Studies on deep-sea Protobranchia (Bivalvia); the family Malletiidae

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Contents

Synopsis

This paper redefines the deep water protobranch bivalve family Malletiidae and describes the functional morphology, growth and geographical distribution of nine species obtained from abyssal and slope depths of the Atlantic. Three new species are described, all from the Guinea Basin.

Subtle differences in the shell shape between different populations are, where possible, quantified and described. The differences are discussed in relation to reproduction and isolation, and taking into account possible slow rates of gene flow and the emergence of sibling species.

Introduction

This is the fifth paper in a series on the biology and ecology of the deep-sea protobranch bivalves of the Atlantic (Allen & Sanders, 1973, 1982; Sanders & Allen, 1975, 1977). Our interest lies in a multiplicity of aspects of the life and evolution of these molluscs, (Allen, 1978), but in particular we have endeavoured to determine the adaptations of these animals to conditions at great depths.

Supported by N.S.F. Grants GB-6027, GA-31105, GA-36554, OCE76-20833 and 20/8837 and NERC Grant GR3/3915A.
Woods Hole Oceanographic Institution Contribution No. 5696

Bull. Br. Mus. nat. Hist. (Zool.) **49** (2): 195–238

Issued 19 December 1985

Thus, much of our study concerns the functional morphology of the animal, its reproduction, the variations in population parameters and the geographical and depth distribution. In addition, because protobranchs dominate the deep sea bivalve fauna with many species present, and because of the large and comprehensive collection at our disposal containing many new species, our work has had of necessity to concern itself with the taxonomy of the group. The presentation of the work is therefore formulated in a taxonomic framework. Our samples come from a variety of sources and the data given under each species section lists these sources. In the main they come from the expeditions of the research vessels of the Woods Hole Oceanographic Institution, U.S.A., the Natural Environment Research Council, U.K., and the Centre National pour Exploitation des Océans (CNEXO), France. Thus, we are greatly indebted to the many scientists and staff of these Institutions for their various contributions.

In this paper we continue our appraisal of the Order Nuculanoidea and consider the family Malletiidae.

It has been the custom by authors of earlier papers on the protobranch Bivalvia to include those nuculanoid species possessing an external ligament within a single subfamily the Malletiinae or family Malletiidae (e.g. Dall, 1898; Verrill & Bush, 1897; Vokes, 1967; McAlester in Moore, 1969). Vokes (1967) included the following recent genera within the Malletiidae:

**Austrotindaria* Fleming, 1948; *Clencheria* (=*Malletia*) Clarke, 1961; *Ctenoconcha* (=*Malletia*) Gray, 1840; *Malletia* des Moulins, 1832; *Malletiella* Soot-Ryen, 1957; *Minormalletia* Dall, 1908; **Neilo* Adams, 1854; **Neilonella* Dall, 1881; **Nucularia* Conrad, 1869; **Protonucula* Cotton, 1930; **Pseudoglomus* Dall, 1898; *Pseudomalletia* (=*Malletia*) Fischer, 1886; *Solenella* (=*Malletia*) G.B. Sowerby, 1833; [*Tindaria* Bellardi, 1875]; **Tindariopsis* Verrill & Bush, 1897.

Our recent studies have shown that this assemblage comprises a variety of unrelated morphologies which have external ligaments as the character in common (Allen, Hannah & Sanders, in prep.). As a result the family Tindariidae was confirmed (Sanders & Allen, 1977). With the asiphonate genus *Tindaria* removed, the remaining siphonate assemblage with external ligaments can be divided into two groups: those marked with an asterisk which have thick shells with strong concentric ornamentation and are not markedly posteriorly elongate; and those without an asterisk which have thin, translucent, ovate or rectangular to ovate shells, with at most, fine concentric striations and which may be rostrate. Some of the species of the first group are probably not closely related; at least two subgroups are present, one ovate and neilonellid in form and the other more rostrate typified by *Malletia (Tindaria) aeolata* Dall as presently named (see p. 234). The second group are unified and are included within the family Malletiidae as here defined.

Family MALLETIIDAE

Nuculanoid protobranchs, shell elongate, ovate or ovate/rostrate, thin, glossy, translucent, usually without marked ornamentation, maybe slender or swollen; umbos, low, anterior, pointing inwards or slightly forward; hinge line slender or, at most moderately developed, with fewer teeth in the anterior as compared with the posterior series, edentulous space between the series; ligament predominantly external, extending beyond the umbos anteriorly and posteriorly, posterior section longer than anterior, small resilium composed of inner and outer layer set in a shallow marginal resilifer; siphonate, specialized posterior mantle feeding area ventral to siphons well developed, single tentacle on right side of siphonal embayment; hind gut in form of single anterior loop on right side, in part contiguous with the anterior adductor, but not penetrating the right mantle; gill axis parallel to anterior-posterior body axis; palps vary in size; cerebro-visceral commissure stout, pedal statocyst large; neck of foot slender, marginal pedal papillae moderately large; 'byssal' gland moderately large.

