Challenger 7/83	232	2195	3	57°17.0'N	10°16.0'W	19.5.83	ES
CANARY BASIN							
Discovery	6701	1934	8	27°45.2'N	14°13.0'W	16.3.68	ES
SIERRE LEONE BASIN							
AtlantisII 31	142	1624–1796	20	10°30.0'N	17°51.5'W	5.2.67	ES
	147	2934	16	10°38.0'N	17°52.0'W	23.2.67	ES
ANGOLA BASIN							
AtlantisII 42	191	1546–1559	52	23°05.0'S	12°31.5'E	17.5.68	ES
	200	2644–2754	7	09°43.5'S	10°57.0'E	22.5.68	ES
	201	1964–2031	41	09°25.0'S	11°35.0'E	23.5.68	ES
	202	1427–1643	21	08°56.0'S	12°15.0'E	15.5.68	ES
Walda	DS20	2514	4	02°32.0'S	08°18.1'E	–.–.71	DS
	DS25	2470	31	02°19.8'S	07°49.2'E	–.–.71	DS

In addition to the material listed above we have examined the following specimens from the Porcupine and Valorous Expeditions housed in the BMNH:– 85.11.5.397–402; 6.9.27,28; 85.11.5.494–5; 89.11.11.10–13; 89.9.5.26–9; 77.11.28.24. We have also examined specimens from the Galathea Expedition housed in the ZMUC, and specimens mostly from the U.S.Fish Commission expeditions housed in the USNM and MCZ.

DISTRIBUTION. Common throughout the Atlantic north of the Argentine and Cape Basins and south of the Norwegian and Arctic Basins. It is also found in the southwestern Pacific. It mainly occurs at slope depths, occasionally at abyssal depths (West European Basin), from 508m to 4829m.

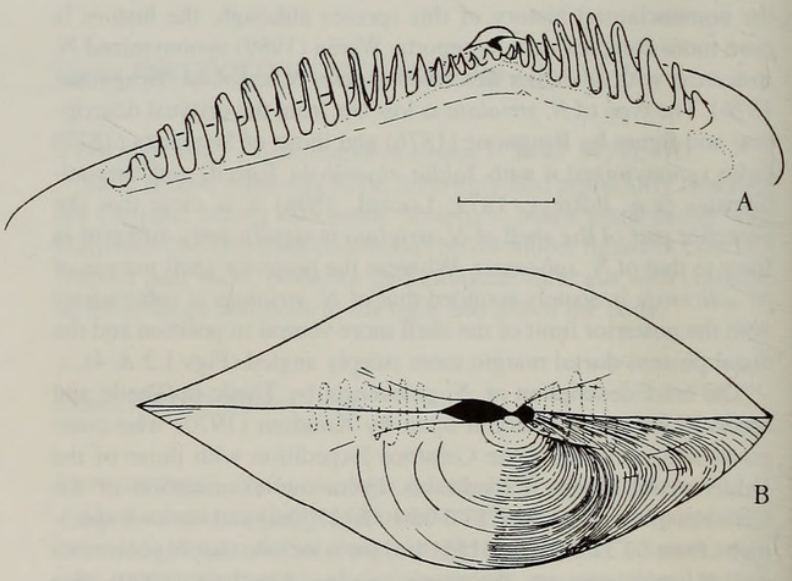

Fig. 3. *Neilonella salicensis.* **a**, internal inclined ventral view of the hinge plate and teeth of a left valve; **b**, dorsal view of shell to show the extent of the external ligament and detail of sculpture. Both specimens taken from Walda station DS 25 in the Angola Basin. Scale = 1mm.

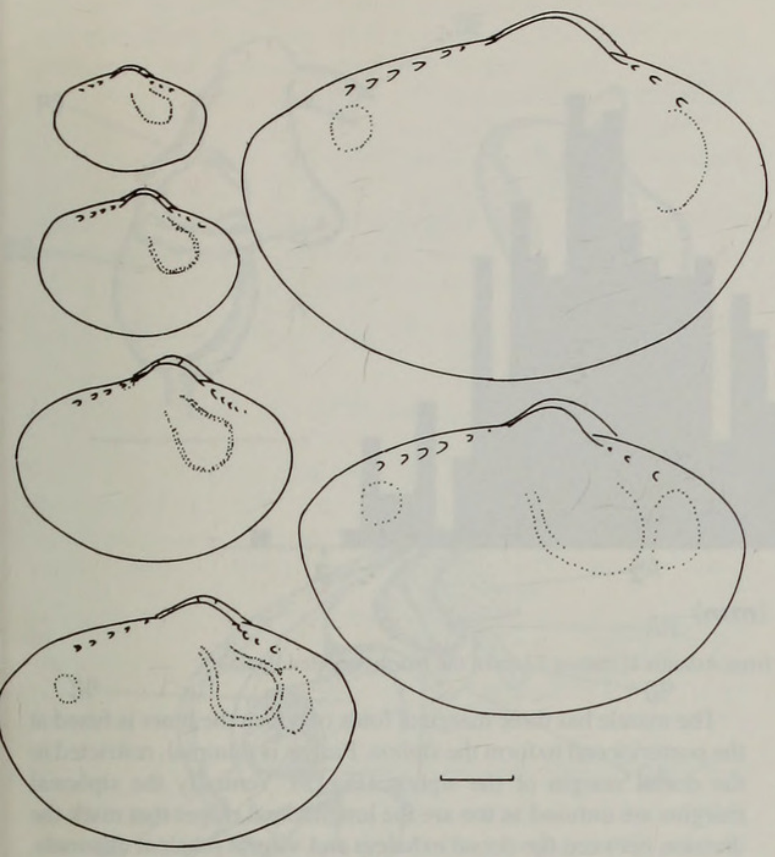

Fig. 4. *Neilonella salicensis.* A series of shells, from Atlantis II station 73 from the North Atlantic Basin, in lateral view from right side to show change in shape with increasing size. Scale = lmm.

SHELL DESCRIPTION (Figs 2–4)

Shell robust, moderately elongate, moderately wide, ornamented with concentric ridges sometimes in groups of three to four well-defined ridges alternating with two to to three slighty less well-defined ridges slightly wider spaced than the former, light to dark straw-coloured periostracum; umbos moderately prominant, somewhat anterior to mid-line (postumbonal length *c.*54% of total length), inward and slightly anterior facing; dorsal shell margins deep set close to umbo but no lunule or true escutcheon, antero-dorsal margin slopes down to join anterior and ventral margins in smooth curve, postero-dorsal margin almost straight, may be slightly angled at posterior limit of hinge short of acutely rounded posterior margin; posterior limit of shell somewhat dorsal to mid horizontal line, anterior limit of shell at mid line; posterior margin of smaller specimens less acutely rounded; hinge plates elongate, moderately broad, increasing slightly in width distally, anterior and posterior hinge teeth series meet below umbo with no edentulous space between, teeth numerous, up to 19 in posterior series and 14 in anterior series depending on size of specimen, obtuse chevron-shape, proximal hinge teeth very small, those more distal elongate and so closely articulated that it maybe impossible to separate valves without damage to them; internal ligament (resilium) microscopic, present ventral to umbo at outer margin of hinge plate, external ligament opisthodetic, relatively short, short anterior part present. Maximum total length of present specimens 8.0mm.

As in most deep-sea protobranchs, there is a change in the shape of the shell outline as growth occurs (Figs 4 & 5), although this is not as marked as in many protobranch species (e.g. *Ledella* spp. Allen and Hannah, 1989). The ratio of postero-umbonal length to total length increases and at the same time the height to total length decreases so that larger shells (>3mm total length) are more posteriorly attenuate than smaller specimens. There is a fair degree of variation in the ratios which is not related to the different populations sampled. Unusually in some samples the length frequency histograms are skewed to the right (Fig. 6) and with clearly

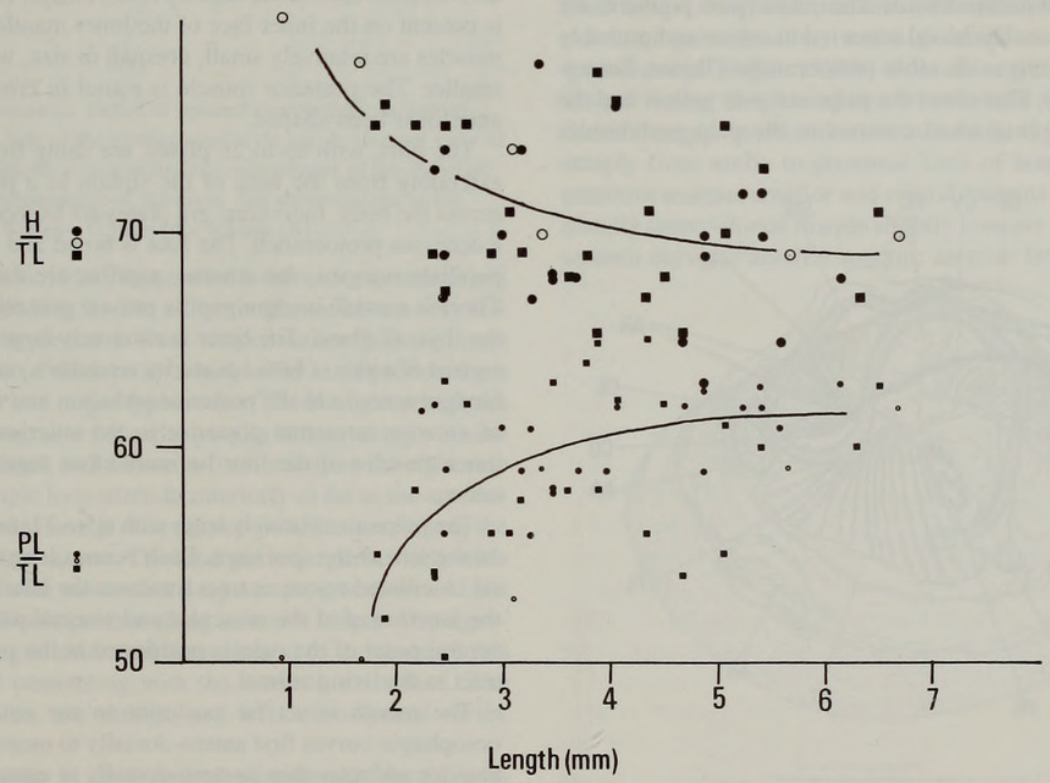

Fig. 5. *Neilonella salicensis.* The ratios height to total length (H/TL)(large symbols) and post-umbonal length to total length (PL/TL)(small symbols) plotted against total length to show changes in shell proportions with increasing length. Open circles are specimens from Biogas III station DS 49 West European Basin, closed circles from Sarsia Station S44 West European Basin and closed squares, from Chain 58 station 103 North America Basin.

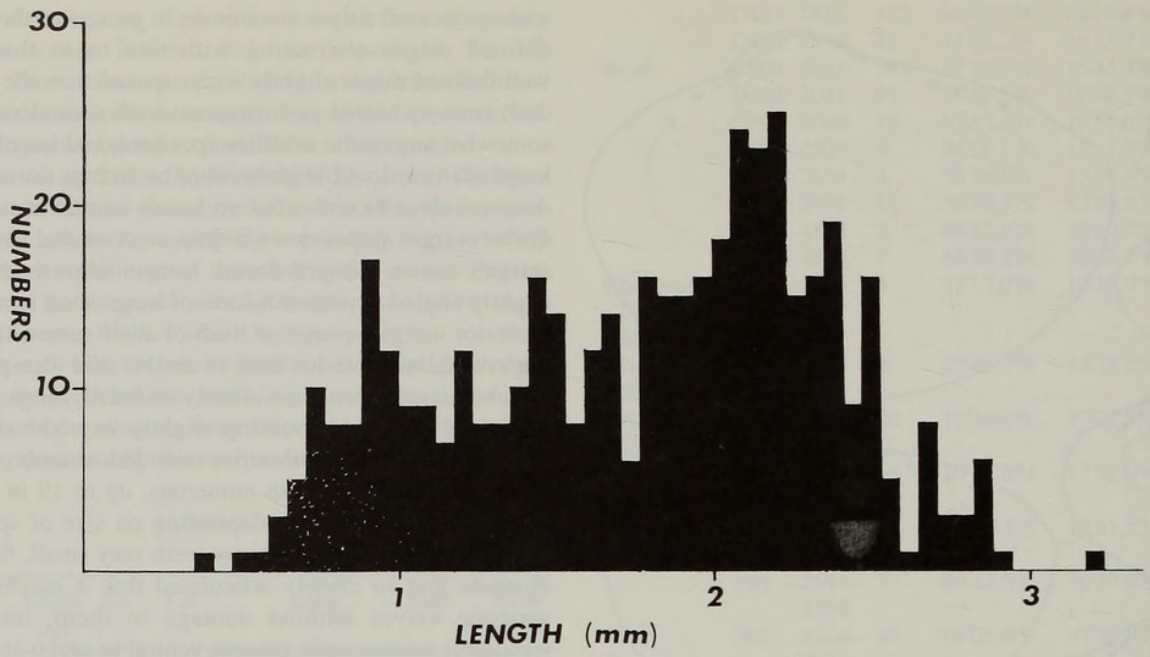

Fig. 6. *Neilonella salicensis.* Length/frequency histogram of a sample taken from Atlantis II station 73 from the North America Basin.

marked size groups. It is unclear whether these latter relate to annual settlements or to fortuitous periodic settlements.

INTERNAL MORPHOLOGY (Figs 7 & 8)

This was one of the few deep-sea species that were kept alive for a few weeks following the processing of the sample. The external drab olive/yellow of the shell is in marked contrast to the spectacularly vivid array of colours of the body organs. The stomach is a bright emerald green, the digestive gland a bright olive green and the gills are bright red. The gill plates are particularly vivid below the frontal cilia and dorso-laterally, in addition the mantle overlying the gills is also red. The margins of the palps are a diffuse pink as too is a band underlying the crest of the inner folds. The red and pink pigments are probably a cytochrome. The blood is not red in colour and probably contains a haemocyanin as do other protobranchs (Taylor, Davenport and Allen, 1995). Elsewhere the palps are pale yellow and the yellow/pink effect is in marked contrast to the palp proboscides which are pure white.

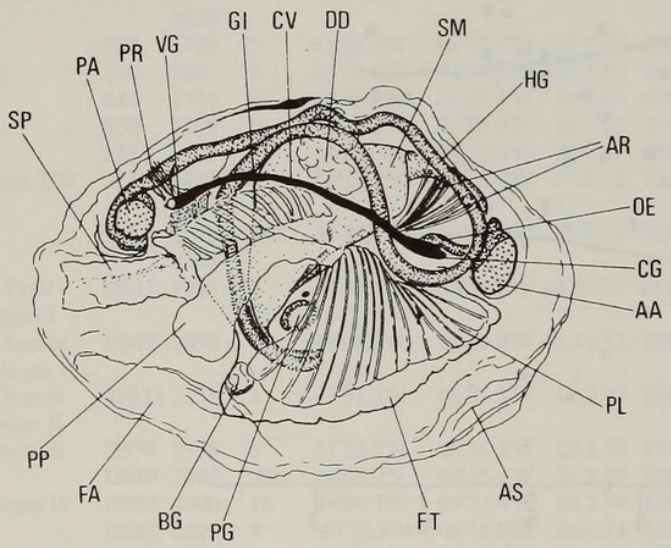

Fig. 7. *Neilonella salicensis.* Semidiagrammatic view of the internal morphology as seen from the right side. See abbreviations to text-figures on p. 102. Scale = 1mm.

The mantle has three marginal folds of which the inner is fused at the posterior end to form the siphon. Fusion is minimal, restricted to the dorsal margin of the siphon (Fig. 8). Ventrally the siphonal margins are unfused as too are the longitudinal ridges that mark the division between the dorsal exhalent and ventral inhalent channels. The gill axes attach to the inner ends of the longitudinal ridges. There is a shallow siphonal embayment and attached to its inner limit on the left or the right side is a siphonal tentacle which in living specimens extends beyond the shell margin at distance equal to a third of the shell length. Ventral to the anterior adductor muscle there is an elongate anterior sense organ, which consists of a flap of tissue derived from the middle sensory fold. A major ciliated rejection tract is present on the inner face of the inner mantle fold. The adductor muscles are relatively small, unequal in size, with the posterior the smaller. The posterior muscle is round in cross-section while the anterior is bean-shaped.

The gills, with up to 26 plates, are slung from a horizontal axis extending from the base of the siphon to a point about half way across the body. Individual gill plates are exceptionally elongate for a deep-sea protobranch. The foot is broad and the divided sole has papillate margins, the anterior papillae are the more pronounced. There is a small median papilla present posterior to the aperture to the 'byssal' gland. The latter is extremely large. The pedal muscles consist of a pair of broad posterior retractors, one on each side of the hindgut anterior to the posterior adductor, and a series of four pairs of anterior retractors posterior to the anterior adductor. The two inner muscles of the four lie more close together than to the two outer.

The palps are relatively large with up to 27 inner ridges depending on the size of the specimen. Each bears a long narrow palp proboscis. A ciliated rejection tract traverses the lateral face of the foot at the junction of of the muscular and visceral parts and the posterior ventral point of the palp is positioned at the posterior limit of this tract in the living animal.

The mouth is set far posterior to the anterior adductor. The oesophagus curves first antero-dorsally to meet the inner face of the anterior adductor then postero-dorsally to open on the anterior face of the stomach. The stomach is large and slung diagonally within the visceral mass. The pedal muscles form a ventral 'basket' in which the stomach rests. The stomach, which is similar to that of other

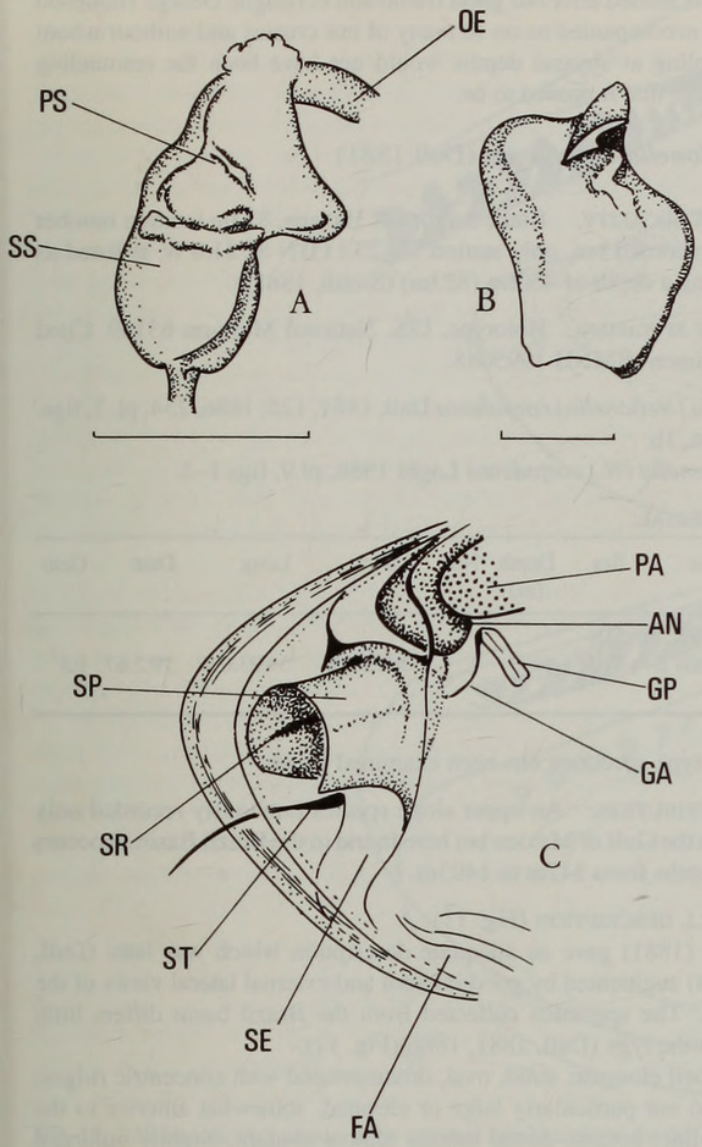

Fig. 8. *Neilonella salicensis.* Detail of internal morphology; **a**, lateral view from the right side of the stomach and style sac; **b**, internal view of a dissected gastric shield; **c**, diagrammatic enlargement of the siphonal region to show the relationship of the parts. See abbreviations to the text-figures p. 102. Scales = 0.5mm (A); 0.1mm (B).

protobranchs (Purchon, 1956), is one third lined with a gastric shield dorsally and to the left (Fig.8). The unlined right wall bears very few sorting ridges. The style sac is flask-shaped rather than the more usual conical outline of other protobranchs. The combined mid gut is guarded by minor and major typhlosoles. The hind gut penetrates the foot to a point ventral to the pedal ganglia before taking a course posterior to the stomach and thence to form a loop to the right side of the body. This single loop extends anteriorly as far as the anterior adductor muscle and where it then takes a dorsal course along the margin of the body to the anus. The hind gut has a particularly wide diameter compared with most other deep-sea protobranchs and has a well-marked typhlosole present along its entire length. The digestive gland which lies anterior and dorso-lateral to the stomach has three sections each connecting with the stomach via a duct. The apertures of the ducts are ventral, and left latero-ventral to the oesophageal aperture.

The nervous system is of a typical protobranch design with elongate pairs of cerebral and visceral ganglia and large ovoid pedal ganglia. These are connected by very stout cerebro-visceral and cerebro-pedal commissures. A statocyst lies dorsal each pedal ganglion. From visceral ganglia three main nerves pass to the gill, hind gut and mantle/siphon, and from the cerebral ganglia nerves pass to the palps and mantle.

The sexes are separate, specimens greater than 4mm total length have gonads. The gonad first develops at the periphery of the visceral mass and as it matures it spreads across the lateral surface of the viscera. On the right side of the body, apart from a small portion postero-dorsal to the loop of the hind gut the gonad does not extend beyond the confines of the of the loop. While different samples show different degrees of maturity, the specimens of each sample appear to be maturing synchronously. The ratio of males to females is approximately 50:50.

Neilonella hampsoni new species

TYPE SPECIMEN. Holotype BMNH 1995049; paratype BMNH 1995050.

TYPE LOCALITY. Atlantis II cruise 31, station 155, Sierra Leone Basin, 00°03.0'S 27°48.0'W, 3730–3783m.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
SIERRA LEONE BASIN							
Atlantis 11 31	155	3730–3783	3	00°03.0'S	27°48.0'W	14.2.67	ES
J.Charcot Vema	DS03	5150	1	10°59.0'N	45°15.0'W	16.11.77	DS

DISTRIBUTION. An abyssal species, to date only found in the Sierra Leone Basin at depths from 3730m to 5150m.

SHELL DESCRIPTION (Figs 9 & 10)
Shell robust, oval, wide, ornamented with concentric ridges, straw-coloured periostracum; umbo prominant, anterior to midline (postumbonal length *c.*60% of total length in large specimens), inward facing; lunule and escutcheon, both well-defined; postero-dorsal margin in lateral view almost straight, slopes relatively steeply from umbo to proximal limit of hinge, rounded angle to posterior margin, anterior and ventral margins form a smooth curve, distally antero-dorsal margin slightly concave then slopes steeply in smooth curve to anterior margin; anterior limit of shell coincides

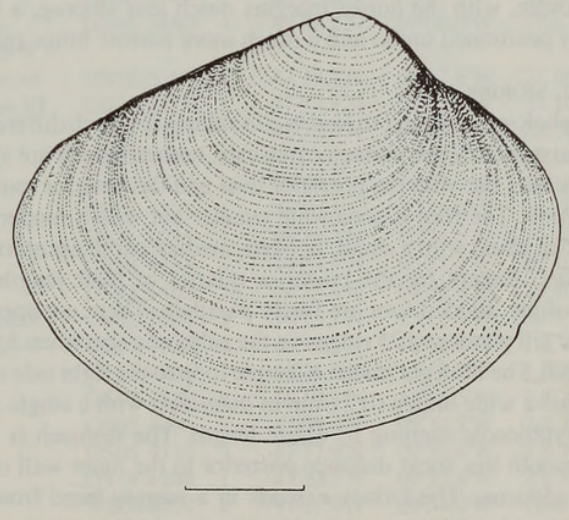

Fig. 9. *Neilonella hampsoni.* Lateral view of the right valve of the holotype, from Atlantis II station 155 from the Sierra Leone Basin. Scale = 1mm.

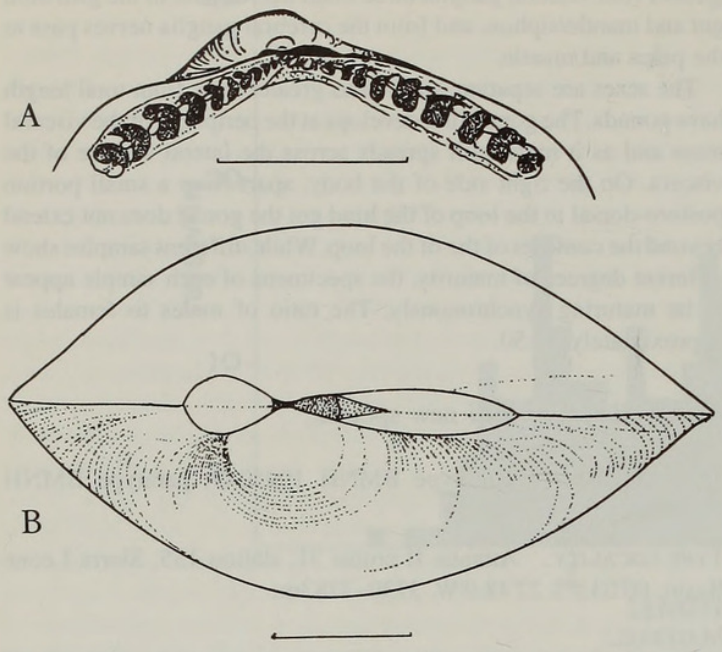

Fig. 10. *Neilonella hampsoni.* **a**, lateral view of the hinge plate of the right valve of a paratype; **b**, dorsal view of the shell of the holotype. Both specimens taken from Atlantis II station 155 from the Sierra Leone Basin. Scales = 1mm.

with horizontal midline, posterior limit of shell immediately ventral to mid line; hinge plate stout extending along most of the dorsal shell margin, anterior and posterior tooth series meet below umbo, with faint suggestion of an edentulous space between, 13 posterior and 10 anterior teeth in specimen 3.9mm total length, teeth increase in size distally, teeth chevron-shaped, obtuse, so much so that teeth appear to be a straight line transverse to hinge plate; ligament opisthodetic, external, short, anterior outer layer extremely short, hidden beneath umbo, no resilium.

Maximum total length of present specimens is 7.5mm.

Apart from *N. salicensis,* from which it differs in having a shorter, wider shape, and well-marked lunule and escutcheon, the only other protobranch species with which it has some similarity is *'Leda' sericea* var *ovata* Jeffreys 1876 (Jeffreys, 1879). One of us (JAA) has examined specimens of this latter species in the Natural History Museum, London, (BMNH 85 11 5483–84) and find that *L. sericea* is more ovate, with the dorsal margins much less sloping, a more anteriorly positioned umbo and a much more narrow hinge plate.

INTERNAL MORPHOLOGY

The morphology is similar to *Neilonella salicensis*. Such differences that do exist include the adductor muscles, both of which are small, similar in size, but with the posterior oval and the anterior round in cross section. The foot is somewhat smaller but with a moderately large byssal gland with a small, hooked, median papilla posterior to its aperture. Except for the posterior quarter of their length, the margins of the divided foot are finely papillate. There are approximately 20 gill plates and 25 ridges on the palps of a specimen 3.9mm total length. The hind gut makes a simple loop to the right side of the body, it has a wide lumen (0.21mm in diameter) with a single well-defined typhlosole running its entire length. The stomach is large and the mouth lies some distance posterior to the inner wall of the anterior adductor. The kidney extends in a narrow band from the posterior margin of the posterior adductor, anteriorly narrowing over the viscera, and terminating at the posterior edge of the digestive diverticula.

It is named after our good friend and colleague George Hampson who accompanied us on so many of our cruises and without whom sampling at abyssal depths would not have been the resounding success that it proved to be.

Neilonella corpulenta (Dall 1881)

TYPE LOCALITY. Blake station off Havana, 823m (station number not recorded but, only station 51, 23°11.0'N 82°21.0'W, is listed as having a depth of 450fm (823m) (Smith, 1888)).

TYPE SPECIMEN. Holotype, U.S. National Museum 63169. Cited specimen: BMNH 1995048.

Leda (Neilonella) corpulenta Dall, 1881, 125; 1886, 254, pl. 7, figs. 1a, 1b.
Neilonella (N.) corpulenta Laghi 1986, pl.9, figs 1–3.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
BRAZIL BASIN							
Atlantis II 31	162	1493	1	08°02.2'S	34°03.0'W	19.2.67	ES

The type specimen has been examined by us.

DISTRIBUTION. An upper slope species previously recorded only from the Gulf of Mexico but here found in the Brazil Basin. It occurs at depths from 347m to 1493m.

SHELL DESCRIPTION (Fig. 11)

Dall (1881) gave an adequate description which was later (Dall, 1886) augmented by good internal and external lateral views of the shell. The specimen collected from the Brazil basin differs little from the type (Dall, 1881, 1886)(Fig. 11):-

Shell elongate, solid, oval, ornamentated with concentric ridges; umbo not particularly large or elevated, somewhat anterior to the mid line; postero-dorsal margin almost straight, slightly upturned posterior to the distal limit of the hinge, then sharply and smoothly curved to posterior margin, ventral margin shallow smooth curve, not posteriorly sinuous, anterior margin smoothly curved, antero-dorsal margin relatively steeply angled, distally slightly raised; hinge plate elongate, relatively wide, hinge teeth chevron-shaped, 9 in anterior and 12 in posterior series; external ligament slightly opisthodetic, short; resilium small ventral to umbo.

Dall (1881) states that there are an equal number of teeth in the anterior and posterior series (15), however the type specimen which is larger than the present specimen, has 17 anterior and 20 posterior teeth.

The total length of present specimen is 3.1mm.

INTERNAL MORPHOLOGY

Both adductor muscles are oval in cross section, the anterior is somewhat larger than the posterior but neither is particulaly large. The foot is relatively short with large marginal papillae. The palps are relatively short with 7 broad internal ridges. The gill is also short. The siphonal embayment is shallow and the siphons similar to those described for *N. salicensis.* The hind gut forms a single loop to the right side of the body and has a typhlosole along its entire length.

Neilonella whoii new species

TYPE SPECIMEN. Holotype BMNH 1995052; paratypes BMNH 1995053.

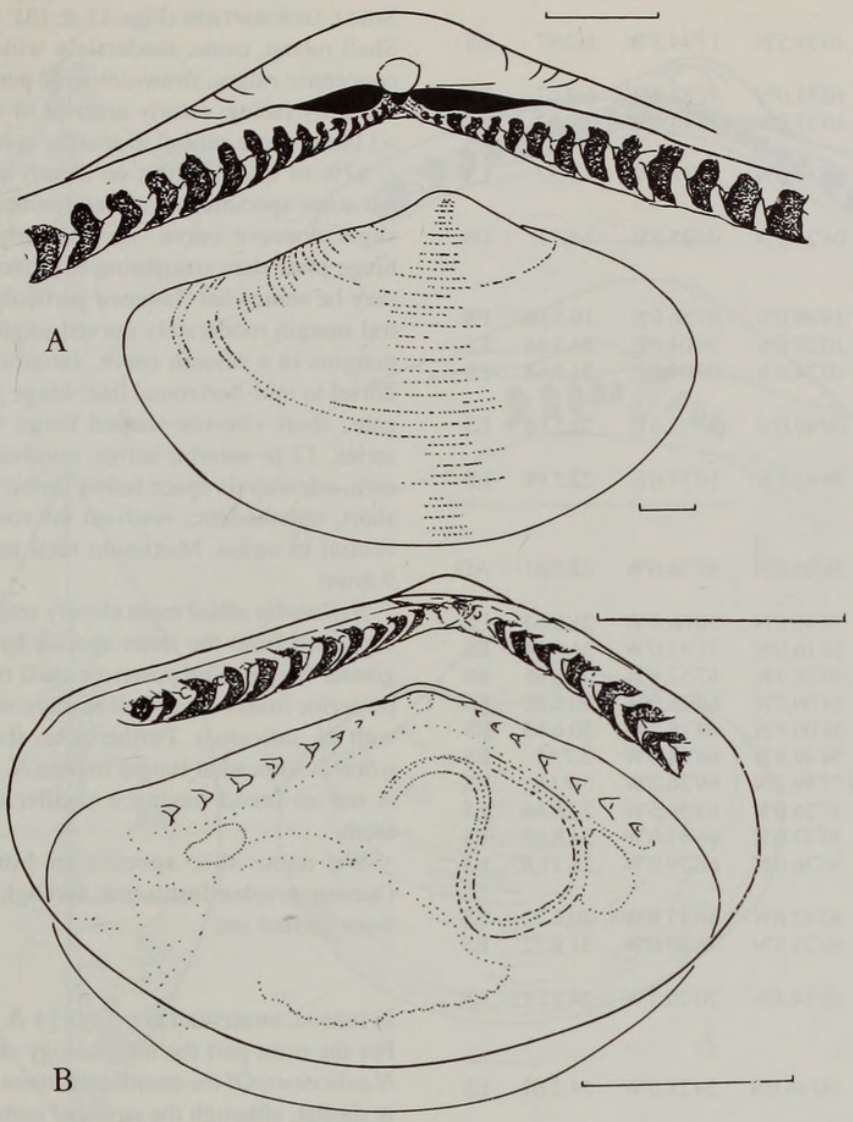

Fig. 11. *Neilonella corpulenta*. **a**, an external lateral view of the right valve of specimen No 63169 from the USNM and an internal lateral view of the central region of the hinge of the same valve; **b**, lateral view of the intact shell, from Atlantis II station 162 from the Brazil Basin, and an internal view of the left valve of the same specimen to show detail of the hinge plate. Scales = 1mm.

CITED SPECIMEN. BMNH 1995054.

TYPE LOCALITY. Chain cruise 50, station 78, North America Basin, 38°00.8'N 69°18.7'W, 3828m.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
WEST EUROPEAN BASIN							
Chain 106	323	3356–3338	7	50°08.3'N	13°53.7'W	21.8.72	ES
	326	3859	5	50°04.9'N	14°23.8'W	22.8.72	ES
	328	4426–4435	6	50°04.7'N	15°44.8'W	23.8.72	ES
	330	4632	16	50°43.5'N	17°51.7'W	24.8.72	ES
J.Charcot	DS20	4226	2	47°33.0'N	09°36.7'W	24.10.72	DS
Polygas	DS22	4144	2	47°34.1'N	09°38.4'W	25.10.72	DS
	DS23	4734	18	46°32.8'N	10°21.0'W	26.10.72	DS
	DS28	4413	1	44°23.8'N	04°47.5'W	2.11.72	DS
J.Charcot	CV23	2034	1	47°32.7'N	08°34.2'W	25.8.73	CV
Biogas III	DS41	3548	4	47°28.3'N	09°04.2'W	26.8.73	DS
	CV27	4023	1	47°34.2'N	09°32.4'W	28.8.73	CV
	CV30	4518	53	46°32.8'N	10°20.0'W	28.8.73	CV
	DS47	4230	2	44°26.8'N	04°50.7'W	31.8.73	DS
J.Charcot	CV34	4406	1	44°27.2'N	04°49.1'W	19.2.74	CV
Biogas IV	DS53	4425	30	44°30.4'N	04°56.3'W	19.2.74	DS
	DS54	4659	13	46°31.1'N	10°29.2'W	21.2.74	DS
	DS56	4050	2	47°32.7'N	09°28.2'W	23.2.74	DS
	DS60	3742	2	47°26.8'N	09°07.2'W	24.2.74	DS
Cryos	DS66	3480	4	47°28.2'N	09°00.0'W	17.6.74	DS
Biogas V							
J.Charcot	DS75	3250	4	47°28.1'N	09°07.8'W	22.10.74	DS
Biogas VI	DS76	4228	8	47°34.8'N	09°33.3'W	23.10.74	DS
	CP14	4237	1	47°32.0'N	09°35.9'W	23.10.74	CP
	DS78	4706	29	46°31.2'N	10°23.8'W	25.10.74	DS
	DS79	4715	10	46°30.4'N	10°27.1'W	26.10.74	DS
	CP18	4721	1	46°30.5'N	10°26.0'W	26.10.74	CP
	DS81	4715	1	46°28.3'N	10°24.6'W	27.10.74	DS
	CP19	4434	3	44°24.9'N	04°51.3'W	28.10.74	CP
	DS82	4462	16	44°25.4'N	04°52.8'W	29.10.74	DS
J.Charcot	OS01	2634	3	50°15.2'N	13°11.0'W	30.7.76	OS
Incal	DS11	4823	1	48°18.6'N	15°12.0'W	1.8.76	DS
	CP11	4823	1	48°21.2'N	15°13.7'W	1.8.76	CP
	OS02	4829	6	48°19.1'N	15°15.5'W	2.8.76	OS
	OS05	4296	3	47°32.9'N	09°34.7'W	7.8.76	OS
	OS06	4316	3	47°27.9'N	09°36.0'W	9.8.76	OS
	DS16	4268	1	47°30.3'N	09°33.4'W	9.8.76	DS
	WS09	4277	2	47°27.9'N	09°34.0'W	10.8.76	WS
CANARY BASIN							
Discovery	6711	2988	1	27°14.9'N	15°36.3'W	19.3.68	ES

SIERRA LEONE BASIN							
Atlantis II 31	146	2842–2891	2	10°39.5'N	17°44.5'W	6.2.67	ES
	147	2934	4	10°38.0'N	17°52.0'W	6.2.67	ES
	148	3814–3828	4	10°37.0'N	18°14.0'W	7.2.67	ES
	149	3861	1	10°30.0'N	18°18.0'W	7.2.67	ES
GUINEA BASIN							
J. Charcot Walda	DS28	1261	2	04°21.2'N	04°35.2'E	?.8.71	DS
ANGOLA BASIN							
Atlantis II 42	195	3797	46	14°49.0'S	09°56.0'E	19.5.68	ES
	197	4595	25	10°29.0'S	09°04.0'E	21.5.68	ES
	198	4559–4566	20	10°24.0'S	09°09.0'E	21.5.68	ES
	199	3764–3779	3	09°49.0'S	10°33.0'E	22.5.68	ES
	200	2644–2754	8	09°43.5'S	10°57.0'E	22.5.68	ES
NORTH AMERICA BASIN							
Atlantis II 264	2	3752	2	38°05.0'N	69°36.0'W	22.5.61	AD
Atlantis II 12	64	2886	2	38°46.0'N	70°06.0'W	21.8.64	ES
	72	2864	9	38°16.0'N	71°47.0'W	24.8.64	ES
Chain 50	76	2862	3	39°38.3'N	67°57.8'W	29.6.65	ES
	77	3806	752	38°00.7'N	69°16.0'W	30.6.65	ES
	78	3828	199	38°00.8'N	69°18.7'W	30.6.65	ES
	80	4970	1	34°49.8'N	66°34.0'W	2.7.65	ES
	85	3834	1150	37°59.2'N	69°26.2'W	5.7.65	ES
Atlantis II 24	124	4862	1	37°26.0'N	63°59.5'W	22.8.66	ES
	126	3806	48	39°37.0'N	66°47.0'W	24.8.66	ES
Atlantis II 40	175	4667–4693	1	36°36.0'N	68°29.0'W	28.11.67	ES
Chain 106	334	4400	3	40°42.6'N	46°13.8'W	30.8.72	ES
	335	3882–3919	5	40°25.3'N	46°30.0'W	31.8.72	ES
Knorr 35	340	3264–3356	95	38°14.4'N	70°20.3'W	24.11.73	ES
BRAZIL BASIN							
Atlantis II 31	156	3459	6	00°46.0'S	29°28.0'W	14.2.67	ES
GUYANA BASIN							
Knorr 25	287	4980–4934	72	13°16.0'N	54°52.2'W	24.2.72	ES
	288	4417–4429	19	11°02.2'N	55°05.5'W	25.2.72	ES
	291	3859–3868	43	10°06.1'N	55°14.0'W	26.2.72	ES
	301	2487–2500	23	08°12.4'N	55°50.2'W	29.2.72	ES
	303	2842–2853	8	08°28.8'N	56°04.5'W	1.3.72	ES
	307	3862–3835	15	12°34.4'N	58°59.3'W	3.3.72	ES
J.Charcot Biovema	DS05	5100	3	10°46.0'N	42°40.3'W	19.11.77	DS
ARGENTINE BASIN							
Atlantis II 60	242	4382–4402	1	38°16.9'S	51°56.1'W	13.3.71	ES
	243	3815–3822	3	37°36.8'S	52°23.6'W	14.3.71	ES
	247	5208–5223	6	43°33.0'S	48°58.1'W	17.3.71	ES
	256	3906–3917	8	37°40.9'S	52°19.3'W	24.3.71	ES
	259	3305–3317	11	37°13.3'S	52°45.0'W	26.3.71	ES

DISTRIBUTION. An abyssal species, found widely within temperate and tropical latitudes at depths ranging from 2487m to 5223m.

SHELL DESCRIPTION (Figs 12 & 13)

Shell robust, ovate, moderately wide, ornamentated with marked concentric ridges, straw-coloured periostracum; umbos prominant, inwardly facing, clearly anterior of vertical midline in specimens >3.0mm, more central in smaller specimens (post-umbonal length *c.* 57% of total length); no clearly marked lunule or escutcheon, but some specimens with faint indications; postero-dorsal margin slight concave curve, very slightly angulate opposite limit of hinge plate then steepening to posterior margin, posterior margin may be somewhat flattened particularly in small specimens, ventral margin moderately curved joining anterior and antero-dorsal margins in a smooth curve, anterior and posterior limits of shell dorsal to mid-horizontal line; hinge plate broad, continuous, elongate, short chevron-shaped hinge teeth, up to 14 in posterior series, 12 in anterior series, numbers varying with size of specimen, edentulous space below umbo very small; external ligament short, opisthodetic, resilium microscopic, close to shell margin, ventral to umbo. Maximum total length of present specimens is 9.8mm.

Neilonella whoii most closely resembles *N. salicensis*. It can be separated from the latter species by its more rounded shape and greater height. The posterior shell margin is not as acute and the posterior limit of the shell is more dorsal in position as compared with *N. salicensis*. Furthermore, the post-umbonal length of *N. whoii* is somewhat longer than in *N. salicensis* and the hinge plate is not so broad having a smaller ratio of anterior to posterior teeth.

We name this species in honour of the Woods Hole Ocenanographic Institution, through whose auspices these studies were carried out.

INTERNAL MORPHOLOGY (Figs 14 & 15)

For the most part the morphology of *N. whoii* is similar to that of *N.salicensis*. Of the mantle structures, the construction of the siphon is similar, although the siphonal embayment is less deep than in *N. salincensis*. The posterior adductor muscle is oval in cross-section and not much smaller than the anterior, probably reflecting the more rounded shell outline of *N. whoii*. The anterior sense organ is poorly developed, the least developed of all the deep-sea nuculanids that have been described to date. The gills and palps of *N. whoii* are similar in size and form to those in *N. salicensis* with up to a maximum of 18 gill plates and 17 palp ridges.

The foot is large with a few moderately deep papillae at the margin. The mouth lies some distance posterior to the anterior adductor. The stomach is large with 9 or 10 ridges forming the porterior sorting area. The hind gut makes a single loop to the right side of the body, the loop being somewhat larger and more smoothly curved than that in *N. salicensis*. The ganglia and commissures are not so stout as they are in the latter species.