There is considerable confusion in the literature concerning the form of the malletiid ligament. Thus Verrill & Bush (1897, 1898) state that 'the resilium is wanting or else is represented by a special part of the ligament external to the teeth', while McAlester (1964) defined the family as comprising Cenozoic and Recent forms 'lacking an internal separated ligament and resilifer'. We confirm that in addition to the elongate anterior and posterior external parts of the ligament there is in all species a small internal ligament or resilium inset superficially into the hinge plate below the umbos.

The family includes species of three genera, *Malletia, Minormalletia* & *Malletiella.* Most species belong to the genus *Malletia.* Of the others *Malletiella* comprises two species and *Minormalletia* one species. The two latter genera are restricted to the eastern Pacific. *Minormalletia* and *Malletiella* may on further study prove to be synonymous with *Malletia.* From the existing descriptions the difference of note from *Malletia* in the case of *Minormalletia* is that the lower edge of the pallial sinus is confluent with the pallial scar and in the case of *Malletiella* the postumbonal length is extreme with 3 to 4 times the number of posterior teeth compared with the number of anterior teeth.

MALLETIA des Moulins, 1832

TYPE SPECIES. *M. chilensis* des Moulins, 1832 by monotypy

TYPE LOCALITY. Valparaiso, 100–110 m mud.

SYNONYMY. Solenella Sowerby, 1833; *Ctenoconcha* Gray, 1840; *Pseudomalletia* Fischer, 1886; *Clencheria* Clarke, 1961

The characters of the genus are those that define the family and additionally the number of posterior hinge teeth are less than three times the number of anterior hinge teeth and the pallial sinus scar is not confluent with the pallial mantle scar. There is sufficient similarity of form within the family to describe one species, *M. abyssorum*, in detail while in the case of other species only those characters that differ from those in *M. abyssorum*, or for reason of better material extend the original description need be given. Species of the genus are among the largest protobranch bivalves of the deep-sea, many exceeding 15 mm in total length.

MINORMALLETIA Dall, 1908

TYPE SPECIES. *M. arciformis* Dall, 1908 by monotypy.

TYPE LOCALITY. *Albatross* Sta 3417, off Acapulco, Mexico.

Shell small, blunt, plump; ligament amphidetic; pallial sinus large, ventrally confluent with pallial line, other shell features as given under the family diagnosis. Anatomy unknown.

MALLETIELLA Soot-Ryen, 1957

TYPE SPECIES. *Malletia pacifica* Dall, 1899.

TYPE LOCALITY. *Albatross* Sta 2791, SW Chile.

Umbones anterior; posterior hinge teeth 3–4 times more numerous than anterior; pallial sinus very short, slightly rostrate; other shell features as for family diagnosis. Anatomy unknown.

Malletia abyssorum Verrill & Bush, 1898

Malletia abyssorum Verrill & Bush, 1898: *Proc. U.S. Natl Mus.* **20:** 875, pl. 97, fig. 7. TYPE LOCALITY. U.S. Fish Comm. Sta 2566, 4791 m, Lat 37°23′N, Long 68°28′W. TYPE SPECIMEN. Holotype, U.S. Nat. Mus. No. 52159.

Tindaria (Clencheria) diaphana Clarke, 1961; *Bull. Mus. Comp. Zool. Harv.* **125:** 374, pl. 1, fig. 2. TYPE LOCALITY. *Vema* Sta 52. 2711 fms Lat 41°03′S 07°49′E. TYPE SPECIMENS. Holotype, Mus. Comp. Zool. Harvard No. 224965; paratype, Natl Mus. Canada No. 4741.

DEPTH RANGE = 2864 m to 5280 m.

Shell description

The original shell description by Verrill & Bush (1898) is both detailed and accurate and requires no enlarging, however for comparative purposes the species is figured (Figs 1, 2, 3 & 4). Maximum recorded length 7·8 mm; prodissoconch length 300 μm–325 μm.