Clearly *Neilonella whoii* is closely related to *N. salicensis*. Although similar in form, they have markedly different depth distributions, *N. salicensis* occurring mainly at lower slope depths and *N. whoii* occurring mainly at abyssal depths. We believe that in the past there may have been misidentifications, and specimens of *N. salicensis* recorded from abyssal depths deserve re-examination.

Specimens which are narrower and relatively smaller in height to length ratio than those described above (Fig.16) are present in some samples and do not occur other than with typical specimens of *N. whoii*. In other respects they are no different in their morphology to *N. whoii*. We consider them to be varients at the limit of a range of shell outlines and not a subspecies.

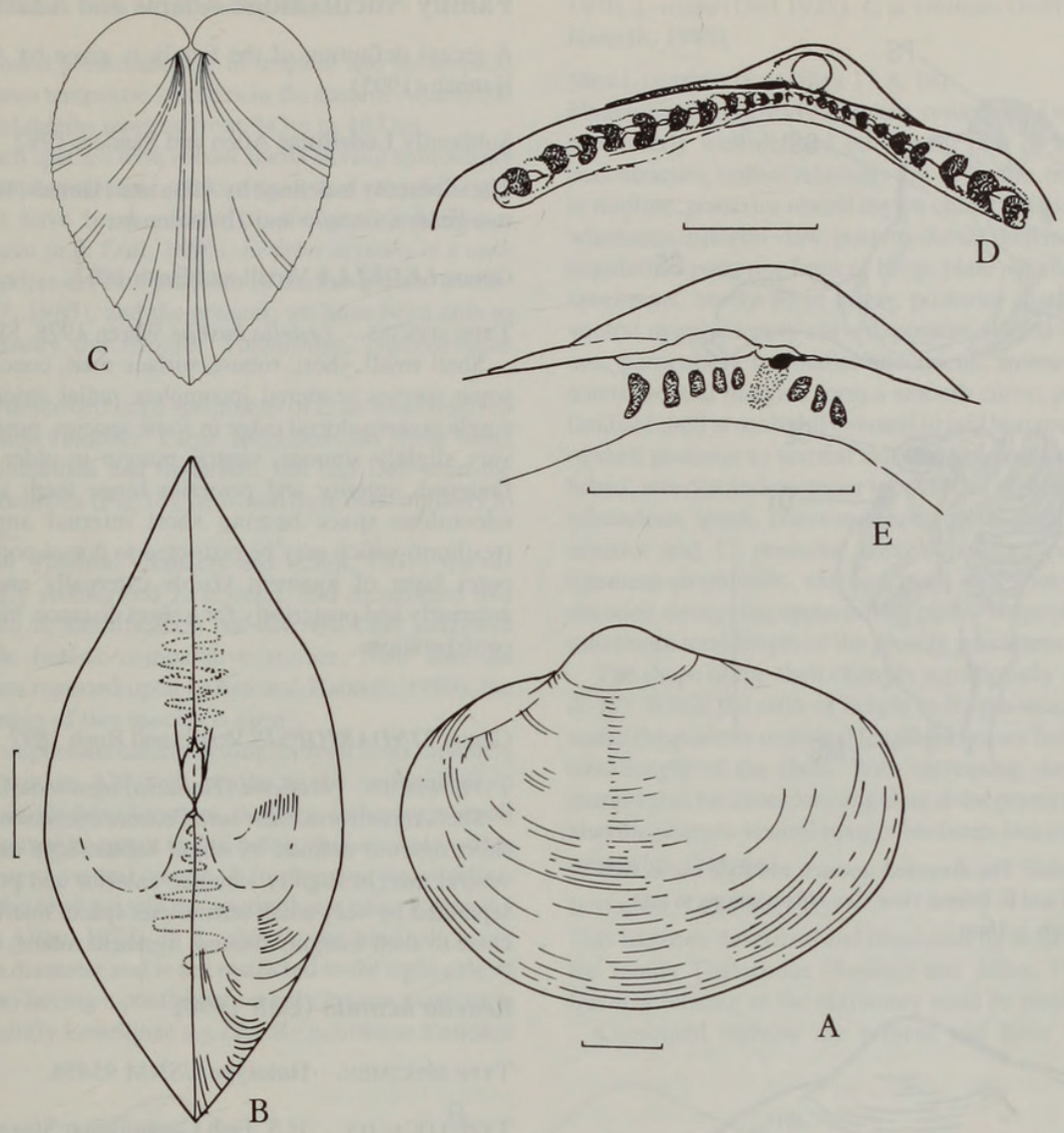

Fig. 12. *Neilonella whoii.* Details of shell form of specimens, from Chain station 78 from the North America Basin, the type locality; **a**, left lateral, **b**, dorsal and **c**, anterior views intact shells; **d**, the hinge plate of a specimen, from Incal station DS05 from the West European Basin; e, detail of the umbonal region of the hinge plate of a specimen, from Chain station 78. Scales = 1mm.

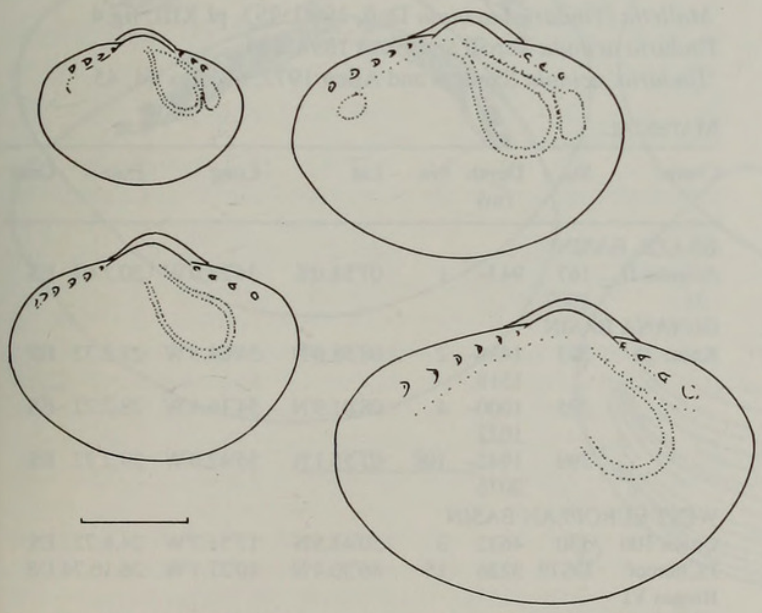

Fig. 13. *Neilonella whoii.* Four shells in outline, from Atlantis II station 72 from the North America Basin, in left lateral view to illustrate the small changes in shape with increasing size. Scale = 1mm.

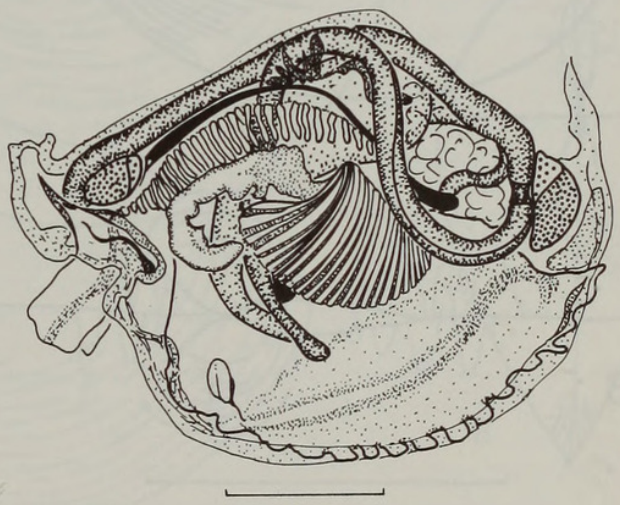

Fig. 14. *Neilonella whoii.* A semidiagrammatic view of the internal morphology as seen from the right side. For the identification of the parts see text-figure 7, p. 106. Scale = 1mm.

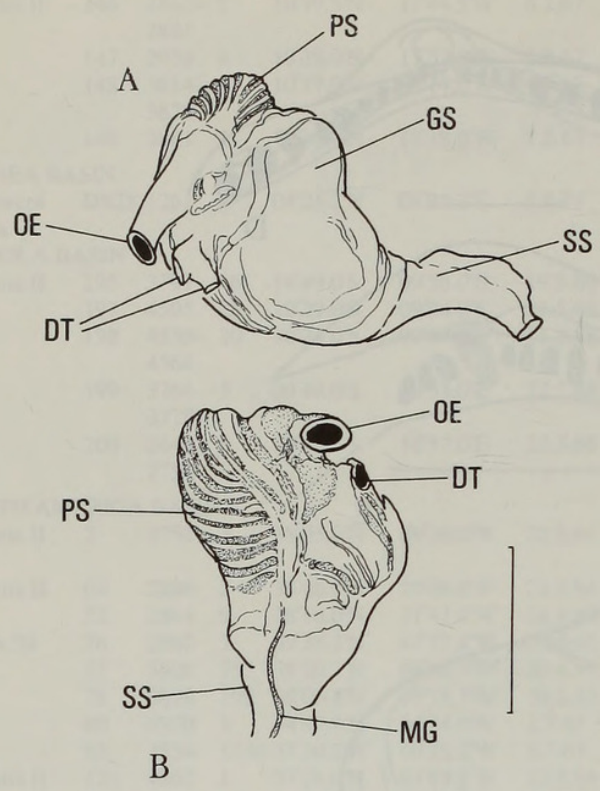

Fig. 15. *Neilonella whoii.* The dissected stomach and style sac as seen from a, in left lateral and b, frontal view. See abbreviations to text figures on p. 102. Scale = 1mm.

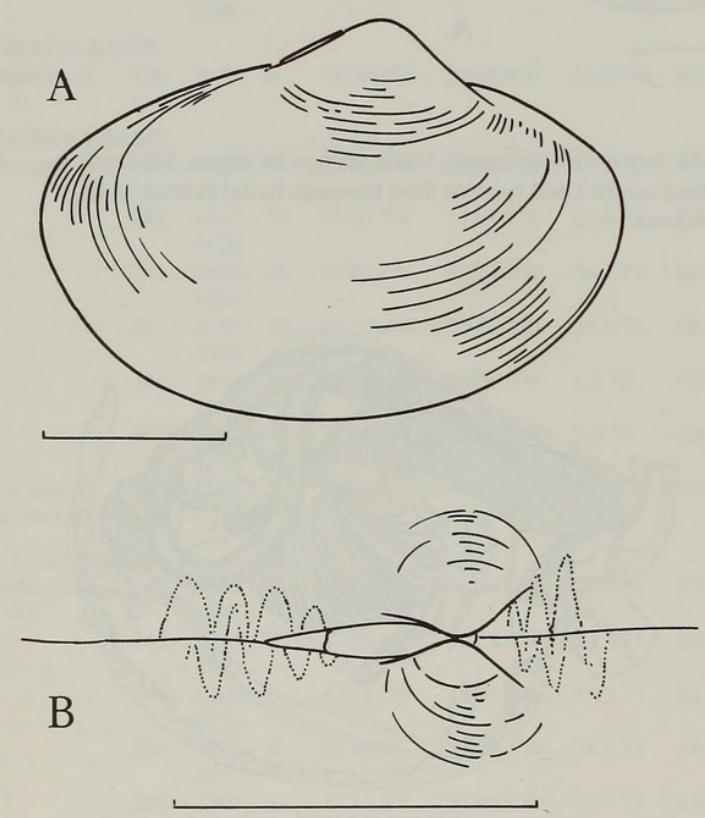

Fig. 16. *Neilonella whoii.* **a**, right lateral view of shell of elongate form, from Atlantis II station 242 from the Argentine Basin, in right lateral view and **b**, detail of the umbonal region of the same shell in dorsal view. Scales = 1 mm.

Family Nuculanidae Adams and Adams 1858

A recent definition of the family is given by Allen, Sanders and Hannah (1995).

Subfamily **Ledellinae** Allen and Sanders 1982

The subfamily is defined by Allen and Hannah (1989) and comprises two genera, *Ledella* and *Tindariopsis*.

Genus ***LEDELLA*** Verrill and Bush 1897

TYPE SPECIES. *Ledella bushae* Warén 1978. SD – Warén 1981.

Shell small, short, robust, surface matt, concentric sculpture, in some species scattered incomplete radial striae, usually rostrate, single postero-dorsal ridge in some species, postero-ventral margin very slightly sinuous, ventral margin in older specimens maybe flattened, anterior and posterior hinge teeth series separated by edentulous space bearing short internal amphidetic ligament (resilium) which may be restricted to dorsal portion of hinge plate, outer layer of ligament visible externally and maybe extended anteriorly and posteriorly for a short distance, hind gut with various configurations.

Genus ***TINDARIOPSIS*** Verrill and Bush 1897

TYPE SPECIES. *Malletia (Tindaria) agatheda* Dall 1889. OD.

Shell veneriform, matt surface, concentric sculpture, umbo large, short rostrum defined by slight radial ridge and furrow, postero-ventral margin slightly sinuous, anterior and posterior hinge teeth separated by very small edentulous space, internal ligament small, close to shell margin, external ligament robust, amphidetic.

Ledella acinula (Dall 1890)

TYPE SPECIMEN. Holotype USNM 95438.

TYPE LOCALITY. U.S. Fish Commission Steamer 'Albatross' Sta. 2754, 11°40'N 58°33'W, East of Tobago, 1609m.

CITED SPECIMENS. BMNH 1995047

Malletia (Tindaria) acinula Dall, 1890, 253, pl.XIII, fig.4.
Tindaria acinula Verrill and Bush 1898, 881.
'Tindaria' acinula Sanders and Allen 1977, 55, figs 44, 45.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
BRAZIL BASIN							
Atlantis II 31	167 1007	943–	1	07°58.0'S	34°28.0'W	20.2.67	ES
GUYANA BASIN							
Knorr 25	293	1456–1518	2	08°58.0'N	54°04.3'W	27.2.72	ES
	295	1000–1022	4	08°01.9'N	54°16.4'W	28.2.72	ES
	299	1942–2076	108	07°55.1'N	55°42.0'W	29.2.72	ES
WEST EUROPEAN BASIN							
Chain 106	330	4632	3	50°43.5'N	17°51.7'W	24.8.72	ES
J.Charcot Biogas VI	DS79	3226	15	46°30.4'N	10°27.1'W	26.10.74	DS
GUINEA BASIN							
J. Charcot Walda	DS28	1261	4	04°21.2'N	04°35.2'E	–.–.71	DS

The type specimen has been examined by us.

DISTRIBUTION. Found predominantly in tropical and subtropical latitudes, and southern temperate latitudes in the eastern Atlantic, at mid-slope to abyssal depths ranging from 943m to 4632m.

Many protobranch species with robust shells having subrostrate or ovate outlines and with concentric ridges and external ligaments, in the past have been referred to the genera *Malletia, Neilonella* or*Tindaria* (e.g. Dall, 1890). *Ledella acinula* is a case in point. Having addressed this problem in earlier papers (Sanders and Allen, 1977, 1985), and the present, we have been able to define more rigorously the families Tindariidae, Neilonellidae and Malletiidae.

Dall (1890) who described large specimens of *L. acinula* referred them to the subgenus *Tindaria.* Large specimens do show some resemblance to neilonellids and tindariids, but had Dall seen the shells of smaller specimens (Fig.18), he would have been unlikely to have made the error.

In our studies on *Tindaria* (Sanders and Allen, 1977) we re-examined and briefly redescribed *L. acinula,* and recognized that there was a problem in identification but deferred final judgment until we had made further comparative studies. Now that the Ledellinae have been reported upon (Allen and Hannah, 1989), the taxonomic relationship of this species is clear.

That *L. acinula* is siphonate clearly distinguishes it from members of the family Tindariidae. Although similar to the neilonellids in having an external amphidetic ligament, it differs in having a small but well-defined internal ligament and in being semi-rostrate with a slightly sinuous postero-ventral margin. A further significant difference is the form of the hind gut and the course that it takes within the body (Sanders and Allen, 1977). In *L. acinula* the hind gut is not particularly wide in diameter and is not restricted to the right side of the body (see below) having a configuration only known to occur in species of the subfamily Ledellinae e.g.*Ledella galatheae* Knudsen 1970, *L. oxira* (Dall 1927), *L. acuminata* (Jeffreys 1870)(Allen and Hannah, 1989).

SHELL DESCRIPTION (Figs 17 & 18)

Shell robust, posteriorly angulate, ornamented with concentric ridges particularly well-defined on ventral part of shell, straw-coloured periostracum; umbos relatively low in profile, inward facing, anterior to midline; posterior rostral region characteristically broad and blunt when seen in dorsal view; postero-dorsal shell margin almost straight, angulate at posterior limit of hinge plate - particularly so in smaller specimens, barely so in larger, posterior margin sharply rounded, ventral margin deeply curved, postero-ventral margin slightly sinuous, particularly in smaller specimens, antero-dorsal, anterior and antero-ventral margins form a smooth curve; posterior and anterior limits of shell at or slightly ventral to mid horizontal axis, ventral limit of shell posterior to vertical axis through umbo; hinge plate elongate, broad, anterior and posterior tooth series separated by relatively long edentulous space, chevron-shaped teeth acutely angled, up to 10 anterior and 12 posterior teeth depending on size of specimen; ligament amphidetic, external parts short, internal resilium small, rounded, occupying upper central part of hinge plate below umbo.The maximum total length of the present specimens is 6.0mm.

The shape of the shell changes significantly with growth (Figs 18 & 19). While the ratio of height to length remains more or less the same, the postero-umbonal length increases from 50% to 60% of the total length of the shell. With increasing size the postero-dorsal margin also becomes less angulate at the posterior limit of the hinge, also the postero-ventral margin becomes less sinuous, at most being somewhat flattened.

INTERNAL MORPHOLOGY

This has been described and illustrated by us in our earlier studies on the family Tindariidae (Sanders and Allen, 1977). Only essential features relating to the taxonomy need be mentioned.

Combined siphons are present and there is a well-developed

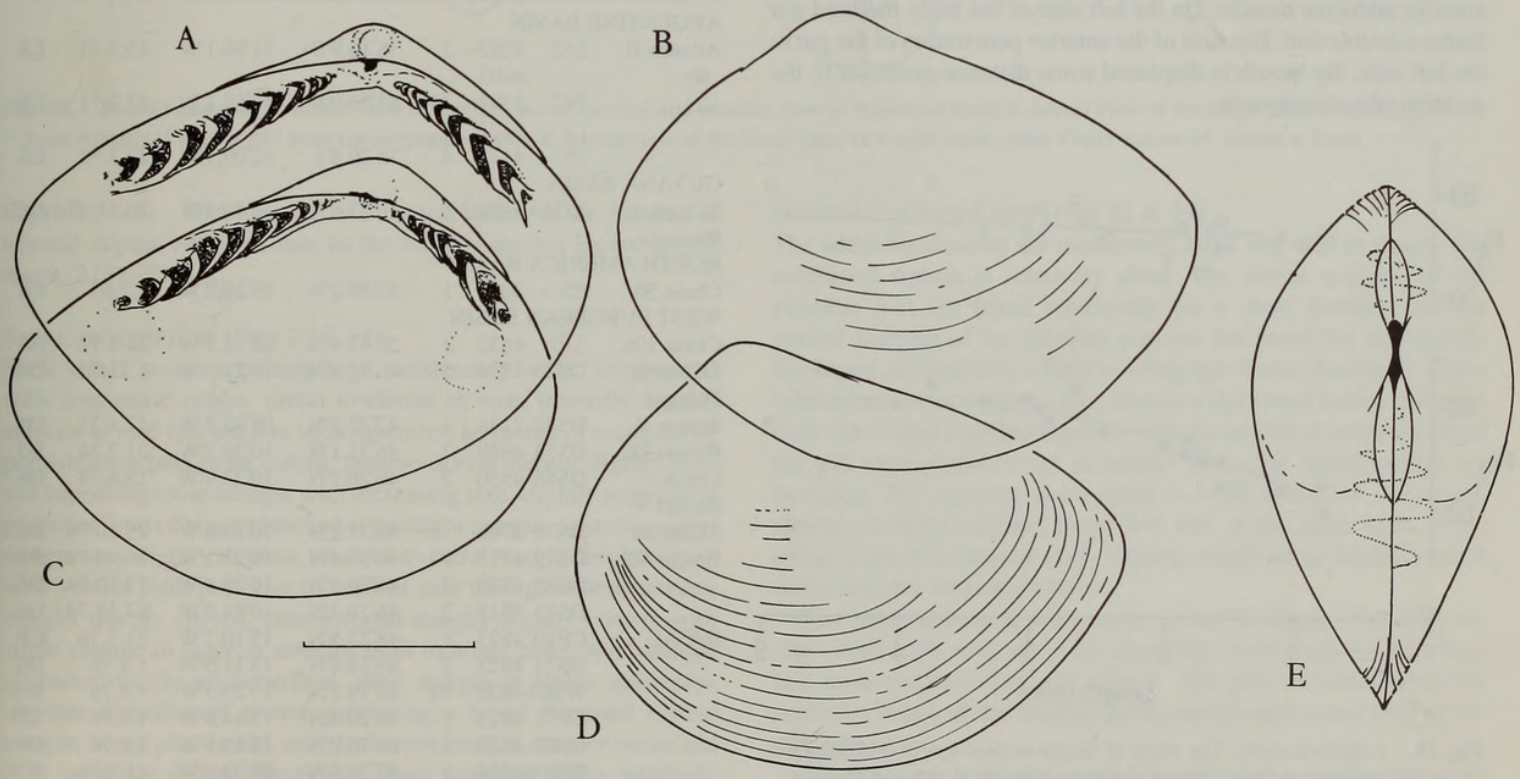

Fig. 17. *Ledella acinula.* **a & b**, internal and external views of a left valve, from the type locality Albatross station 2754, USNM 95438; c, internal view of left valve of specimen, from Atlantis II station 167 from the Brazil Basin; **d & e**, lateral view of left side and dorsal view of a shell, from Knorr station 299 from the Guyana Basin. Scale = 1mm.

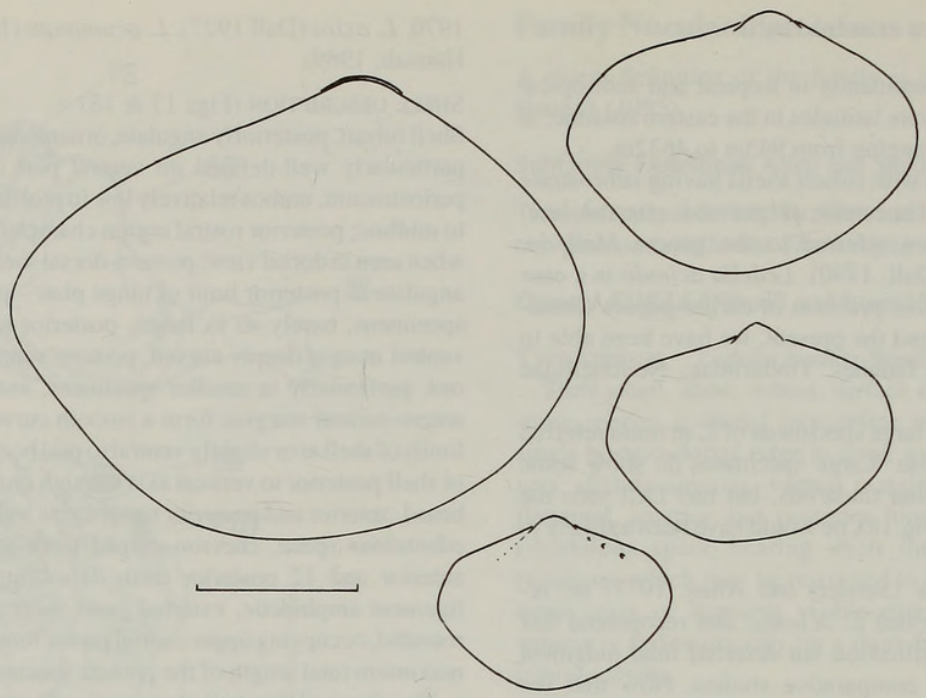

Fig. 18. *Ledella acinula.* Four shells in outline, from Knorr station 299 from the Guyana Basin, in right lateral view to illustrate changes in shape with increasing size. Scale = 1mm.

feeding aperture ventral to the siphonal embayment. The adductor muscles are relatively large, the anterior ovate and the posterior more circular in cross section. The anterior sense organ lies far anterior, ventral to the anterior adductor. The palps and gills are moderate in size with relatively few ridges (up to 15) and plates (up to 17) respectively. The foot has a well-defined neck, this is probably related to the relatively large height of the shell. There is a large 'byssal' gland present in the heel of the foot. The hind gut first makes a single loop on the right side of the body before passing to the left side of the body between the oesophagus and the inner face of the anterior adductor muscle. On the left side of the body the hind gut forms a double coil. Because of the anterior penetration of the gut to the left side, the mouth is displaced some distance posterior to the anterior adductor muscle.

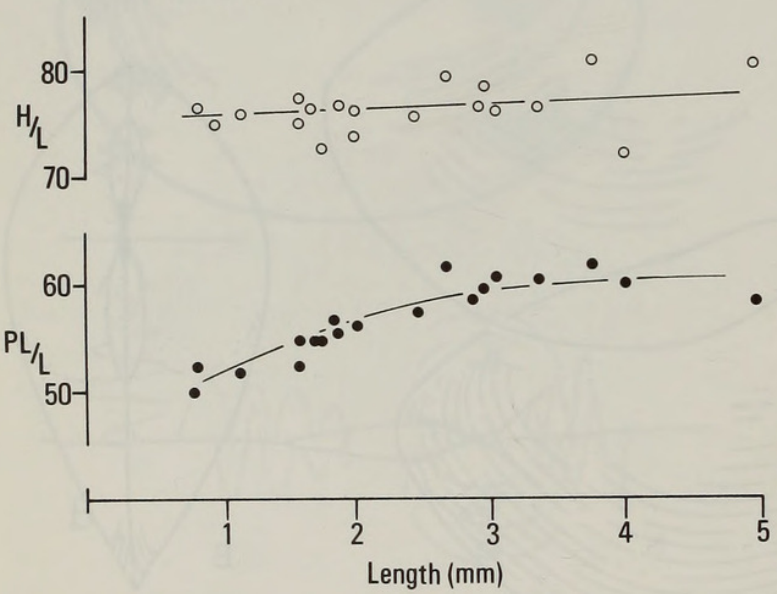

Fig. 19. *Ledella acinula.* The ratios of height to total length (H/L)(open circles) and post-umbonal length to total length (PL/L)(closed circles) plotted against total length to show changes in shell proportions with increasing length. Specimens from Knorr station 299 from the Guyana Basin.

Ledella aberrata (new species)

TYPE SPECIMEN. Holotype BMNH 1995045; paratypes BMNH 1995046.

TYPE LOCALITY. Chain cruise 60, station 247, Argentine Basin, 43°33.0'S 48°58.1'W, 5208–5223m

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
ARGENTINE BASIN							
Atlantis II 60	242	4382–4402	2	38°16.9'S	51°56.1'W	13.3.71	ES
	247	5208–5223	34	43°33.0'S	48°58.1'W	17.3.71	ES
	252	4435	4	38°29.8'S	52°09.1'W	22.3.71	ES
GUYANA BASIN							
J.Charcot Biovema	KG13	5100	1	10°47.6'N	42°40.4'W	20.11.77	KG
NORTH AMERICA BASIN							
Chain 50	85	3834	1	37°59.2'N	69°26.2'W	5.7.65	ES
WEST EUROPEAN BASIN							
Chain 106	330	4632	3	50°43.4'N	17°51.7'W	24.8.72	ES
J.Charcot Polygas	DS23	4734	5	46°32.8'N	10°21.0'W	1.11.72	DS
Biogas II	DS32	2138	1	47°32.2'N	08°05.3'W	17.4.73	DS
Biogas IV	DS54	4659	7	46°31.1'N	10°29.2'W	21.2.74	DS
Cryos Biogas V	DS68	4550	2	46°26.7'N	10°23.9'W	19.6.74	DS
J.Charcot Biogas VI	DS78	4706	18	46°31.2'N	10°23.8'W	25.10.74	DS
	DS79	4715	17	46°30.4'N	10°27.1'W	26.10.74	DS
	DS80	4720	3	46°29.5'N	10°29.5'W	27.10.74	DS
	DS81	4715	2	46°28.3'N	10°24.6'W	27.10.74	DS
INCAL	CP10	4823	1	48°25.5'N	15°10.7'W	31.7.76	CP
	DS11	4823	2	48°18.8'N	15°11.5'W	1.8.76	DS
	WS03	4829	18	48°19.2'N	15°23.3'W	1.8.76	WS
	CP11	4823	1	48°20.4'N	15°14.6'W	1.8.76	CP
	OS02	4829	1	48°19.2'N	15°15.9'W	2.8.76	OS
	WS10	4354	1	47°27.3'N	09°39.9'W	11.8.76	WS
CAPE BASIN							
J.Charcot Walvis	DS05	4560	2	33°20.5'S	02°34.9'E	30.12.78	DS

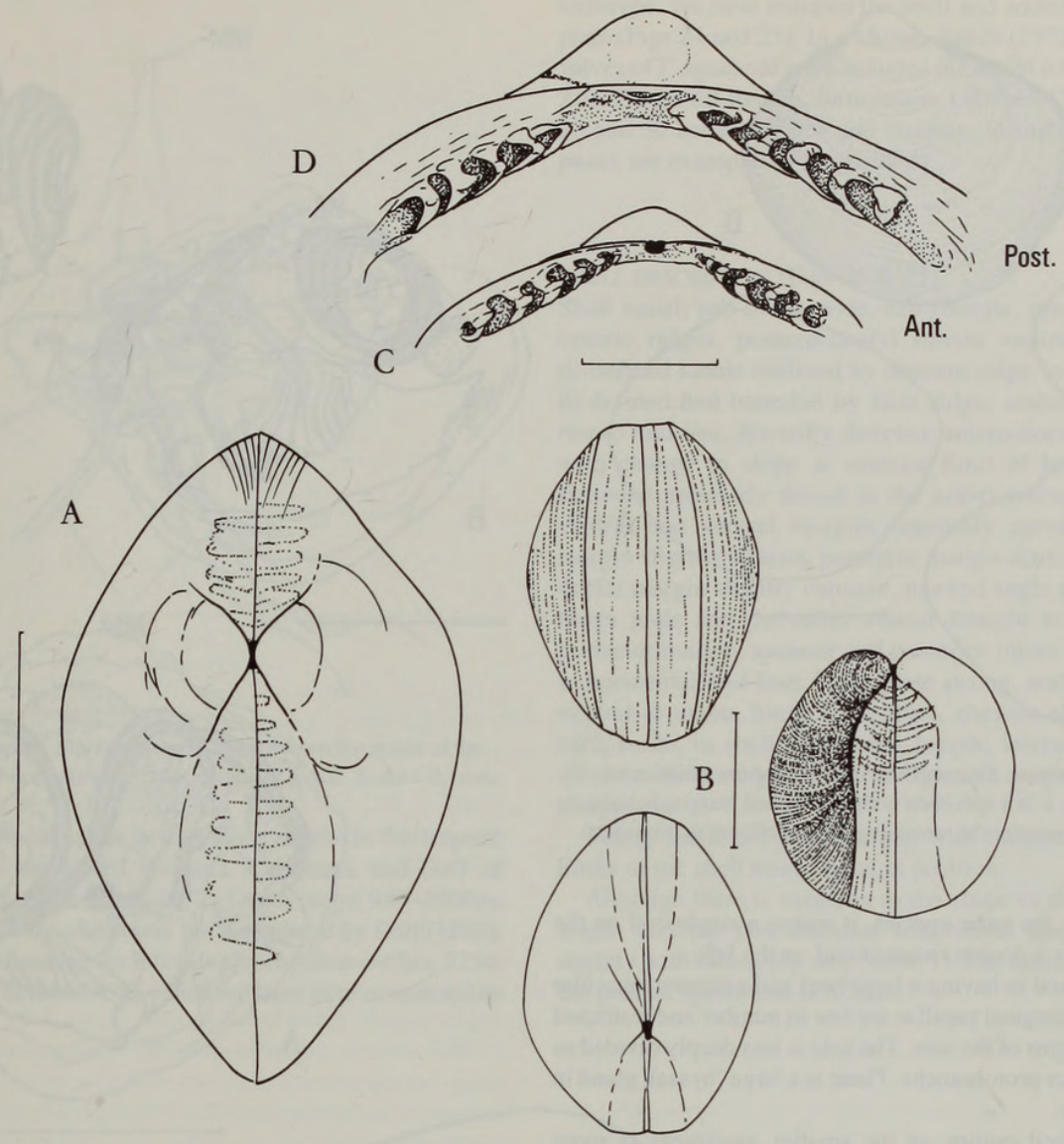

Fig. 20. *Ledella aberrata.* **a**, dorsal view of shell; **b**, dorsal, ventral and anterior view of thickened shell; **c**, lateral view of the hinge plate of a left valve, all from Atlantis II station 247 from the Argentine Basin; **d**, lateral view of the hinge plate of a right valve, from Chain station 85. Scales = 1mm.

DISTRIBUTION. In temperate and tropical basins of the Atlantic at abyssal depths >4000m, rare in the North America Basin. Depth range, 2138–5223m.

SHELL DESCRIPTION (Figs 20 & 21)
Shell small, ovate, relatively high, moderately wide, ornamented with concentric ridges; umbo moderate in size, inwardly turned, anterior to mid-line but less so in juveniles; no lunule or escutcheon; periostracum pale straw colour; postero-dorsal margin slightly convex becoming more straight with increasing size, slightly angulate at posterior limit of hinge plate and at posterior margin, postero-ventral margin very slightly sinuous, otherwise ventral margin deeply curved with ventral limit posterior to vertical axis through umbo, anterior margin sharply curved, antero-dorsal margin slightly convex with slight change in slope at anterior limit to hinge plate; shell outline characteristically asymmetrical, shell margin in larger specimens changes direction of growth producing a broad flattened ventral margin; hinge plate broad, up to 6 chevron teeth in anterior series and 7 in posterior series, edentulous space between series relatively broad; ligament small, amphidetic, internal part restricted to upper part of hinge plate, external part extremely short situated below umbo. The maximum length of the present specimens is 2.6mm.

INTERNAL MORPHOLOGY (Figs 22 & 23)
The adductor muscles are moderately large and oval in shape. The combined siphon is relatively short. The dorsal margins of the exhalent part are fused proximally for a short distance and the ventral margins of the inhalent part are not fused but are slightly thickened and probably adhere in living specimens. Internally where inhalent and exhalent parts join, there is a thickened median ridge on each side which together together with the posterior continuation of the gill axes probably act as guides when the faecal pellets are extruded. The siphonal embayment is small and there is a small, slender, tentacle attached to the left side at the inner limit of the embayment. The anterior sense organ is small and is situated ventral to the anterior adductor muscle.

The palps are small with up to 11 broad ridges. The gills are also small each with up to 11 plates the most posterior of which lies some distance from the siphon. The gills are attached to the posterior limits of the median guides by slender extensions of the gill axis.

The hind gut is greatly extended and takes a similar but more complex course to that described for *L. acinula*. Like the latter, the hind gut passes from the right side of the body to the left immediately posterior to the anterior adductor muscle and returns by the

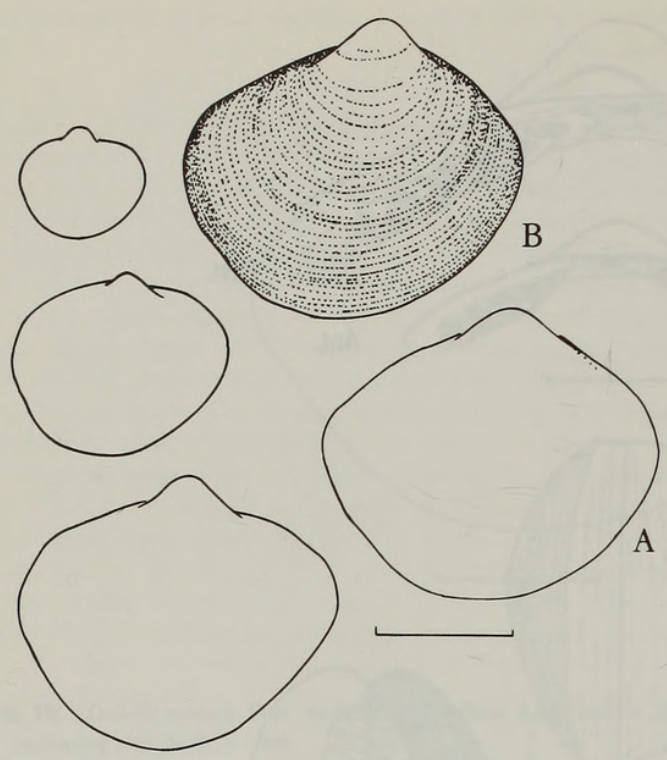

Fig. 21. *Ledella aberrata.* Five shells in outline to show variation in shape with growth. a, is a specimen with a thickened margin; b, has a slightly thickened margin; the remaining three shells are unthickened. Scale = 1mm.

same route. Unlike the latter species, it makes a single coil on the right side as well as a double twinned coil on the left.

The foot is unusual in having a large heel and a narrow muscular anterior part. The marginal papillae are few in number and restricted to the anterior margins of the sole. The sole is less deeply divided as compared with other protobranchs. There is a large 'byssal' gland in the heel of the foot.

Although the shell outline of the smaller specimens is more characteristic of the genus *Ledella* than in larger mature specimens, the general shell outline of *L aberrata* (and *L. acinula*) is much deeper and more ovate than in other described species (Figs 18 & 21) nor is it markedly rostrate. Despite this, the characters place them in the Ledellinae (Allen and Hannah, 1989) and we see no reason for erecting another genus.

Apart from *L. aberrata,* only two species of protobranchs, have been reported as exhibiting a change in shell growth to produce a flattened shell margin (Fig. 20). Both are ledellids, namely *L. ultima* (Smith 1885) and *L. solidula* (Smith 1885) (Allen and Hannah, 1989). Like *L. aberrata* these two latter species also have elongate hind guts. The hind gut of *L. solidula* is very similar to that of *L. aberrata* in having double twinned coils to the left side of the body (Fig.22), although it does not have an additional single coil to the right as does the present species. The type of course taken by the hind gut in *L. acinula* is also found in other species of *Ledella* (e.g. *L. oxira*) (Allen and Hannah, 1989).

We named this species after the familiar appelation to which it was referred during our original analysis of the samples.

Tindariopsis agatheda (Dall 1889)

TYPE SPECIMEN. USNM 95437, lectotype here designated.

TYPE LOCALITY. U.S.Fish Commission Sta. 2754, east of Tobago, 11°40'N 58°33W, 1609m.

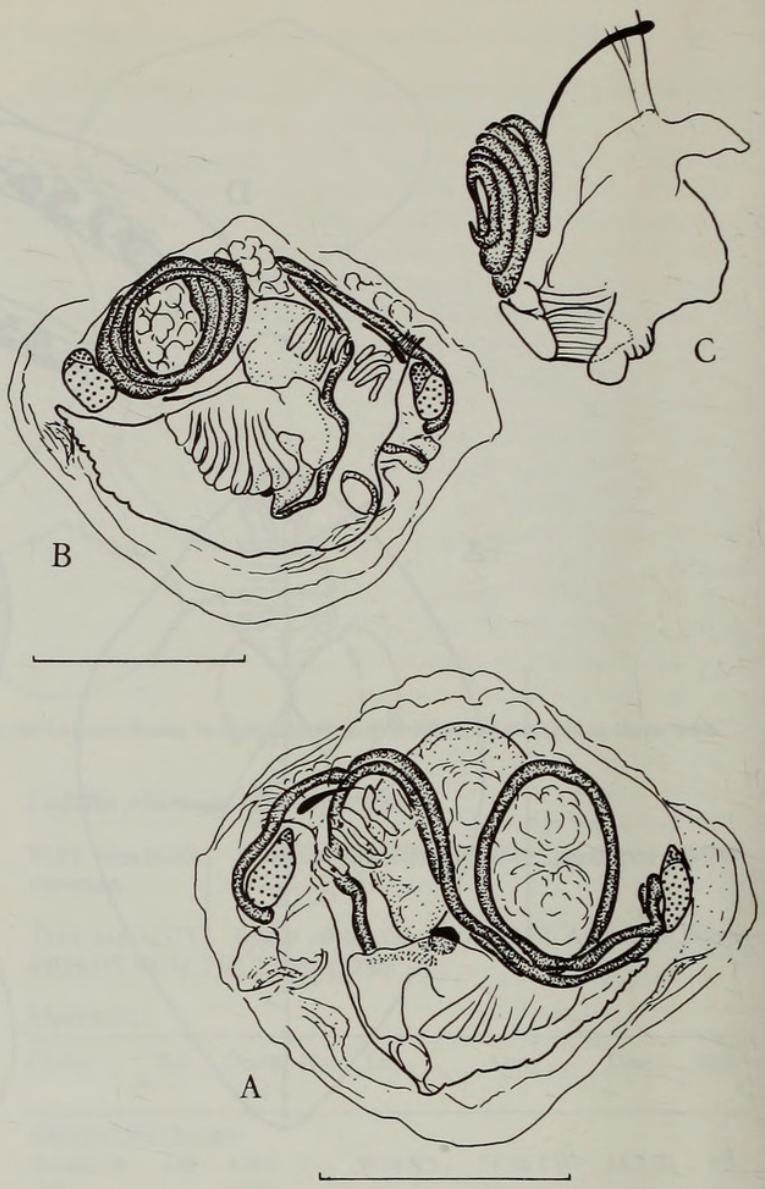

Fig. 22. *Ledella aberrata.* Internal morphology as seen in **a**, right lateral view, **b**, left lateral view and **c**, left ventro-lateral view. For identification of the parts see text-figure 7, p. 106. Scales = 1mm.

CITED SPECIMEN. BMNH 1995062.

Malletia (Tindaria) agatheda Dall 1890, 252, pl. xiii, fig. 10.
Tindaria (Tindariopsis) agatheda Verrill and Bush 1897, 59.
Saturnia (Tindariopsis) agatheda McAlester 1969, N235.
Tindariopsis agatheda James 1972, 98, figs 60–62.
Neilonella (Tindariopsis) agatheda Laghi 1986, 190, pl.8, figs 2–6.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
BRAZIL BASIN							
Atlantis II 31	167	943–1007	1	07°58.0'S	34°28.0'W	20.2.67	ES
GUYANA BASIN							
Knorr 25	293	1456–1518	14	08°53.1'N	54°04.3'W	27.2.72	ES
	299	1942–2067	8	07°55.1'N	55°42.0'W	29.2.72	ES
	301	2487–2500	7	08°12.4'N	55°50.2'W	1.3.72	ES

The type specimen has been examined by us.

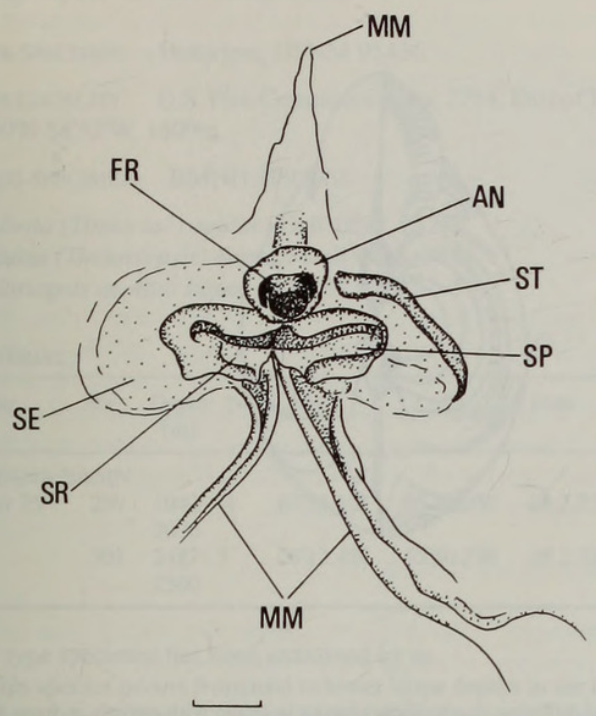

Fig. 23. *Ledella aberrata.* Siphonal region, as seen from the inside of the mantle cavity. See abbreviations to the text-figures p. 102. Scale = 0.1mm.