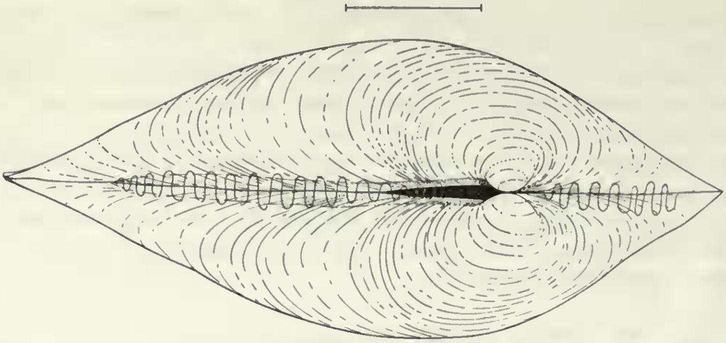

Fig. 1 *Malletia abyssorum*. Dorsal view of shell. From Station BG VI DS.79. (West European Basin). Scale 1 mm.

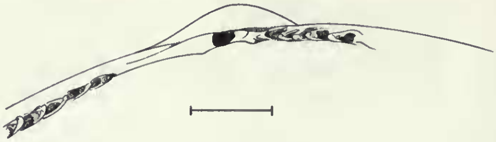

Fig. 2 *Malletia abyssorum*. Lateral view of hinge of right valve in umbonal region. From Station BG VI DS.79. Scale 0·25 mm.

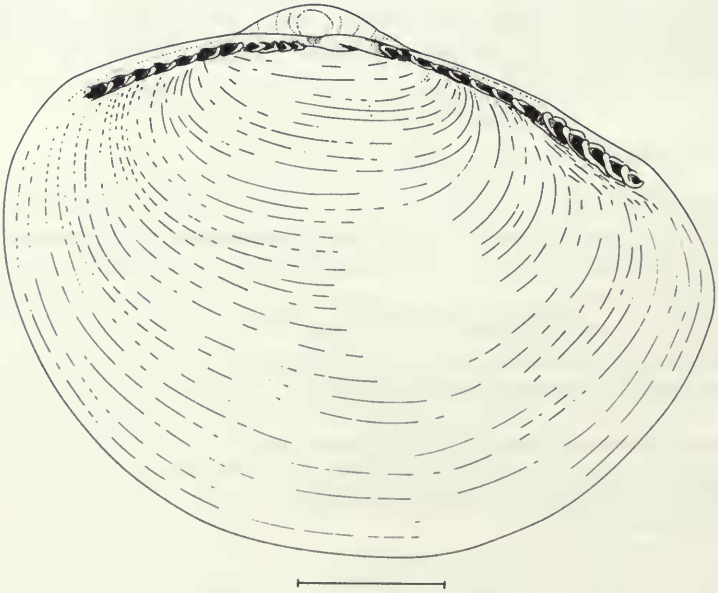

Fig. 3 *Malletia abyssorum*. Lateral internal view of left valve of shell. From Station BG VI DS.79. (West European Basin). Scale 1 mm.