This species occurs at upper to mid slope depths in the tropical western Atlantic in the Brazil, Guyana, Caribbean and Gulf of Mexico Basins (Dall, 1889; James 1972). Depth range; 943–2500m.

The holotype for *T. agatheda* was not designated by Dall (1890), nevertheless he did illustrate the left valve from Albatross Sta. 2754, 11°40'N 58°33'W (USNM 95437) which we have here nominated as lectotype. We have redrawn the shell and added detail of the hinge plate (Figs 24 and 25). In addition, James (1972) reported that two valves of *T. agatheda* were included in USNM 63149 from Blake sta. 236, 2909m off Bequia, furthermore USNM 94326 from Blake stas 26 and 30 between Cuba and Yucatan, identified by Dall as *Leda pusio,* are examples of *T. agatheda.*

SHELL DESCRIPTION (Figs 24 & 25)

Shell small, sub-ovate, wide, sub-rostrate, ornamented with concentric ridges, postero-lateral furrow ventral to sub-rostrum, ill-defined lunule outlined by obscure ridge, escutcheon similarly ill-defined and bounded by faint ridge; umbo prominant, posterior to mid-line, inwardly directed; antero-dorsal margin concave, with change in slope at anterior limit of hinge plate, slightly flattened anteriorly dorsal to the anterior limit of shell, antero-ventral and ventral margins smoothly curved, postero-ventral margin slightly sinuate, posterior margin acutely angled, postero-dorsal margin slightly concave, marked angle at posterior limit of hinge plate and thereafter almost straight to form sub-rostrate posterior margin; anterior and posterior limits of shell are ventral to horizontal mid-line; hinge plate strong, with edentulous space ventral to umbo, hinge teeth stout, chevron-shaped, up to 12 in each series in shell 6mm total length; internal ligament small, close to shell margin, external ligament amphidetic, moderately short, stout.

Young shells are less rostrate, with the posterior and anterior limits of the shell more dorsal in position.

Although there is variation in the shape of the shell, the height/length and the post-umbonal length/total length ratios increase slightly with increasing size (Table 1). The maximum total length of the present specimens is 6.0mm.

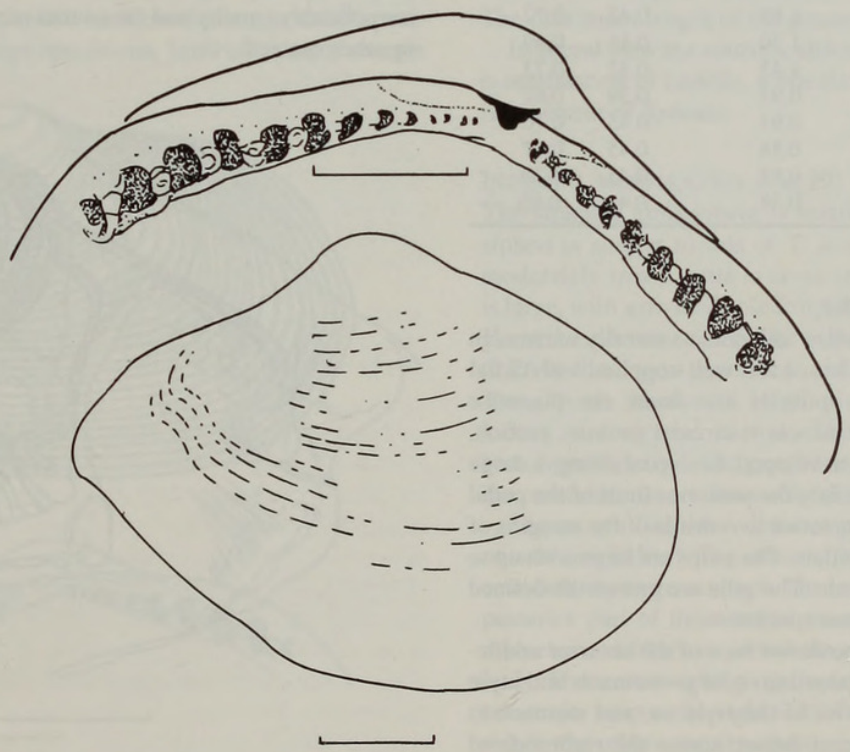

Fig. 24. *Tindariopsis agatheda.* External lateral view of the right valve of the lectotype and an internal view of the hinge plate of the same valve, from U.S.Fish Commission station 2754 East of Tobago, USNM 95437. Scales = 1mm.

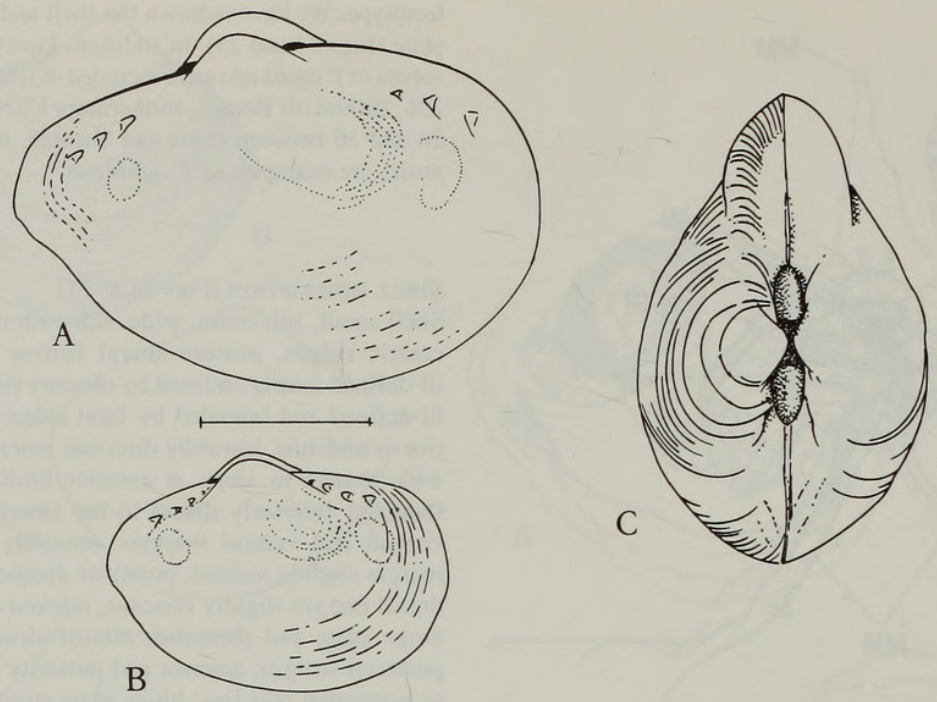

Fig. 25. *Tindariopsis agatheda.* External lateral views of right side of two specimens of differing size to show change in shape with growth. a, from Knorr station 301 and b, from Knorr station 293, both from the Guyana Basin; c, external dorsal view of a shell also from station 293. Scale = 1mm.

Table 1. Measurements and ratios of shell parameters of the sample from Knorr sta. 293.

Length (L) (mm)	Height (H) (mm)	Post-umbonal (PL) length (mm)	PL/L	H/L
6.00	4.95	3.00	0.50	0.83
5.60	3.95	2.65	0.47	0.71
5.00	3.65	2.20	0.44	0.73
4.90	3.65	2.05	0.42	0.75
4.70	3.15	1.95	0.42	0.67
4.50	3.10	1.85	0.41	0.69
4.45	3.20	1.85	0.42	0.72
3.70	2.55	1.70	0.46	0.69
3.45	2.50	1.45	0.42	0.73
2.35	1.58	0.93	0.39	0.67
2.05	1.43	0.93	0.45	0.70
1.95	1.30	0.88	0.45	0.67
1.83	1.28	0.83	0.45	0.70
1.10	0.88	0.48	0.43	0.80

INTERNAL MORPHOLOGY (Fig.26)

The siphonal embayment is shallow and dorso-ventrally narrow. In contrast, the feeding aperture is broad and well-supplied with radial pallial muscles. The adductor muscles are small, the posterior muscle is oval and the anterior muscle is circular in cross section. The foot is large with a well-developed heel containing a large 'byssal' gland. The gland opens into the posterior limit of the pedal groove via a small papilla. The anterior two-thirds of the margins of the divided sole are broadly papillate. The palps are large with up to 25 ridges in the largest specimens. The gills are narrow ill-defined with about 16 plates in the largest specimens.

The mouth lies close to the posterior face of the anterior adductor muscle. The oesophagus opens into a large stomach and style sac. The hind gut passes posterior to the style sac and stomach to the dorsal side of the viscera and thence across the right side of the body where it forms 8 coils before returning along the same path to the dorsal side of the viscera and from there through the heart and then dorsal to the posterior adductor muscle to the anus. Usually not more than six coils are visible, the others being overlain by those to the outside of them. The form of the hind gut is derived by 4 complete turns of the closely parallel anterior and posterior lengths of the hind gut on the right of the body. This particular disposition of the hind-gut is to be found in other ledellids (e.g. *L. ultima*) and yoldiellids (e.g. *Y. ella* Allen, Sanders and Hannah 1995) (Allen and Hannah, 1989; Allen, 1992; Allen, Sanders and Hannah, 1995).

The nervous system is similar in its arrangement to that of other deep-sea protobranchs, however the cerebral and visceral ganglia are noticably smaller and the commissures much finer than observed in other species.

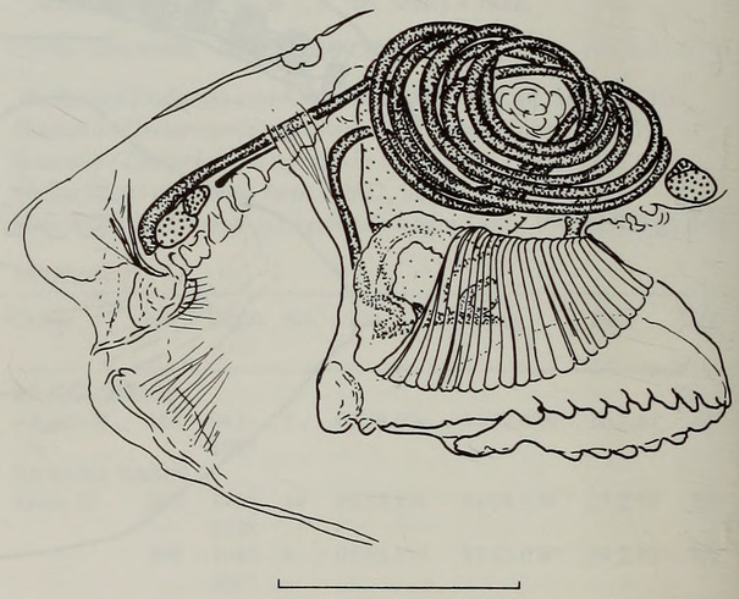

Fig. 26. *Tindariopsis agatheda.* Internal morphology as seen from the right side of a specimen from Knorr station 293. For identification of the parts see text-figure 7, p. 106. Scale = 1mm.

Tindariopsis aeolata (Dall 1890)

TYPE SPECIMEN. Holotype, USNM 95436.

TYPE LOCALITY. U.S. Fish Commission Sta. 2754, East of Tobago, 11°40'N 58°33'W, 1609m.

CITED SPECIMEN. BMNH 1995061.

Malletia (Tindaria?) aeolata Dall 1890, 252.
Tindaria (Tindariopsis) aeolata Dall 1898, 582.
Tindariopsis aeolata James 1972, 97, figs 57–59.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
GUYANA BASIN							
Knorr 25	299	1942–2076	4	07°55.1'N	55°42.0'W	29.2.72	ES
	301	2487–2500	5	08°12.4'N	55°50.2'W	29.2.72	ES

The type specimen has been examined by us.

This species occurs from mid to lower slope depths in the tropical western Atlantic in the Guyana and Caribbean Basins and the Gulf of Mexico. Depth range: 1609–3466m.

SHELL DESCRIPTION (Figs 27 & 28)
Shell small, subquadrate, rostrate, ornamented with marked concentric ridges; periostracum pale yellow; umbos moderately large, posterior to midline (post-umbonal length 45–48% of total length), facing inwards, slightly separated by external ligament; distally antero-dorsal shell margin horizontal, then curves smoothly and steeply to anterior margin, postero-ventral margin sinuous, ventral margin somewhat flattened, postero-dorsal distal margin slopes gently to limit of hinge plate then curves sharply to rostral point, latter rounded and somewhat eroded in large specimens, more pointed in smaller, rostrum in mid horizontal plane in small specimens and dorsal to it in large specimens, limit of anterior margin ventral to the mid horizontal plane; hinge plate stout, small edentulous space between tooth series, 9 chevron-shaped teeth in anterior series and 10 in posterior series in largest specimens; ligament amphidetic, external except for small resilifer at margin ventral to umbo, external part thickened, particularly so in large specimens. The maximum length of the present specimens is 5.8mm.

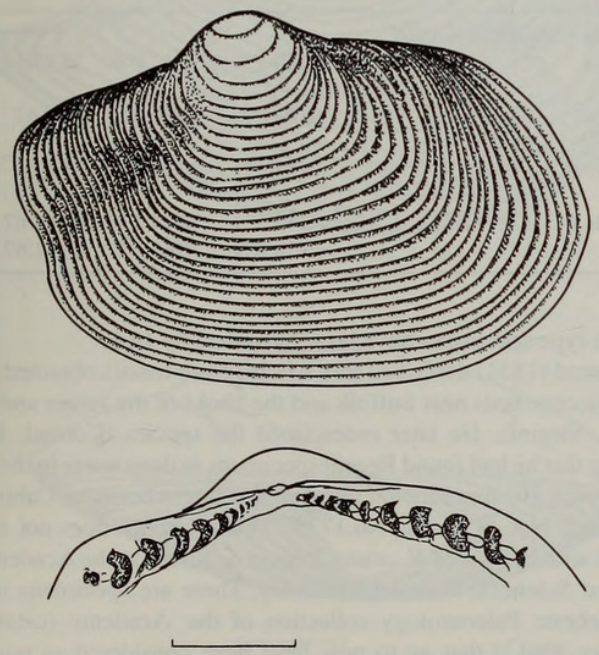

Fig. 27. *Tindariopsis aeolata.* External lateral view of the right valve and the hinge plate of the left valve of the holotype, from U.S. Fish Commission station 2754, USNM 95436. Scale = 1mm.

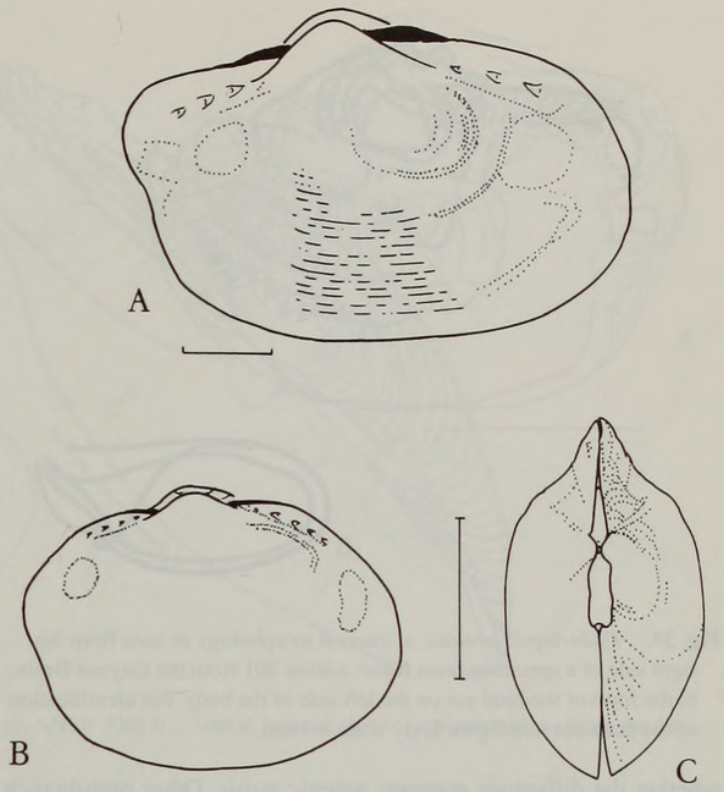

Fig. 28. *Tindariopsis aeolata.* External lateral views of the right side of shells of differing size to change in shape with growth. a, from Knorr station 301 and b, from Knorr station 299 from the Guyana Basin; c, external dorsal view of a shell also from Knorr station 299. Scales = 1mm.

In lateral view the rostrum, although dorsal to mid horizontal line, is reminiscent of *Ledella*, while the robust external ligament is more reminiscent of *Spinula*.

INTERNAL MORPHOLOGY (Fig.29)
The siphonal embayment is relatively shallow and the contained siphon is similar to that of *T. acinula.* The adductor muscles are moderately small, ovate in cross-section and equal in size. The foot is large, with a divided sole fringed with large papillae. The 'byssal' gland is moderate in size. The palps are very large with many ridges (c 26 in the largest specimen) and the palp proboscides are broad. The gills are small with 11 gill plates in the largest specimen. The kidney is long and narrow. The nervous system is of typical protobranch design. The ganglia are relatively large and, in contrast, the commissures are unusually slender.

The mouth lies some distance posterior to the anterior adductor muscle (see below). The oesophagus opens on to the anterior face of a moderately large stomach. The latter lies almost vertical within the posterior part of the visceral mass. The hind gut is very small in diameter and takes an extraordinarily complex course through the body. There are two loops to the left side of the body (Fig.29B) and one major loop to the right side of the body, all three pass from one side to the other ventral to the umbo. There is also a complex series of loops anterior and to the right of the stomach. This morphology has not been encountered before in the protobranch bivalves and is very different from that seen in *T. agatheda*. Yet, it is debateable

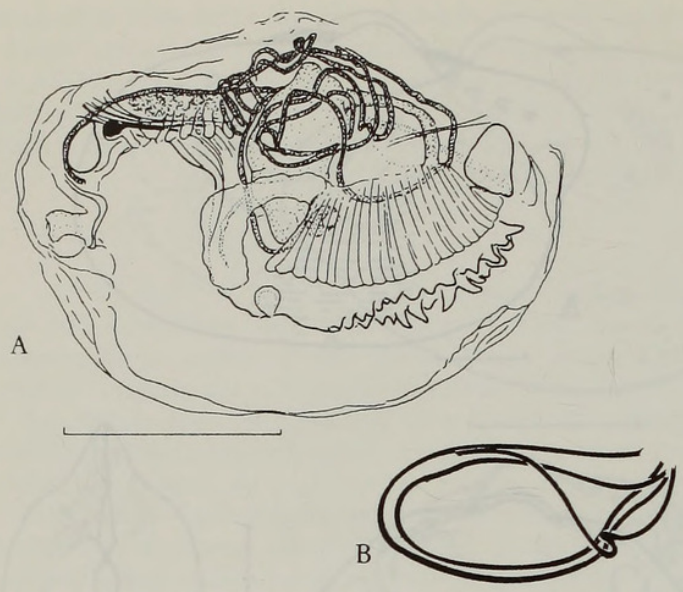

Fig. 29. *Tindariopsis aeolata.* a, internal morphology as seen from the right side of a specimen from Knorr station 301 from the Guyana Basin; b, the form of the hind gut on the left side of the body. For identification of the parts see text-figure 8, p.. Scale = 1mm.

whether the difference warrents generic status. Other protobranch genera show an array of hind gut morphologies (e.g. Yoldiellidae, Allen, 1992; Allen, Sanders and Hannah, 1995) which we believe relate to changes in the benthic food resource as depth increases. For this reason we are reluctant to erect a new genus when in other respects *T. aeolata* is clearly within the genus *Tindariopsis.*

Subfamily **Nuculaninae** Allen and Sanders 1982

The subfamily is defined by Allen and Hannah (1986) and comprises three genera *Nuculana, Propeleda* and *Adrana.*

Genus ***NUCULANA*** Link 1807

TYPE SPECIES. *Arca rostrata* Gmelin 1791 = *Arca pernula* Müller 1779. OD.

Shell robust, moderately elongate, concentric sculpture, occasionally with radial ribs, slightly rostrate, usually bicarinate; umbo anterior; postero-dorsal margin straight or somewhat concave, posterior margin may be slightly sinuous; escutcheon present; no internal ridge from umbo to posterior margin; hinge moderately robust, teeth chevron-shaped; ligament small, for most part internal, usually amphidetic and vertical, sometimes posteriorly oblique.

Genus ***PROPELEDA*** Iredale 1924

TYPE SPECIES. *Leda ensicula* Angas 1877. OD.

Shell very elongate, thin, glossy, concentric sculpture may be ill-defined, 3/4 shell post-umbonal, usually with two marked carinae from umbo to upper and lower limit of rostrum, posteriorly truncate; umbo small; postero-dorsal margin concave, postero-ventral margin not sinuous; internal ridge usually from umbo, skirts ventral margin of posterior adductor to posterior margin, second ridge may be present from hinge plate to rostral margin; hinge plate slender, hinge teeth chevron-shaped, one or both arms of the chevron may be elongate, anterior tooth series curve round the outer margin of the anterior adductor, posterior series extends posterior to adductor; ligament in large part internal, opisthodetic and oblique.

Genus ***ADRANA*** Adams & Adams 1858

TYPE SPECIES. *Nucula lanceolata* Lamarck 1819. SD Stoliczka 1871.