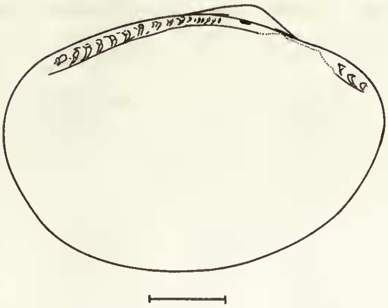

Fig. 4 *Malletia abyssorum.* Lateral internal view of left valve of type specimen. (Hinge broken since figured by Verrill & Bush, 1898), U.S. Nat. Mus. 52159. Station 2566, 4791 m off Martha's Vinyard. Scale 1 mm.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
NORTH AMERICA BASIN							
Atlantis II	64	2886	5	38°41·0′N	70°06·0′W	ES	21.8.64
	70	4680	26	36°23·0′N	67°58·0′W	ES	23.8.64
	72	2864	9	38°16·0′N	71°47·0′W	ES	24.8.64
Chain	77	3806	10	38°01·0′N	69°16·0′W	ES	30.6.65
	78	3829	144	38°01·0′N	69°19·0′W	ES	30.6.65
	80	4970	21	34°49·8′N	66°34·0′W	ES	2.7.65
Atlantis II	81	5042	19	34°41·0′N	66°28·0′W	ES	2.7.65
	83	5000	8	34°39·0′N	66°26·0′W	ES	3.7.65
Chain	84	4749	256	36°24·0′N	67°56·0′W	ES	4.7.65
	85	3835	1475	37°59·0′N	69°26·0′W	ES	5.7.75
Atlantis II	92	4694	37	36°20·0′N	67°56·0′W	ES	13.12.65
	93	5007	17	34°39·0′N	66°26·0′W	ES	14.12.65
	121	4800	178	35°50·0′N	65°11·0′W	ES	21.8.66
	122	4833	199	35°52·0′N	64°14·0′W	ES	21.8.66
	123	4853	69	37°29·0′N	64°14·0′W	ES	22.8.66
	124	4862	37	37°26·0′N	63°59·5′W	ES	22.8.66
	125	4825	284	37°24·0′N	65°54·0′W	ES	23.8.66
	126	3806	139	39°37·0′N	66°47·0′W	ES	24.8.66
	175	4693	81	36°36·0′N	68°31·0′W	ES	29.11.67
Chain	331	4793	21	41°13·2′N	41°38·7′W	ES	29.8.72
Knorr	340	3356	65	38°17·6′N	70°22·8′W	ES	24.11.73
WEST EUROPEAN BASIN							
Chain	328	4435	2	50°04·7′N	15°44·8′W	ES	23.8.73
	330	4632	10	50°43·4′N	17°52·9′W	ES	24.8.73
Polygas	DS20	4226	14	47°33·0′N	9°36·7′W	ES	24.10.72
(J. Charcot)	DS21	4190	16	47°31·5′N	9°40·7°W	ES	24.10.72
	DS22	4144	12	47°34·1′N	9°38·4′W	ES	25.10.72
	DS23	4737	163	46°32·8′N	10°21·0′W	ES	26.10.72
Biogass II	DS30	4106	4	47°38·3′N	9°33·9′W	ES	18.4.73
Biogass III	DS46	4521	12	46°28·6′N	10°23.0′W	ES	29.8.73
	CV30	4518	6	46°32·8′N	10°20.0′W	BT	29.8.73
	DS48	4203	7	44°29·0′N	4°54.0′N	ES	31.8.73

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Biogas IV	DS53	4425	25	44°30·4′N	4°56.3′W	ES	19.2.74
	DS54	4659	68	46°31·1′N	10°29·2′W	ES	21.2.74
	DS55	4125	65	47°34·9′N	9°40·9°W	ES	22.2.74
	CV36	4209	1	47°34·1′N	9°38·5′W	ES	22.2.74
Biogas V (Cryos)	DS67	4150	7	47°31·0′N	9°35·0′W	ES	17.6.74
	DS68	4550	2	46°26·7′N	10°23·9′W	ES	19.6.74
	DS69	4510	1	44°21·9′N	4°52.4′W	ES	20.6.74
Biogas VI (J. Charcot)	DS75	3250	1	47°28·1′N	9°07·8′W	ES	22.10.74
	CP13	4134	9	47°34·4′N	9°38·0′W	FT	23.10.74
	DS76	4228	8	47°34·8′N	9°33·3′W	ES	23.10.74
	DS77	4240	10	47°31·8′N	9°34·6′W	ES	24.10.74
	DS78	4706	201	46°31·2′N	10°23·8′W	ES	25.10.74
	DS79	4715	127	46°30·4′N	10°27·1′W	ES	26.10.74
	CP17	4706	9	46°30·8′N	10°29·5′W	ES	26.10.74
	DS80	4720	35	46°29·5′N	10°29·5′W	ES	27.10.74
	DS81	4715	8	46°28·3′N	10°24·6′W	ES	27.10.74
	CP19	4434	1	44°24·9′N	4°51·3′W	FT	28.10.74
	DS82	4462	94	44°25·4′N	4°52·8′W	ES	29.10.74
	DS84	4466	11	44°22·4′N	4°51·0′W	ES	29.10.74
	DS85	4462	4	44°30·0′N	4°53·9′W	ES	29.10.74
	CP21	4453	1	44°21·2′N	4°49·3′W	FT	30.10.74
	CP22	4475	21	44°22·9′N	4°54·8′W	FT	30.10.74
GUIANA BASIN							
Knorr	288	4429	2	11°04·0′N	55°05·0′W	ES	25.2.72
Biovema (J. Charcot)	DS04	5150	5	10°47·5′N	42°40·74′W	ES	24.3.71
ARGENTINE BASIN							
Atlantis II	243	3820	23	37°36·8′S	52°23·6′W	ES	14.3.71
	256	3917	86	37°40·0′S	52°19·0′W	ES	24.3.71
SIERA LEONE BASIN							
Atlantis II	148	3828	2	10°37·0′N	18°14·0′W	ES	7.2.67
	149	3861	13	10°30·0′N	18°18·0′W	ES	7.2.67
ANGOLA BASIN							
Campagne Walvis I	DS07	5157	1	27°00·0′S	1°06·4′E	ES	3.1.79
CAPE BASIN							
Campagne Walvis I	DS05	4560	9	33°20·5′S	2°34·9′E	ES	30.12.78
	DS06	4585	13	33°24·5′S	2°32·9′E	ES	31.12.78
	DS02	5280	9	33°54·7′S	5°07·5′E	ES	25.12.78
NEWFOUNDLAND BASIN							
Knorr	334	4400	121	40°43·3′N	46°14·2′W	ES	30.8.72
	331	4793	21	41°13·1′N	41°37·7′W	ES	29.8.72

*BT Blake Trawl. ES Epibenthic sledge. FT 'Honfleur' Trawl.

Filatova & Shileiko (1981) record four specimens of *M. abyssorum* (= *Clencheria diaphana*) from 5020 m in the South Australian Basin of the Indian Ocean. This is the only record of this species outside the Atlantic Ocean.

Morphology

No account of the anatomy has been given hitherto. The mantle is typically nuculanoid (Sanders & Allen, 1973). There is a marginal anterior sense organ developed from the middle sensory lobe which consists of two epithelial folds with a ciliated glandular region between them similar to that described for other nuculanoid species (Allen & Sanders, 1982). It is antero-ventral in position

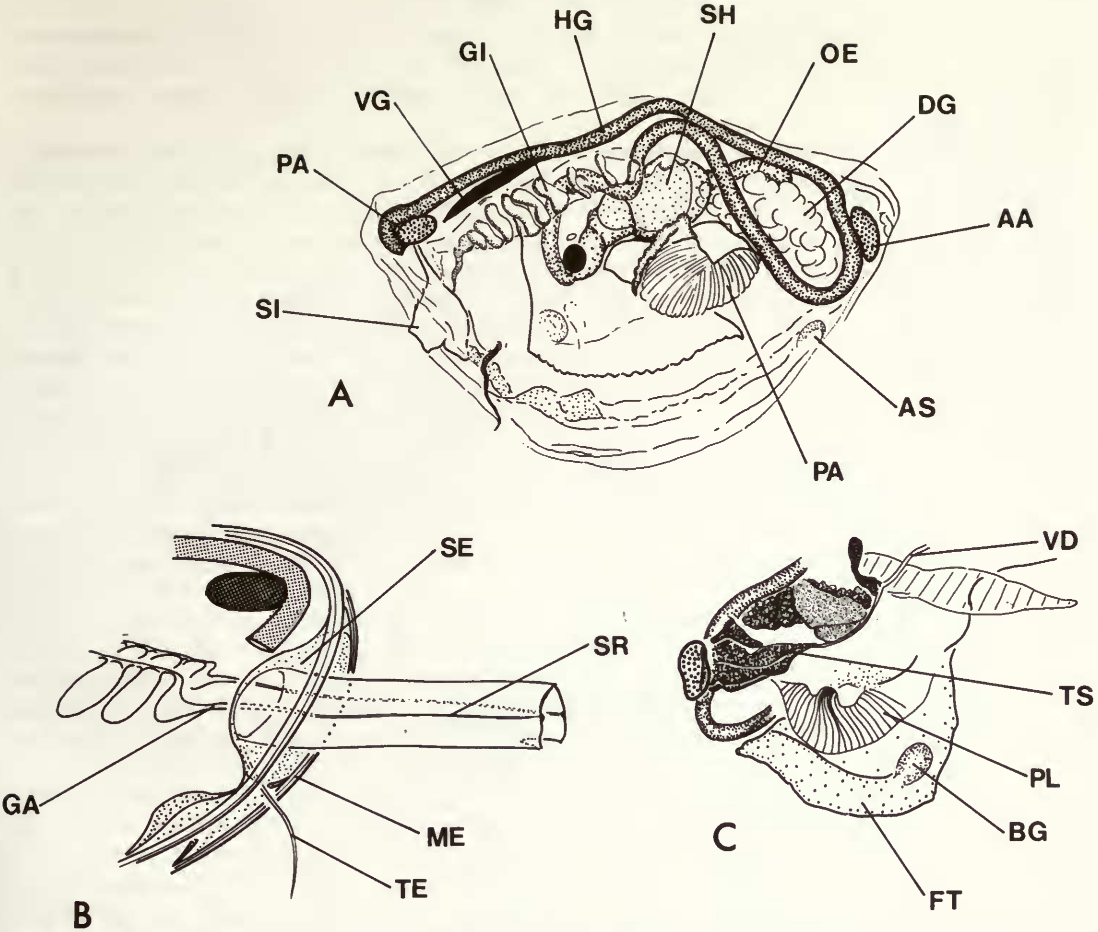

Fig. 5 *Malletia abyssorum.* (a) Lateral view of the anatomy from the right side; (b) diagrammatic lateral view of the posterior part of the body showing the relationship of the gill axis with extended siphon; (c) lateral view showing the early development of testis on the left side of the viscera. Abbreviations see Appendix.