Shell extremely elongate, slender, lanceolate, fragile, smooth or with fine concentric and sometimes oblique sculpture, without carinae, glossy; umbo almost central, barely raised; escutcheon elongate, flattened, narrow; postero-dorsal margin straight, antero-dorsal margin slightly convex, postero-ventral margin sinuous; hinge plate slender, hinge teeth fine, obtuse, chevron-shaped; chondrophore present; ligament internal, amphidetic.

Nuculana acuta (Conrad 1831)

TYPE SPECIMEN. Lectotype here designated, chosen from ANSP 30613, remainder of lot designated paralectotypes.

CITED SPECIMEN. BMNH 1995055.

TYPE LOCALITY. Tertiary fossil beds, near Suffolk, Virginia.

Nucula acuta Conrad 1831, 32, pl.6, fig.1.
Nucula cuneata Sowerby 1833, 198.
Nucula carinata H.C.Lea 1843, 163, (non M'Coy 1844).
?Leda jamaicensis d'Orbigny 1846, 263, pl.XXIV, figs 30–32.
?Leda inornata A.Adams 1856, 48.
Leda unca Verrill 1880, 401, (?non Gould 1862).
Leda acuta Dall 1886, 251, pl.7, figs 3a, 3b and 8.
Nuculana acuta Morris 1951, 7, pl.6, fig.2.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
NORTH AMERICA BASIN							
Atlantis 264	C1	97	2+2v	40°20.5'N	70°47.0'W	25.5.61	AD
Atlantis 283	Slope sta.2	200	8+6v	40°01.8'N	70°42.0'W	28.8.62	AD
Atlantis II 24	114	197	8	40°04.1'N	70°27.8'W	15.8.66	ES
Atlantis II 40	172	119	7+2v	40°12.3'N	70°44.7'W	27.11.67	ES
	173	123	4	40°10.8'N	70°43.6'W	28.11.67	ES

The type specimens have been examined by JAA.

Conrad (1831) described this species from fossils obtained from the Miocene beds near Suffolk and the banks of the James and York rivers, Virginia. He later redescribed the species (Conrad, 1845) adding that he had found Recent specimens in deep water in the Gulf of Mexico. His first account refers to specimens being in 'Cabinet of the Acad. Nat. Sciences, No.1738.' This reference does not correspond with any lot of *N. acuta,* Recent or fossil, in the Academy of Natural Sciences, Philadelphia today. There are specimens in the Invertebrate Paleontology collection of the Academy (catalogue number 30613) that up to now have been considered as possible syntypes of the species. The lot comprises 4 right valves, 3 left valves 1 left and 1 right broken valve, 1 intact shell, 1 shell with rostrum tip missing and 3 fragments. These specimens, labelled by

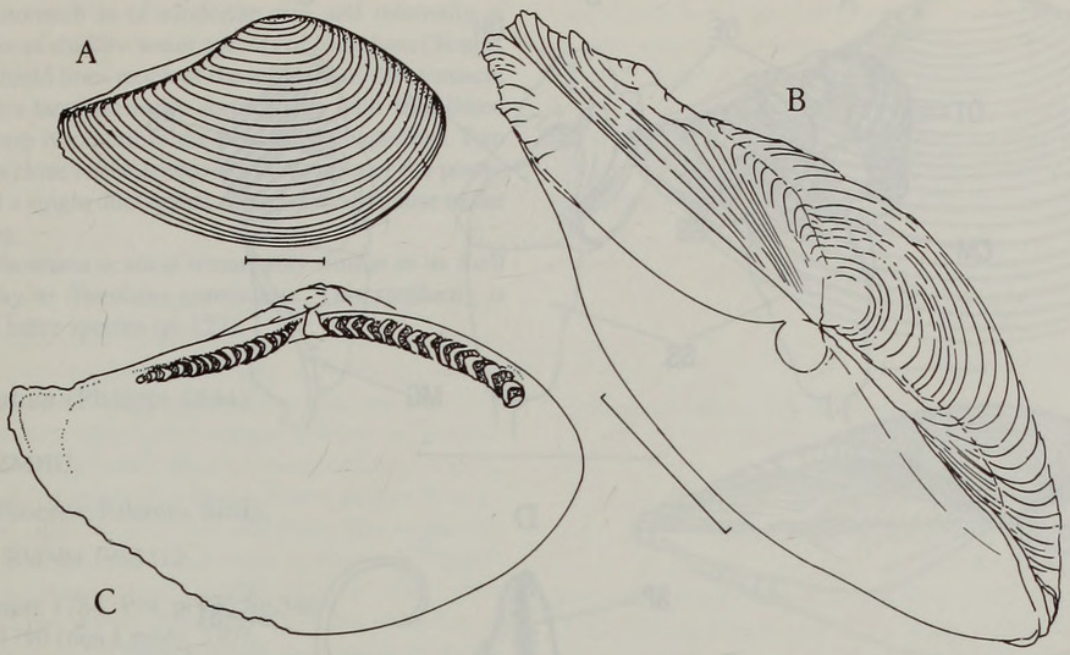

Fig. 30. *Nuculana acuta.* a & b, lateral and dorsal external views of the lectotype, ANSP 30613; c, lateral internal view of a paralectotype from the same lot. Scales = 1mm.

Conrad, may include those figured by him. Comparison with the figures (Conrad, 1831 and 1845) shows that it is impossible to say which, if any one, was figured nor is it possible to be absolutely certain that these are the specimens from which the original description was made, although we believe that they are. Thus, the intact shell from lot 30613 has been chosen as the lectotype, the remainder being paralectotypes.

Campbell (1993) listed *Leda jamaicensis* d'Orbigny 1846, *Leda inornata* A.Adams 1856 and *L.unca* Gould 1862 as synonyms of *N. acuta.* Verrill (1882) describes in detail differences that he found between *N. acuta* and *L.jamaicensis* and *L.unca* which cast doubt as to the synonymy, although Dall (1886) maintains the synonymy of *L. jamaicensis.* Similarly, we have doubts as to synonymy with *L.inornata* A.Adams which is a 'gibbose', 'fuscous', 'sulcate' species from New Guinea, Thus, although *Nuculana acuta* is a well-described species (e.g. Verrill 1882, 1884; Dall, 1886; Abbott, 1974) because there are closely related species in the Atlantic and elsewhere, we include a description here. It occurs off the East coast of North America, in the Caribbean Sea and off Brazil at depths from the outer shelf to lower slope depths, 97–2909m (James, 1972).

SHELL DESCRIPTION (Figs 30, 31)

Shell moderately large, elongate, somewhat inflated, rostrate, ornamented with deep concentric ridges flattened at the apex, rostral ridge from umbo to ventral limit of rostrum, very faint radial ridge from umbo to antero-ventral margin, yellow periostracum; lunule

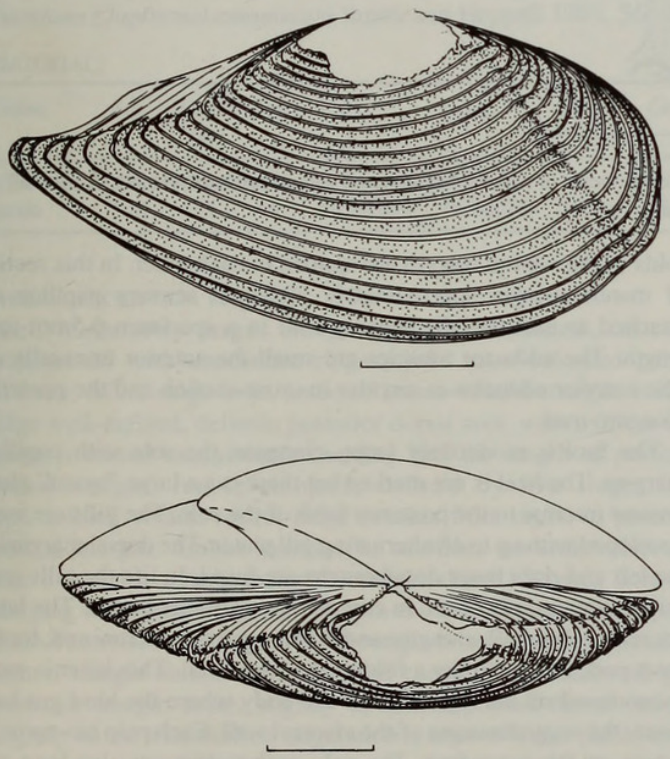

Fig. 31. *Nuculana acuta.* Lateral and dorsal external views of a shell, from Atlantis 283 station 2 from the North America Basin. Scales = 1mm.

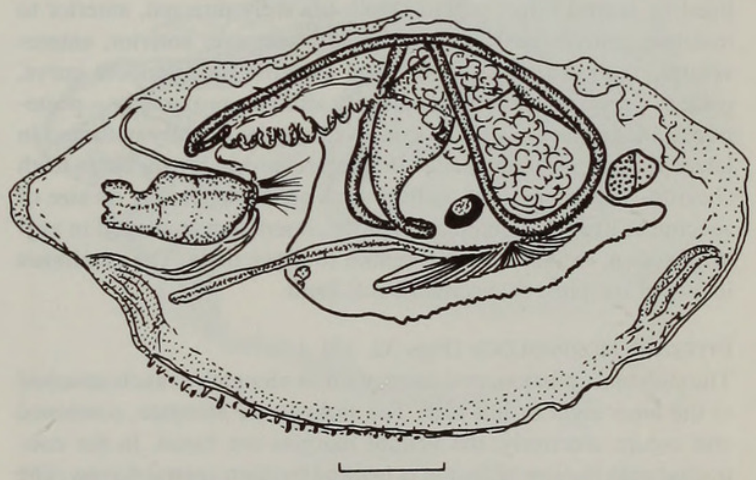

Fig. 32. *Nuculana acuta.* Internal morphology as seen from the right side of a specimen from Atlantis II station 197 from the North America Basin. For identification of the parts see text-figure 7, p. 106. Scale = 1mm.

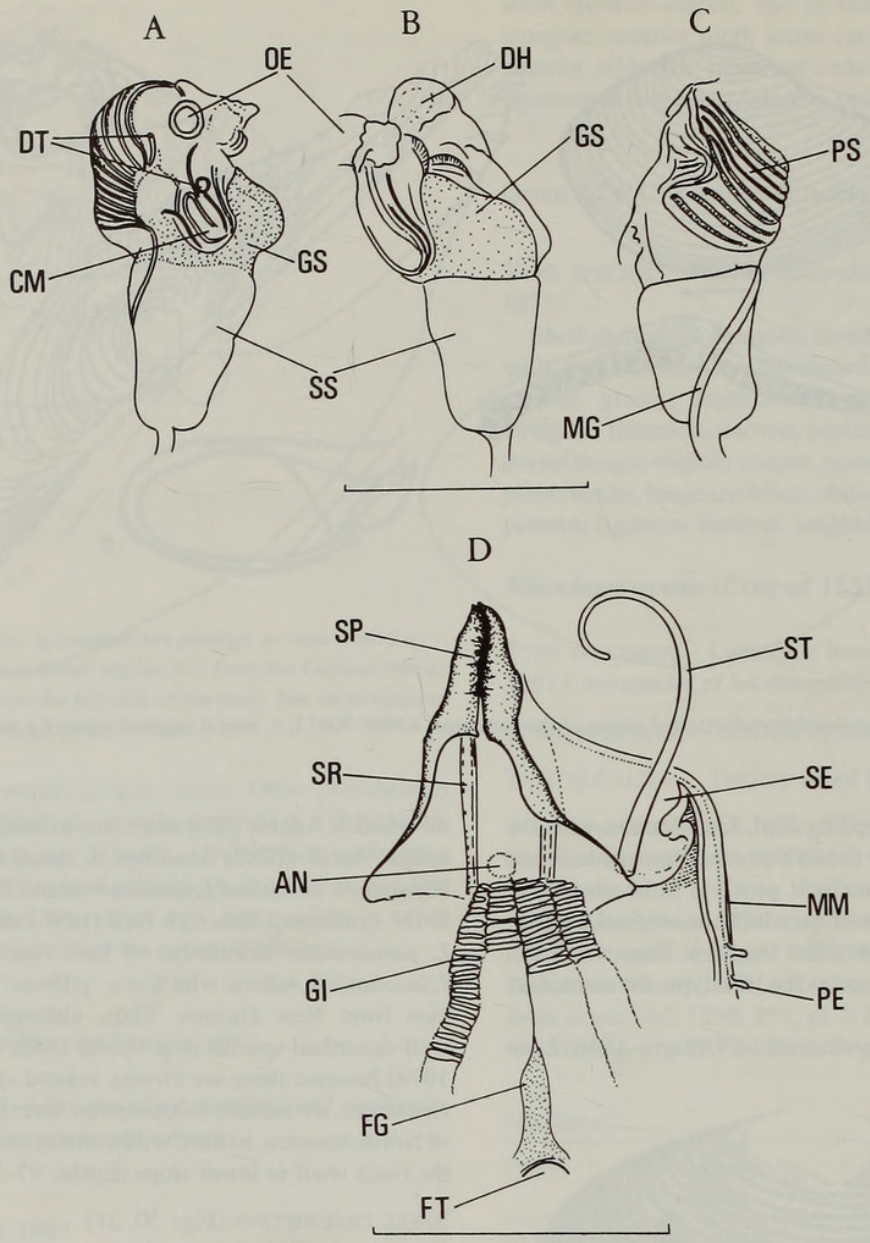

Fig. 33. *Nuculana acuta.* Internal morphology, a, anterior, b, left lateral & c, posterior views of a dissected stomach and combined style sac; d, ventral view of siphonal region. See abbreviations to text-figures on p. 102. Scales = 1mm.

broad, elongate, outlined with faint ridge, escutcheon broad, outlined by rostral ridge; umbos small, inwardly directed, anterior to mid-line; antero-dorsal margin broadly concave, anterior, antero-ventral, ventral and postero-ventral margins form smooth curve, postero-dorsal margin raised, distally straight, proximally – posterior to hinge plate – slightly concave, may be slightly upturned in larger specimens; hinge plate elongate, relatively broad, hinge teeth chevron-shaped, up to 18 teeth in each series depending on size of specimen; ligament small, amphidetic, internal pear-shaped in sagittal section, extends slightly ventral to hinge plate. The maximum length of the present specimens is 9.2mm.

INTERNAL MORPHOLOGY (Figs 32, 33)

The siphonal embayment is deep, with an elongate tentacle attached to the inner right or left side. The siphons are elongate, combined and except anteriorly, the ventral margins are fused. In the contracted state the line of fusion is marked by deep ventral furrow. The anterior sense organ is far anterior, situated at the point where the radial ridge meets with the shell margin. Between the feeding (ventral to the siphonal embayment) and the pedal gape, the inner folds of the ventral margin are applied to each other. In this section of mantle margin approximately 30 small sensory papillae are attached to each middle sensory fold in a specimen 6.5mm total length. The adductor muscles are small the anterior unusually so. The anterior adductor is circular in cross-section and the posterior elongate-oval.

The foot is moderately large, elongate, the sole with papillate margins. The heel is not marked but there is a a large 'byssal' gland present internal to the posterior limit of the sole. The gills are well-developed with up to 48 alternating gill plates. The dorsal margins of the left and right inner demibranchs are fused. In life the gills are a bright orange-red colour. In contrast the palps are cream. The latter are relatively small, elongate and dorso-ventrally narrow and, for the most part, hidden under a fold of the body wall. This latter is more pronounced on the right side of the body where the hind gut loop meets the ventral margin of the visceral wall. Each palp has up to 24 ridges on the inner face. The palp proboscides are also long and tapering.

The digestive gland is bright orange in life. As in other species of *Nuculana*, the course of the hind gut describes a single loop to the

right side of the viscera. There is a single typhlosole present along its entire length. The stomach is of moderate size and internally is similar in form to that of shallow water species of *Nuculana* (Yonge, 1939). The gastric shield lines much of the left wall of the stomach. To the right there is a large posterior sorting area with 13 ciliated ridges. A deep caecum is ventral to the oesophageal aperture. Two digestive ducts open close to the antero-dorsal margin of the posterior sorting area and a single duct opens antero-dorsally close to the oesophageal opening.

As will be seen *Nuculana acuta* is remarkably similar in its shell features and anatomy to *Nuculana commutata.* This similarity is discussed under the latter species (p. 123).

Nuculana commutata (Philippi 1844)

TYPE SPECIMEN. ZMHU.

TYPE LOCALITY. Pliocene, Palermo, Sicily.

CITED SPECIMEN. BMNH 1995212

Arca fragilis Chemnitz 1784, 199, pl.LV, fig.546.
Arca pella Gmelin 1790 (non Linné), 3307.
Arca minuta Brocchi 1814 (non Fabricius), 482, pl.XI,fig.4.
Nucula pella Payraudeau 1826 (non Linné), 64.
Lembulus deltoideus Risso 1826 (non Lamarck), 320, pl. XI, fig. 164.
Nucula minuta Scacchi 1836 (non Fabricius), 4.
Nucula striata Philippi 1836 (non Lamarck), 64.
Nucula commutata Philippi 1844, 101.
Leda fragilis Jeffreys 1879, 575.
Leda minuta Jeffreys 1856 (non Fabricius), 25.
Leda commutata Hanley 1863, pl.CCXVIII, figs, 80, 81.
Lembulus commutatus Monterosato 1878, 6.
Leda (Portlandia) tenuis Sturany 1896, 6.
Nuculana (Jupiteria) fragilis Nordsieck 1969, 9, pl.I, fig.02.25.
Nuculana (Jupiteria) commutata Smith and Heppell 1991, 56.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
WEST EUROPEAN BASIN							
Sarsia	S29	119	16	47°40.0'N	05°00.0'W	12.8.67	ES

SHELL DESCRIPTION (Fig.34)
Shell moderately large, elongate, slightly inflated, rostrate, ornamented with concentric ridges, pale straw-coloured periostracum; radial ridge from umbo to antero-ventral margin; rostral ridge well-defined, delimits posterior dorsal area, within this area a faintly outlined escutcheon extending half the length of postero-dorsal margin; lunule elongate, defined by fine ridge; less well-defined ventral rostral ridge extends from umbo to postero-ventral margin; umbos anterior to midline, inwardly directed; antero-dorsal margin proximally straight, distally slightly concave merging with rounded anterior margin to where it meets with ventral limit of anterior radial ridge, ventral margin broadly concave, postero-ventral margin sinuate where ventral rostral ridge meets margin, posterior margin acute, slightly upturned, postero-dorsal margin slightly raised with shallow angulation at limit of hinge plate; hinge plate elongate, relatively broad, acute chevron teeth, 16 on both anterior and posterior hinge plates of specimen 8.3mm total length; ligament internal, amphidetic, triangular, extends slightly ventral to hinge plate.

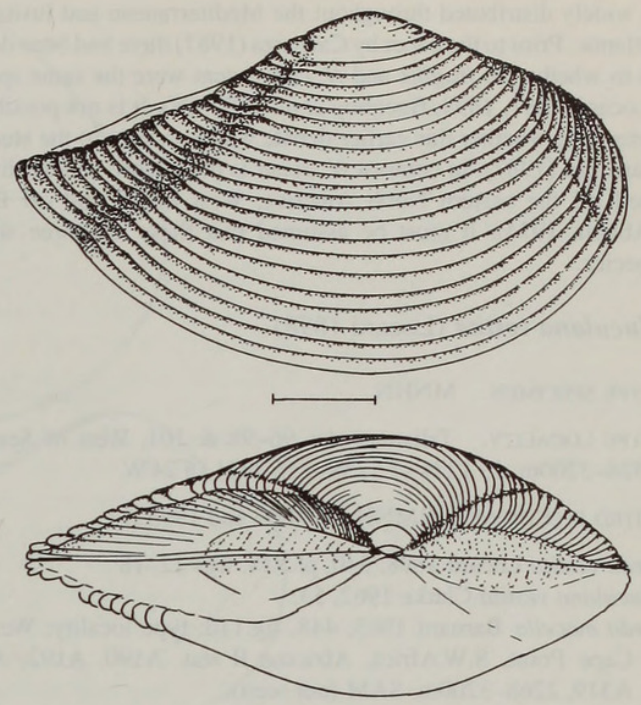

Fig. 34. *Nuculana commutata.* Lateral and dorsal views of a shell, from Sarsia station S29 from the West European Basin. Scale = 1mm.
Maximum length of present specimens is 8.3mm.

INTERNAL MORPHOLOGY (Fig.35)
The internal morphology differs little from that of *N. acuta* (Fig.32). The most noticable differences are that *N. commutata* has less attenuate palps with fewer palp ridges and larger adductor muscles than does *N. acuta.*

Other differences between the two species are that in *N. commutata* the ridge from the umbo to the antero-ventral margin is more marked, the apices of the concentric ridges are less broad, the postero-dorsal margin is not so raised and the shell is somewhat less elongate in relation to its height.

These differences are of degree and at that point where separation into species rather than subspecies is a subjective judgement. Nevertheless, these differences are more marked than those between *N. commutata* and *N. illirica* Carrozza 1987 (paratypes BMNH 1995213 examined by JAA), a species that has been recently described from the northern Adriatic Sea (Carrozza, 1987). In contrast *N. commutata*

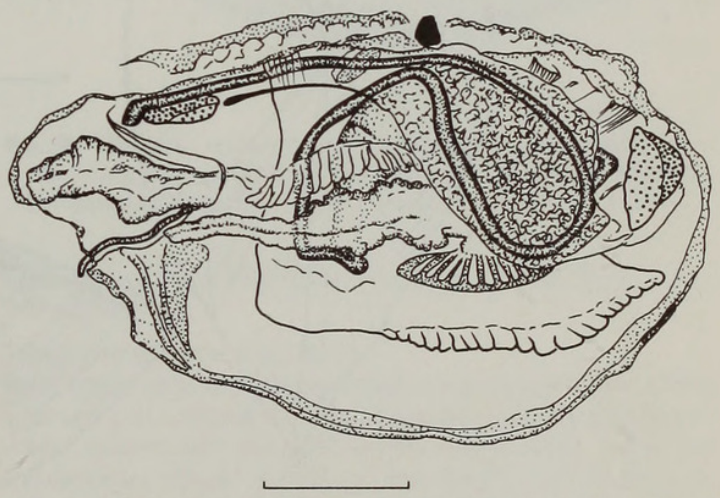

Fig. 35. *Nuculana commutata.* Internal morphology as seen from the right side of a specimen from Sarsia station S29 from the West European Basin. For identification of the parts see text-figure 7, p. 106. Scale = 1mm.

is widely distributed throughout the Mediterranean and lusitanean Atlantic. Prior to the paper by Carrozza (1987) there had been debate as to whether *N. fragilis* and *N. commutata* were the same species (Locard, 1891, 1898; Bucquoy *et al,* 1887–98). It is not possible to determine whether this earlier debate was a presage to the study of Carrozza (1987). In contrast *N. acuta* is even more widely distributed off the eastern North America, West Indies and off Brazil (Abbott, 1974). It must be assumed that these are three sibling species.