and lies ventral to the ventral limit of the hind gut loop (Fig. 5). The posterior mantle edge is highly specialized and comprises a combined incurrent and excurrent siphon with a feeding region ventral to it. The latter is a specialized aperture created by the aposition of the mantle margins. The siphonal embayment and the feeding region do not encroach mantle space to any marked degree. Siphon formation involves fusion of the inner mantle lobes both dorsally and ventrally, however, that ventral to the inhalent siphon is not complete distally and here is limited to the adhesion of the opposing inner mantle lobes. The internal division into incurrent and excurrent lumena is not complete but the integrity of the passages is probably maintained by a pair of opposed longitudinal midlateral ridges (Fig. 5b). A single tentacle similar to that described for other nuculanoids (Allen & Sanders, 1982) is present on the right side and originates at the inner part of the siphonal embayment ventrally at the base of the siphon.

The adductor muscles are approximately equal in size and oval in shape. The 'quick' and 'catch' portions are approximately equal in size. The gill axis lies parallel to the dorsal margin of the shell and is attached posteriorly to the midlateral siphonal ridges and anteriorly to the body wall. There is no axial membrane posterior to the foot to physically separate a suprabranchial region from the rest of the mantle cavity. The gill plates number 24 in a specimen 3·0 mm total length. The palps, in preserved specimens, are relatively small. The palp ridges are slender in cross-section, lie close together and number 40 in a specimen 3 mm in length. The anterior limit of the palps, i.e. the position of the mouth, is far removed from the ventral face of the anterior adductor muscle (Fig. 5a). Judged by their small size, the palp proboscides when extended must be very slender.

The gut configuration follows the primitive protobranch form in which the hind gut makes a single loop to the right hand side of the body (Fig. 5a). The oesophagus first takes an anterior dorsal course towards the anterior adductor and just short of the muscle turns posteriorly to join the anterior face of the stomach dorsally. The stomach is elongate and not greatly inflated. The number of ciliated sorting ridges on the right side are few. The style sac is elongate penetrating the foot as far as the ventral limit of the neck. The hind gut further penetrates the foot ventral to the pedal ganglion (Fig. 5a) and, thereafter passes immediately posterior to the stomach dorsally to the umbo before taking an anterior and ventral course to the posterior face of the anterior adductor where it turns to follow the line of the dorsal shell margin, dorsal to the posterior adductor muscle to the anus which lies close to the posterior limit of the gill. Hind gut and body tissue do not penetrate mantle space as they do in *Tindaria* (Sanders & Allen, 1977). Voided faeces are guided by the gill axes and siphonal ridges. The greater part of the digestive gland is anterior to the stomach although overlapping it to some extent antero-laterally. That part on the right side is contained within the loop of the hind gut. The configuration of the section of the hind gut that lies posterior to the stomach is related to the attitude of the foot. In specimens in which the foot is fixed so that it lies in the posterior part of the mantle cavity there is a double bend in the course of the gut (Fig. 5a), when the foot is anterior the bends are pulled straight. A single typholosole that is little more than a faint ridge is present along the entire length of the hind gut. The epithelial cells of the hind gut are vacuolated. The foot is moderately large with a narrow neck, and the margins of the sole of the foot are papillate. The 'byssal' gland is well developed and spherical in outline. The pedal musculature consists of a broad band of posterior retractors attached to each valve between the posterior adductor muscle and the heart and three pairs of anterior reactors lying close together and attached to the valves between the anterior adductor and the anterior wall of the stomach. All these muscles closely flank the ventral walls of the stomach and pass into the foot (see Fig. 22). In addition there are subepithelial circular muscles and inner transverse muscles similar to those described in other protobranchs (Sanders & Allen, 1977; Allen & Sanders, 1982). The nervous system is well developed, the ganglia are stout and the cerebro-visceral commissure relatively thick. As in all malletiids the statocysts dorsal to the pedal ganglia are large and can be clearly seen in whole mounts. The sexes are separate and gonads develop peripheral to the digestive gland. Initially the gonads appear at anterior and ventral margins of the gland, but as they mature they spread laterally across its entire surface. A simple duct passes dorsal to the gill to a point directly above the posterior edge of the neck of the foot (Fig. 5c). Eggs are moderately large and measure approximately 140 μm maximum diameter as measured from sections of mature specimens. The kidneys are small, slender paired sacs that do not abut the posterior adductor but lie anterior to the visceral ganglion and extend anteriorly to the level of the hind gut posterior to the stomach.

The difference in size range of the samples is considerable (Fig. 6). The maximum length of specimens from the well sampled Gayhead-Bermuda transect is 6·5 mm and from the Bay of Biscay, also well sampled, is 7·8 mm. This difference may be but a reflection of the sampling techniques of the CNEXO compared with the Woods Hole ships. Histograms show various maxima over the size range of the samples. These may indicate discrete larval settlements and are not necessarily annual events (Fig. 6). The smallest specimen with developing gonads was 3·8 mm total length. No spent individuals were seen in any sample nor was there any evidence that brooding of the young occurs. In an analysis of specimens from Stations DS79, all specimens of 4·6 mm and above had gonads present, most of which were judged to be either half or three quarter mature. However, it was apparent that the testis was of greater volume than the ovary (Fig. 7). This is probably a reflection of the slow accumulation of egg reserves in an animal living at abyssal depths where food is limited and this may be generally true of animals living in abyssal depths. Sections indicate the eggs in individual specimens develop in unison.

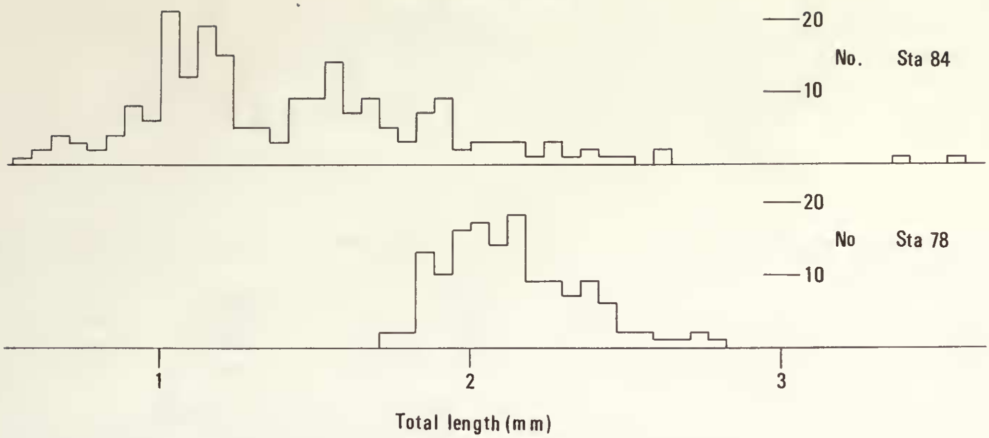

Fig. 6 *Malletia abyssorum*. Comparison of the size frequencies of samples from two Stations on the Woods Hole-Bermuda transect across the North American Basin.

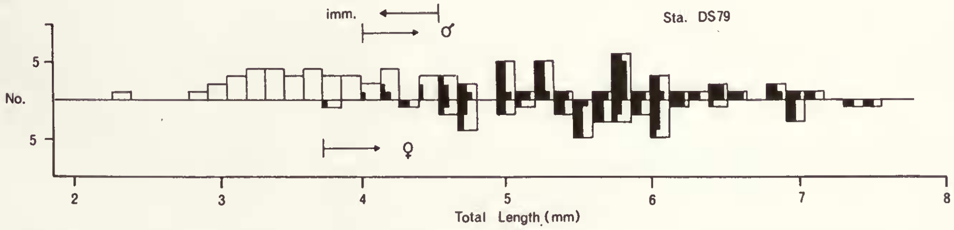

Fig. 7 *Malletia abyssorum*. Analysis of the maturity of a sample taken from Station DS.79 in the West European Basin. The degree of maturity is indicated by the proportion, blacked out on each size frequency.

The prodissoconch measures 300 µm,–325 µm. As in all species of *Malletia* the shell changes in shape with increasing size. Young specimens are oval in shape, while large specimens tend to become very slightly rostrate (Figs 8 & 9). Analysis of various populations shows that there is also a very gradual increase in shell height as reference to a plot of the height to length ratio to length shows (Fig. 9). The same figure also plots the ratio of posterior umbonal length and total length against total length and from this it is apparent that the shell is not fully rostrate until it is half grown, thereafter the rostral increase is much slower matching the increase in height length ratio. There is relatively little variation in shell shape in specimens from different geographical localities. *M. abyssorum* is one of the commoner protobranchs living at abyssal depths and therefore the number of larvae released might be expected to be relatively large. On that count alone, there should be a favourable spread of larvae for the maintenance of gene flow.