Nuculana vestita (Locard 1898)

TYPE SPECIMEN. MNHN

TYPE LOCALITY. Talisman stas 96–98 & 101, West of Senegal, 2324–3200m, 19°12'N 17°57'W – 16°38'N 18°24'W

CITED SPECIMENS. BMNH 1995056 and 1995211

Leda vestita Locard 1898, 340, pl.XIV, figs 12–18
Nuculana vestita Clarke 1962, 53.
Leda macella Barnard 1963, 448, fig.11d; type locality: West off Cape Point, S.W.Africa, Africana II stas A190, A192, A317, A319, 2268–3200m, SAM (not seen).

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
SIERRA LEONE BASIN							
Atlantis II 31	146	2842 –2891	1	10°39.5'N	17°44.5'W	6.2.67	ES
ANGOLA BASIN							
Atlantis II 42	201	1964 –2031	1	09°29.0'S	11°34.0'E	23.5.68	ES
	203	527 –542	742	08°46.0'S	12°47.0'E	23.5.68	ES

Specimens taken by the Galathea Expedition described by Knudsen (1970) examined by JAA, ZMUC. Knudsen (1970) following examination of specimens synonymized *L. macella* with *N. vestita.*

Nuculana vestita is a well-described species (Locard, 1898; Theile and Jaeckel, 1931; Knudsen, 1970) occurring off West and Southwest Africa at lower slope depths (715–2891m) in the Sierra Leone, Guinea and Angola basins.

SHELL DESCRIPTION (Figs 36 & 37)
Shell moderately large, inflated, somewhat elongate, rostrate, ornamented with concentric ridges, pale brownish-yellow periostracum; umbos large, inwardly directed, anterior to midline; antero-dorsal distal margin horizontal for short distance, proximal margin broadly convex forming smooth curve with anterior margin, ventral margin broadly convex to rostrum, postero-dorsal margin, raised in small specimens but less so in large, proximally straight or slightly concave, in small specimens angulate at limit of posterior hinge plate, distally slightly concave to posterior limit of rostrum; broad ridge extends from umbo to rostrum forming outer limit of escutcheon; anterior and posterior hinge plates broad, meet shell margin ventral to umbo, hinge teeth broad chevrons, up to 19 and 16 in anterior and posterior series respectively in specimen 8.3mm total length; ligament internal, amphidetic, pear-shaped in sagittal vertical section, extends ventral to hinge plate. The maximum length of the present specimens is 13.8mm.

INTERNAL MORPHOLOGY (Fig. 38)
The adductor muscles are moderately large and oval. The siphonal embayment is deep with the siphonal tentacle to the right side. The siphons are entire. The feeding aperture is small but well-defined with the mantle surface ridged internally. Radial mantle muscles are well-developed forming a broad band internal to the inner lobe

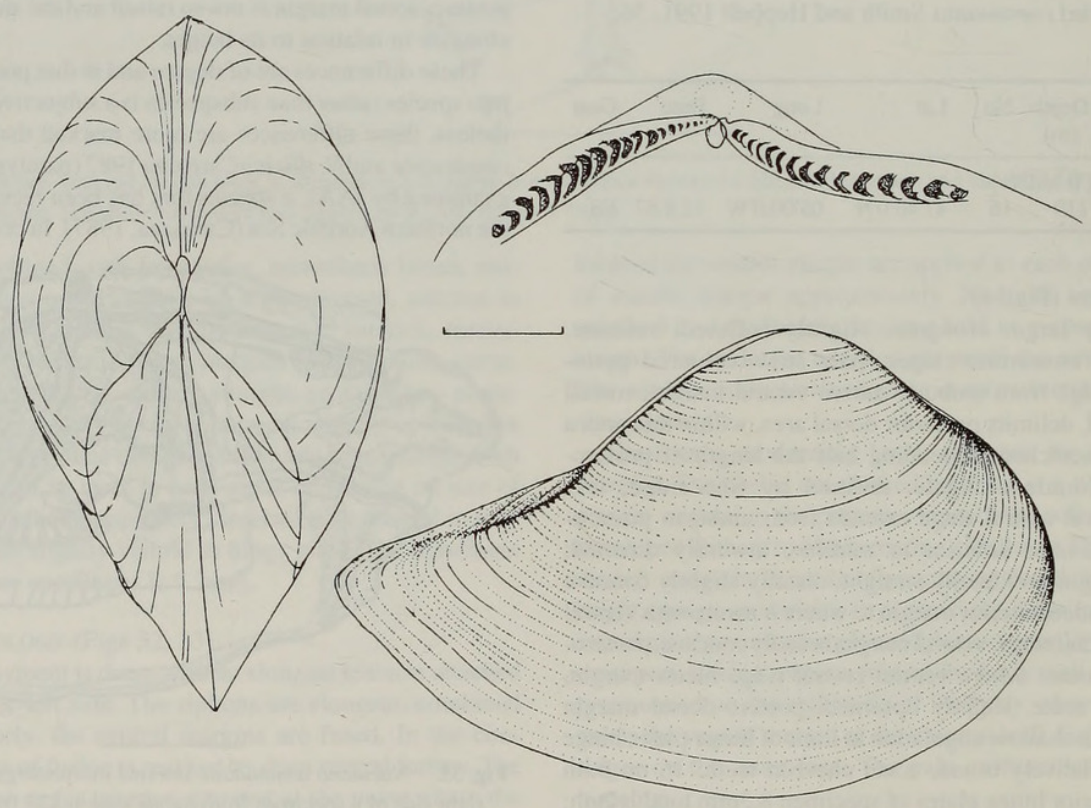

Fig. 36. *Nuculana vestita.* External right lateral and dorsal view of a large adult shell and a lateral view of the hinge plate of a right valve. Specimens are from Atlantis II station 203 from the Angola Basin. Scale = 1mm.

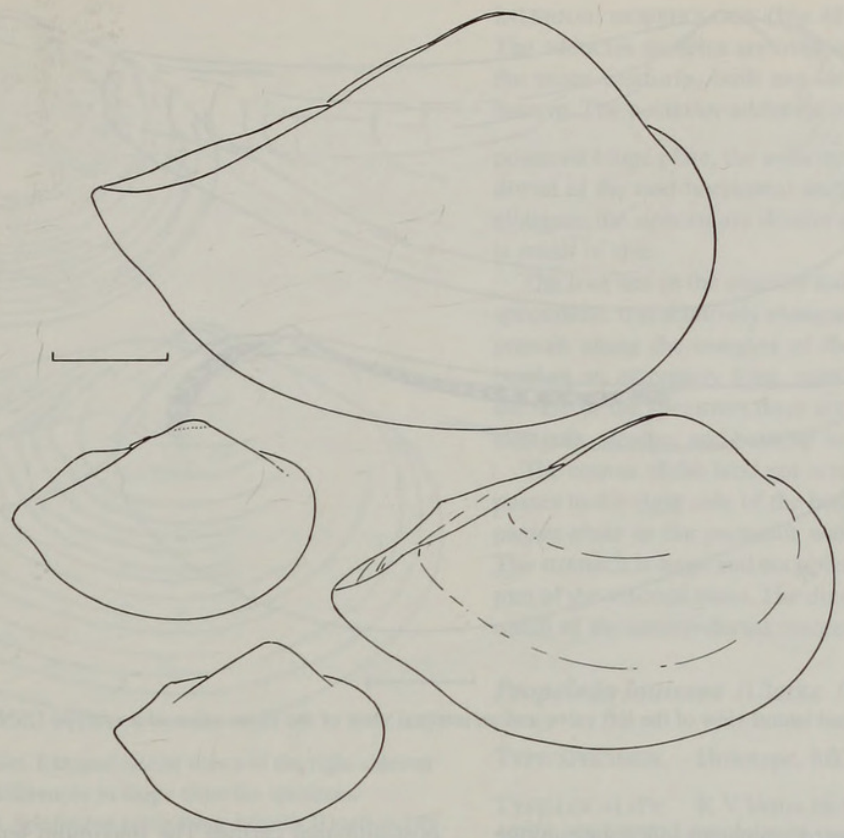

Fig. 37. *Nuculana vestita.* Lateral views of right side of four shells in outline to show differences in shape with increasing size. Specimens from Atlantis II station 203 from the Angola Basin. Scale = 1mm.

of the mantle edge. The anterior mantle sense organ is well-developed.

The foot is large with the margins of the sole finely papillate. The palps are very small with up to 12 broad folds. The palp proboscides are stout and elongate, even in the contracted state. The gills are elongate and broad with up to 36 gill plates.

Propeleda carpenteri (Dall 1881)

TYPE SPECIMEN. Syntypes, USNM 63151 and MCZ 7936–7938.

TYPE LOCALITY. Off Barbados, 'Blake' stations 5, 9, and 21, 100fm–287fm.

CITED SPECIMENS. BMNH 1995057

Leda carpenteri Dall 1881, 125; 1886, 249, pl.8, fig.10, pl.9, fig.3.
Nuculana carpenteri Johnson 1934, 16.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
ARGENTINE BASIN							
Atlantis II 60	237	993–1011	194	36°32.6'S	53°23.0'W	11.3.71	ES
	239	1661–1679	8	36°49.0'S	53°15.4'W	11.3.71	ES
	240	2195–2323	8	36°53.4'S	53°10.2'W	12.3.71	ES

Specimen USNM 63151 examined by JAA.

Previously reported off N. Carolina, Gulf of Mexico and Eastern Caribbean (Dall, 1889; Rice and Kornicker, 1965; James, 1970), the present specimens are from the Argentine Basin. This species has a somewhat unusual distribution from shelf to lower slope depths, 200–2323m

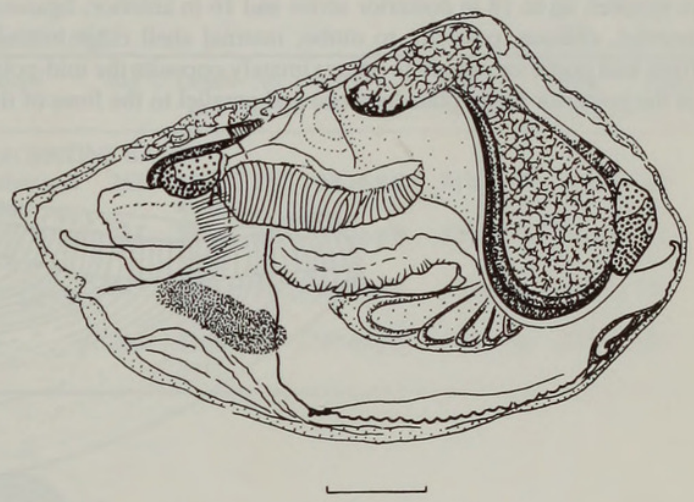

Fig. 38. *Nuculana vestita.* Internal morphology as seen from the right side of a specimen from Atlantis II station 203 from the Angola Basin. For identification of the parts see text-figure 7, p. 106. Scale = 1mm.

SHELL DESCRIPTION (Figs 39–41)

Shell fragile, semi-transparent, slender, moderately elongate, rostrate with two post umbonal carinae, ornamented with faint concentric ridges; periostracum pale straw colour; umbos small, far anterior (postumbonal length 60–68% of total length), inwardly facing; antero-dorsal margin slightly flattened, ventral margin smoothly curved, postero-dorsal margin raised, slightly sinuous, concave proximally, convex distally, meets posterior margin at limit of dorsal post-umbonal carina, posterior margin concave between posterior

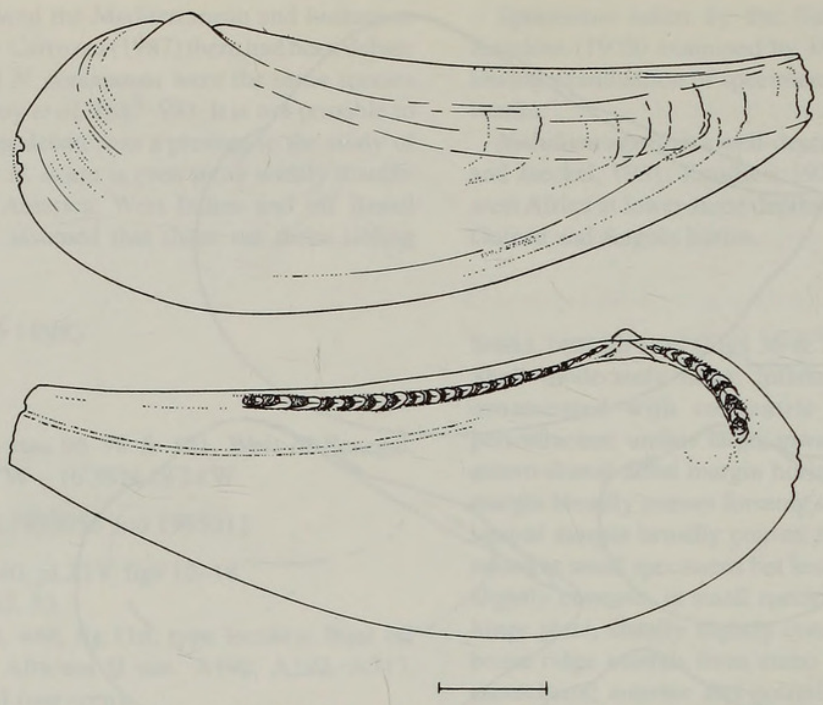

Fig. 39. *Propeleda carpenteri.* External lateral view of the left valve and an internal view of the same valve of a syntype USNM 63151, from off Barbados in 100fms. Scale = 1mm.

limits of dorsal and ventral carinae; escutcheon lanceolate; hinge plates relatively broad, posterior plate short, occupying little more than half of postero-dorsal margin, anterior plate approximately half length of posterior, hinge teeth acute chevron-shape, relatively few in number, up to 18 in posterior series and 16 in anterior; ligament internal, oblique, posterior to umbo; internal shell ridge extends from mid posterior margin to approximately opposite the mid-point of the posterior hinge plate between and parallel to the lines of the post-umbonal carinae.The maximum length of the present specimens is 15.3mm.

In most specimens the posterior shell margin is damaged, often being markedly shortened and specimens frequently show regeneration of the shell posterior to the posterior adductor. The repaired shell is without concentric ornamentation. It is possible that extended siphons are predated upon and that the shell is damaged when this occurs.

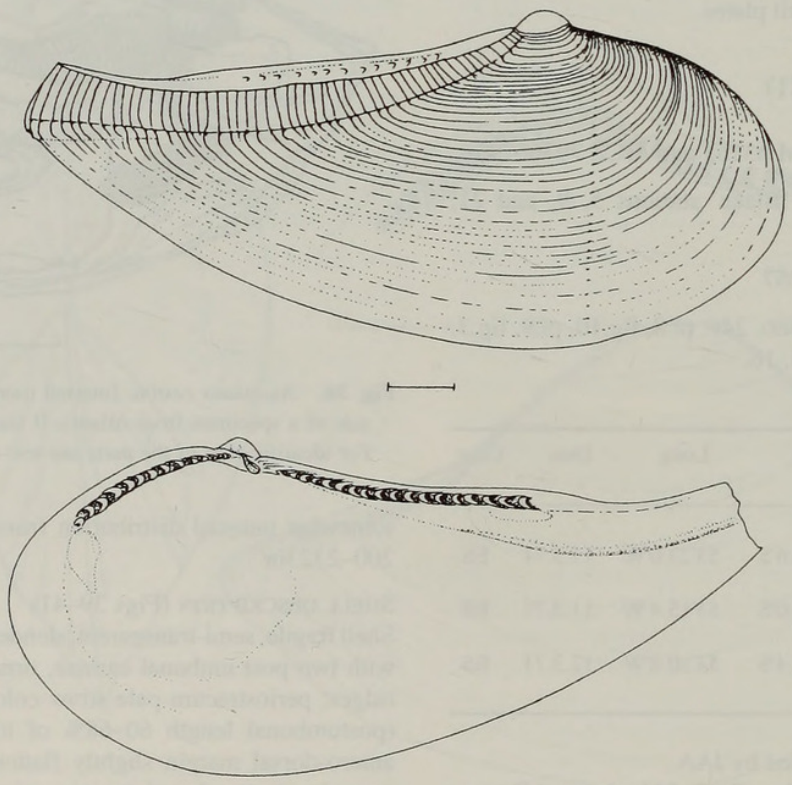

Fig. 40. *Propeleda carpenteri.* External lateral view of the right side of a shell and an internal lateral view of a right valve from Atlantis II station 237 from the Argentine Basin. Scale = 1mm.

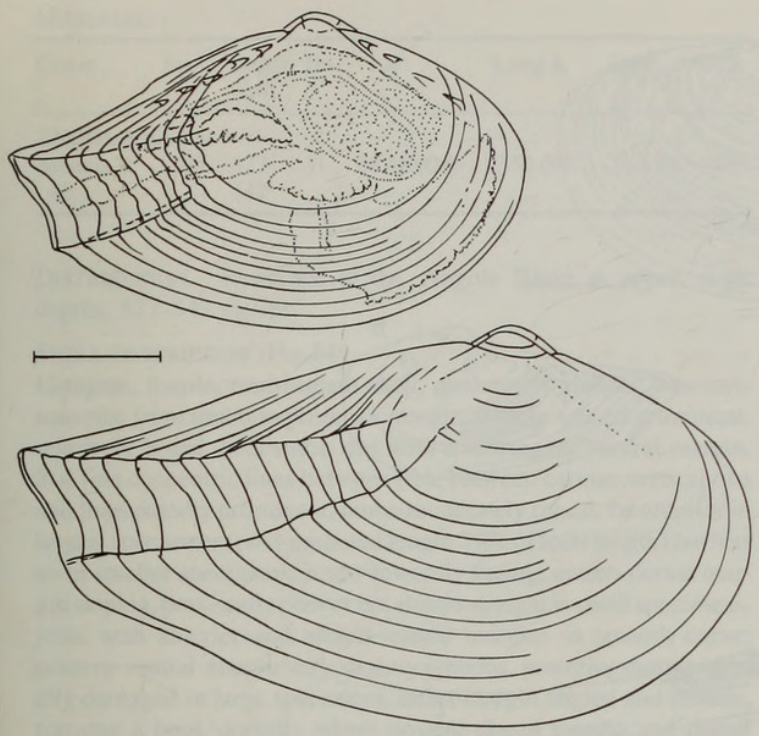

Fig. 41. *Propeleda carpenteri.* External lateral views of the right sides of two small shells to show differences in shape from the specimen illustrated in text-figure 40. Specimens taken from Atlantis II station 239 from the Argentine Basin. Scale = 1mm.

The concentric ridges on the shell of the present specimens while not particularly marked are more so than those described by Dall, though the syntypes that we have examined are dead valves that are somewhat worn (Fig.39). Our specimens also are very slightly more anteriorly extended than the syntypes, though the characteristic antero-dorsal curvature of the shell margin is the same. Our specimens correspond well with the figures given by James (1972, figs 67 and 68). These latter come are from similar depths (2340–2627m) to some of our own. It would appear that specimens from mid to lower slope differ slightly from those taken at shallower depths however, we regard the differences as being at most infrasubspecific.

There is a marked change in shape during growth. Juveniles are much shorter than the adults and subsequent growth involves increasing elongation of the post-umbonal shell. The prodissoconch is extremely large measuring 630μm in length.

INTERNAL MORPHOLOGY (Fig.42)

The adductor muscles are oval in cross-section, the posterior being the more fusiform, both are set some distance in from the shell margin. The posterior adductor muscle lies opposite the limit of the posterior hinge plate, the anterior muscle is attached to the shell just dorsal of the mid-horizontal shell axis. The siphonal embayment is elongate, the siphons are slender and entire. The anterior sense organ is small in size.

The foot lies in the anterior half of the mantle cavity in preserved specimens, it is relatively elongate and has numerous small papillae present along the margins of the sole. The palps are small, each bearing an extremely long, narrow, palp proboscis. Depending on the size of the specimen there are up to 17 palp ridges. The gills are elongate, slender, and have up to 17 plates.

The course of the hind gut is similar to that in *Nuculana* in that it passes to the right side of the body where it forms a broad loop that passes close to the posterior wall of the anterior adductor muscle. The stomach is large and occupies a vertical position in the posterior part of the visceral mass. The digestive gland is extensive occupying much of the antero-dorsal visceral space.

Propeleda louiseae (Clarke 1961)

TYPE SPECIMEN. Holotype, MCZ 224958.

TYPE LOCALITY. R.V.Vema biology station 121, Argentine Basin, 1000 miles ESE of Buenos Aries, 5105 metres.

CITED SPECIMENS. BMNH 1995058

Nuculana (Thestyleda) louiseae Clarke 1961, 375, pl.1, fig. 7.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
ARGENTINE BASIN							
Atlantis II 60	242	4382–4402	25	38°16.9'S	51°56.1'W	13.3.71	ES
	243	3815–3822	2	37°36.8'S	52°23.6'W	14.3.71	ES
	247	5208–5223	2	43°33.0'S	48°58.1'W	17.3.71	ES
	256	3906–3917	3	37°40.9'S	52°19.3'W	24.3.71	ES

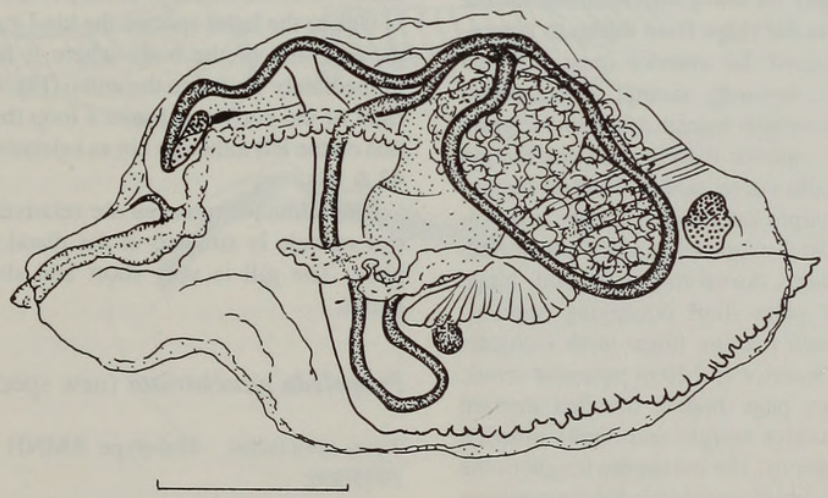

Fig. 42. *Propeleda carpenteri.* Internal morphology as seen from the right side of a specimen taken from Atlantis II station 239 from the Argentine Basin. For identification of the parts see text-figure 7, p. 106. Scale = 0.5mm.

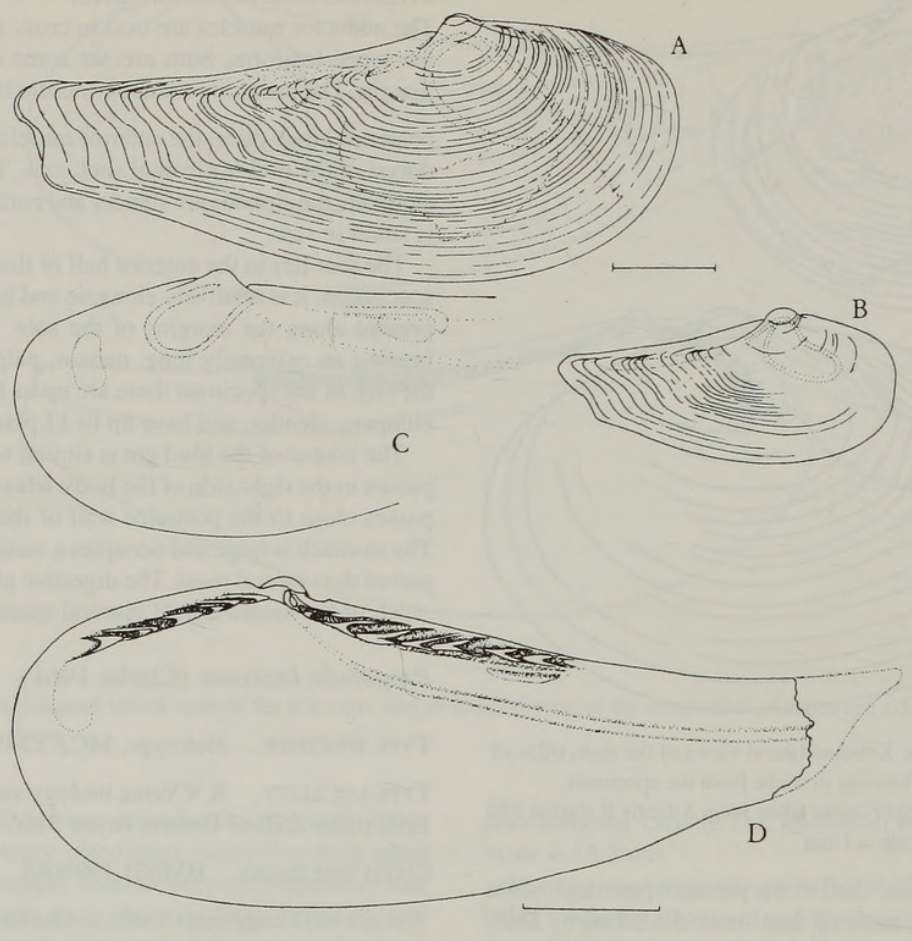

Fig. 43. *Propeleda louiseae.* a & b, external lateral views of the right sides of shells of differing size to show differences in shell proportions with growth; note outline internal morphology through semi-transparent shells, in particular the form of the hind gut and position of the adductor muscles; c, outline of shell from the left side showing the outline of hind gut and adductor muscles; d, internal view of a left valve. All specimens taken from Atlantis II station 242 from the Argentine Basin. Scales = 1mm.

Type specimen examined by HLS.

Distributed at abyssal depths in the Argentine Basin; depth range: 3815–5223 metres.

SHELL DESCRIPTION (Fig.43)

Shell extremely elongate, slender, fragile, semi-transparent, ornamented with moderately spaced concentric ridges, two post-umbonal rounded ridges, one dorsal and one ventral at posterior shell margin and crossed vertically by wavy continuations of the concentric ridges, faint anterior radial ridge from umbo to antero-ventral margin; umbo slightly raised, far anterior (post-umbonal length 65–70% of total length), inwardly facing; antero-dorsal margin with short proximal notch, distally margin raised and slightly concave, faint angulation before anterior margin, anterior margin joins with ventral margin in smooth curve, postero-ventral margin very slightly sinuate, posterior margin angled and sinuate, postero-dorsal margin notched at umbo, distally somewhat raised and keeled, concave overall but slightly sinuous dorsal to hinge plate; hinge plate relatively broad, posterior plate short occupying approximately half the postero-dorsal shell margin, hinge teeth elongate, acute chevron shape, up to 12 in anterior and 20 in posterior series; ligament small, internal, oblique, pear-shaped; rounded internal ridge extends from umbo to posterior margin and marks junction between inhalent and exhalent siphons. The maximum length of the present specimens is 20.3mm. The prodissoconch is large measuring 300μm in length.

Clarke (1961) records a long, thin, external ligament in the type specimen – the latter being a single large valve. We find no evidence of an external part to the ligament and believe that Clarke mistakenly confused periostracum along the postero-dorsal margin for ligament.

INTERNAL MORPHOLOGY

With one notable exception the internal morphology of *P.louiseae* differs little from that of *P. carpenteri.*

Unlike the latter species the hind gut of *P. louiseae* first passes to the left side of the body where it forms a relatively small loop immediately ventral to the umbo (Fig.43). From there it passes to the right of the body and forms a loop that is considerably larger than that on the left although not as extensive as that in *P. carperteri* (Figs 42 & 43).

The adductor muscles are relatively large, the elongate posterior muscle is situated at the distal limit of the posterior hinge plate. The gill is very short and slender with few (c. 13) gill-plates.

Propeleda paucistriata (new species)

TYPE SPECIMEN. Holotype BMNH 1995059; Paratypes BMNH 1995060.

TYPE LOCALITY. Atlantis II station 203, Angola Basin, 08°48.00'S 12°52.00'E, 527–542m.

MATERIAL:

Cruise	Sta	Depth (m)	No	Lat	Long	Date	Gear
ANGOLA BASIN							
Atlantis II 42	203	527–542	31	08°48.00'S	12°52.00E	23.5.68	ES

DISTRIBUTION. Restricted to the Angola Basin at upper slope depths, 527–542 metres.

SHELL DESCRIPTION (Fig.44)

Elongate, fragile, transluscent shell, moderately slender, two carinate ribs from umbo to posterior margin, widely spaced prominant, relatively broad, concentric ribs with overhanging ventral margin, 2–4 fine concentric lines between ribs, between carinae vertical ribs and lines equally prominant; umbo moderately raised, far anterior in largest specimens (post-umbonal length 79% of total length) but less so in smaller specimens, beaks inwardly facing; antero-dorsal margin sloping, proximally convex but almost straight in small specimens, joins with anterior and antero-ventral margins in smooth curve; postero-ventral margin very slightly sinuous, posterior margin usually damaged in large specimens, intact margin angled and sinuate, forming a hook dorsally where postero-dorsal margin and dorsal carina meet, postero-dorsal margin concave, proximally raised, elongate escutcheon outlined by dorsal carina; hinge elongate, moderately broad, large, acute chevron-shaped teeth up to 16 in anterior series and up to 28 in posterior series, anterior series extends to anterior limit of anterior adductor muscle, posterior series extends approximately half length of postero-dorsal margin to anterior limit of posterior adductor muscle, ventral margin of hinge plate corresponds to line of dorsal carina, ventral to umbo teeth approach shell margin, anterior and posterior hinge plates continuous; ligament internal, ventral to umbo and close to shell margin, slightly inclined posteriorly; rounded internal ridge extends from umbo to posterior margin. The maximum recorded shell length is 14.1mm. The prodissoconch is very large and measuring 560μm in length.

Juvenile shells are more ovate and, before posterior elongation occurs, could be mistaken for a yoldiellid (Fig.44).

INTERNAL MORPHOLOGY (Fig.45)

The anterior adductor muscle is oval in cross section, while the posterior adductor is smaller and more elongate. Both are set in from the shell margin, the posterior is positioned at approximately two-thirds the distance between the umbo and the posterior limit of the shell. There is a small anterior sense organ formed from the sensory fold of the mantle, ventral to the anterior adductor. The siphons are joined with their ventral margins fused to form entire lumina. They are slender and particularly elongate and when contracted are contained in the elongate siphonal embayment. The foot and viscera lie in the anterior half of the mantle cavity. The foot is elongate and directed anteriorly. In most preserved specimens the tip of the foot lies between the anterior adductor and the shell margin. The margins of the sole are fringed with numerous relatively small papillae. There are three anterior and two posterior pedal retractor muscles. The palps and gills are markedly narrow and elongate. The are at least 22 palp ridges in the largest specimens and the palp proboscides are attenuate each with a straight dorsal margin and a papillate ventral margin. In a few preserved specimens the palp proboscides extend from the feeding aperture. The gills are similarly attenuate

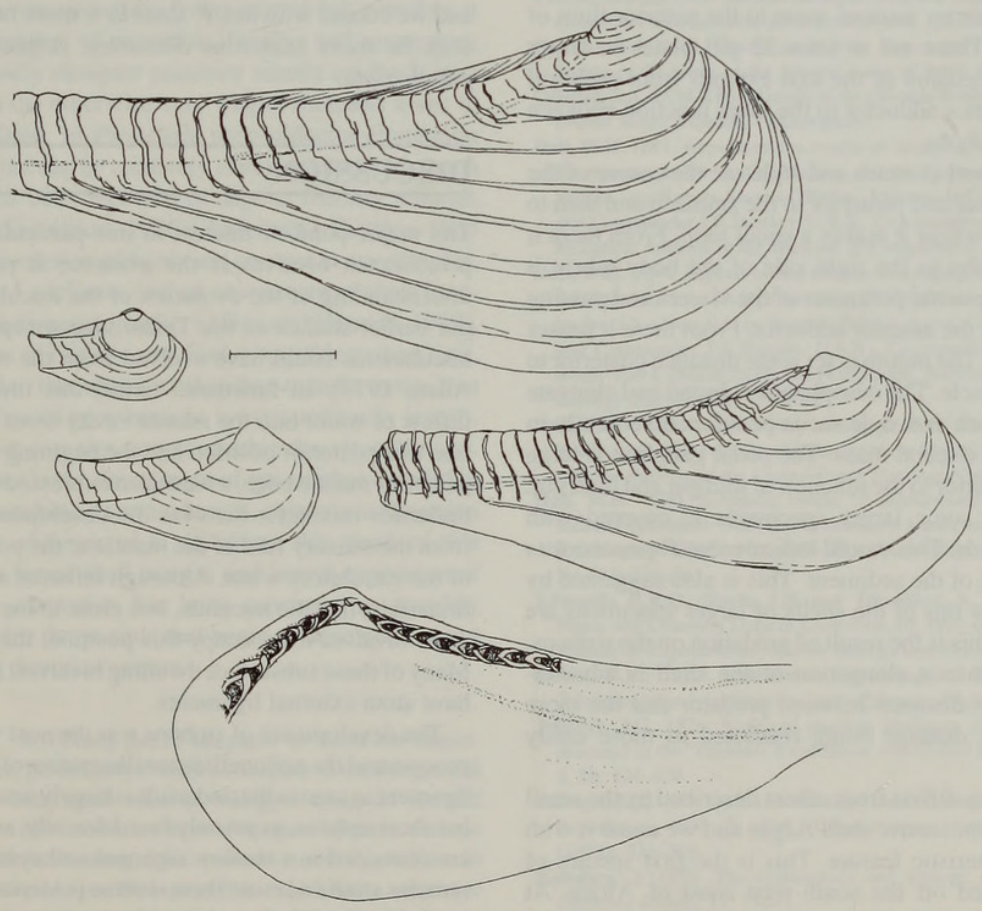

Fig. 44. *Propeleda paucistriata.* External lateral views of the right sides of four shells of differing size to show change of shape with growth and an internal view of a right valve. All specimens taken from Atlantis II station 203 from the Angola Basin. Scale = 1mm.

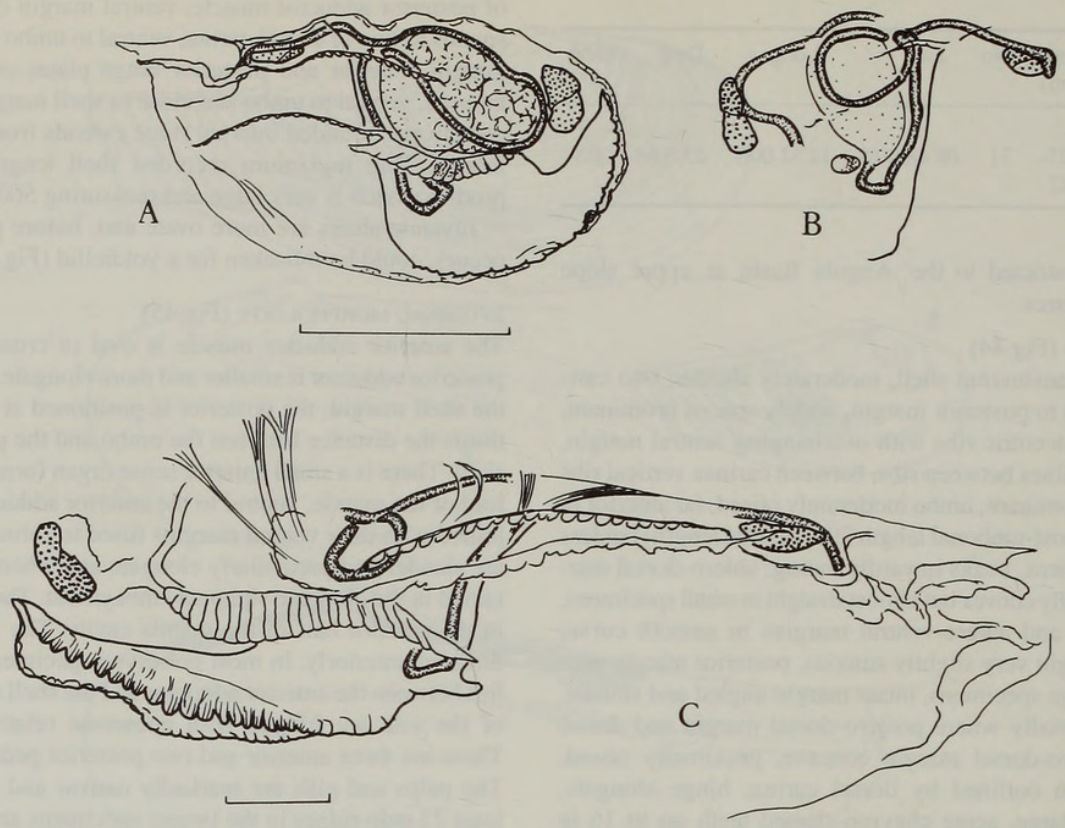

Fig. 45. *Propeleda paucistriata.* a, internal morphology as seen from the right side; b, part of the left side of the same specimen to show details of the course of the gut; c, the internal morphology as seen from the left side of a much larger specimen. All specimens taken from Atlantis II station 203 from the Angola Basin. For identification of the parts see text-figure 7, p. 106. Scales = 1mm.

and extend from the posterior visceral mass to the anterior limit of the posterior adductor. There are at least 22 gill plates in larger specimens. A slender extension of the axis extends from each gill from ventral to the posterior adductor to the inner junction between inhalent and exhalent siphons.

From the large combined stomach and style sac the course of the hind gut takes it first dorsal and posterior to the stomach and then to the left side of the body where it makes a small loop. From there it passes ventral to the umbo to the right side of the body where it makes a much larger loop at the perimeter of the viscera and passing close to the inner face of the anterior adductor. From there it passes mid-dorsally to the anus. The mouth is set some distance posterior to the anterior adductor muscle. The oesophagus is broad and elongate and the combined stomach and style sac is positioned vertically in the posterior part of the visceral mass. The pedal ganglion is large and lies immediately anterior to the junction of mid gut and hind gut.

The shell surface in some larger specimens is covered with epifaunal solitary hydroids. This would indicate that *P. paucistriata* lives close to the surface of the sediment. This is also suggested by the fact that the posterior tips of the shells of larger specimens are broken. We believe that this is the result of predation on the siphons.

The extreme post-adductor elongation of the shell is advantageous in that it provides distance between predator and the more vulnerable viscera with damage being restricted to more easily generated tissue.

The shell of this species differs from others described by the small number of pronounced concentric shell ridges and we name it with reference to this characteristic feature. This is the first species of *Propeleda* to be recorded off the south-west coast of Africa. At approximately the same latitude off the east coast of Natal a species named *Leda lanceta* by Boshoff (1968) occurs at upper slope depths. Nijssen-Meyer (1972) believes that this latter species is a *Propeleda*, and we concur with her. *P. lanceta* is more robust, more arcuate and with far more numerous concentric ridges than is the case in *P. paucistriata.*

DISCUSSION

The major point of interest in this particular account of deep-sea protobranch bivalves is the evidence it provides to further our understanding of the evolution of the nuculanoid protobranchs. In our earlier studies on the Tindariidae we speculated as to how the nuculanoids could have evolved from the nuculoids (Sanders and Allen, 1977). In functional terms, this involved a change in the inflow of water into the mantle cavity from an antero-ventral position to a posterior position and the begining of specialization of the posterior mantle edge, a view also expressed by Yonge (1939). In the tindariids this latter involves the development of sensory papillae from the sensory fold of the mantle at the points of ingress and exit of the circulatory water. Although infaunal and deposit feeding, the tindariids, like the nuculids, live close to the surface and, like many other bivalves that occupy this position, they are ovate and robust. Many of these subsurface dwelling bivalves, including the tindariids, have stout external ligaments.

The development of siphons was the next step in the evolutionary process and the neilonellids are illustrative of this. The shell form and ligament as seen in the tindariids is largely retained in the neilonellids, but short siphons, as yet only fused dorsally, are now present and these are contained in a shallow siphonal embayment. Although the shell remains stout and ovate there is some posterior elongation and an area ventral to the inhalent siphon from where the palp proboscides are extended is more defined. Like the tindariids the neilonellids are deposit feeders living close to the surface of the sediment.

The hind gut in *Neilonella*, like that in *Tindaria*, has a wide lumen and single pronounced typhlosole. Although the course that the hind gut takes in neilonellids makes a single loop on the right side of the body, it does not penetrate mantle space as it does in tindariids (Sanders and Allen, 1977). In this respect the hind gut of neilonellids probably represents the more primitive condition. We have argued elsewhere (Allen, 1992) that elongation and the complexity of form of hind gut configuration are related to food procurement at great depths, and this applies to the tindariids (Sanders and Allen, 1977). The neilonellids are for the most part upper slope species and the hind gut would be expected to be less specialized and less elongate.

In *Nuculana* posterior elongation becomes more extreme and the ventral margins of the combined siphons are fused such that the exhalent and inhalent lumena are separate and entire. The shell remains robust, but is more slender The ligament is restricted to a small internal structure separating elongated anterior and posterior series of hinge teeth. We believe that elongation is correlated to the almost vertical orientation of the animal in the sediment but which retains contact with the surface via the extended posterior body and siphons. The genus *Nuculana* is found mainly in shelf and upper slope sediments and as such the available food resources are relatively abundant. The hind gut is not greatly extended and remains as a single loop to the right side of the body.

In *Propeleda* the evolutionary trend of posterior body elongation seen in *Nuculana* becomes is more extreme, particularly posterior to the posterior adductor muscle. The posterior adductor muscle is more elongate and dorso-ventrally narrow, and the gill, gill axes, siphons and the palp proboscides are exceptionally long and slender. The shell of *Propeleda*, particularly in abyssal species, is much more fragile and is further specialized in that it possesses an internal posterior longitudinal ridge. The function of this ridge is not entirely clear and has await examination of the living animal but, possibly, it is involved in the separation of excretion, feeding and respiratory functions in the extremely elongate posterior mantle cavity. It may also help to strengthen the otherwise very fragile shell and assist in predation damage limition. In *Propeleda* post-adductor elongation involves body tissues that can be relatively easily regenerated, much in the same way as has been reported in deposit feeding tellinids (Edwards, Steele and Trevallion, 1970). Specimens showing shell repair posterior to the posterior adductor are present in our samples.

The evolution of the Ledellinae and an assessment of their functional morphology was discussed earlier (Allen and Hannah, 1989). In respect of the species of *Ledella* and *Tindariopsis* described here, little needs to be added to that account other than to note, again, that the hind gut in these abyssal protobranchs is extraordinarily lengthened and takes the most complex courses within the visceral mass.

The other item of note is the description of yet another ledellid in which the shell, after reaching a certain length, changes its direction of growth. In *Ledella aberrata* as in *L. ultima* the result of this change is to produce a broad shell margin and lateral expansion of the shell cavity. This adaptation has been construed as possibly providing more space for the gonads that begin to develop at about the time the change in direction occurs.

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