Malletia abyssorum is widely distributed throughout the abyssal depths of the Atlantic Ocean and is probably present in all its deep basins at depths in excess of 3500 m. The depth range for the entire suite of samples yielding specimens extends from 2864 m to 5280 m. In depths smaller than 3500 m, this species is a minor numerical constituent of the protobranch fauna and is often absent from well-sampled stations. At depths greater than 3500 m, however, *M. abyssorum* is a more constant element and often comprises a numerically significant percentage of the protobranch bivalves present (10-30%).

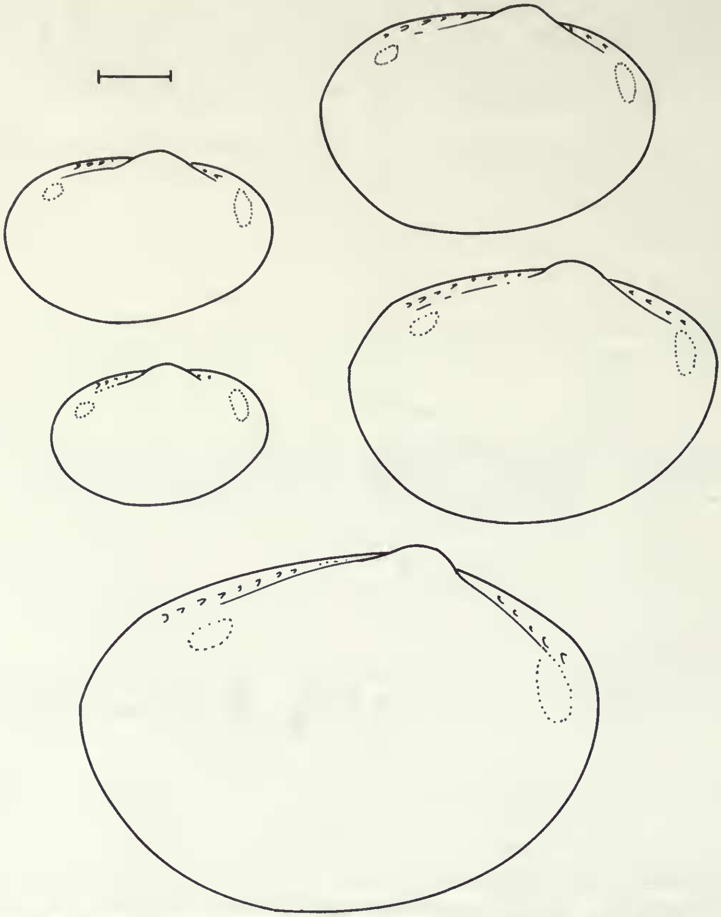

Fig. 8 *Malletia abyssorum*. Lateral outlines of specimens to show change in shape with increasing size. Scale 1 mm.

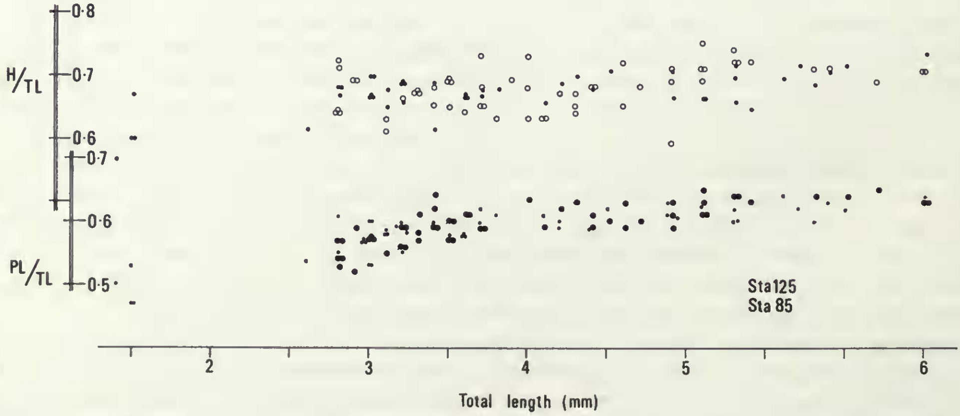

Fig. 9 *Malletia abyssorum*. Analysis of shell proportions of samples taken from Station 85, small closed circles, and Station 125, large open and closed circles, (North Atlantic Basin) showing a change in the ratio umbo-rostum length to total length PL/TL with increasing length, but little change in the ratio of height to total length H/L during growth.

The deeper depth limit of *M. abyssorum,* 5280 m, is an arbitrary boundary in the sense that it is merely the manifestation of the deepest abyssal station sampled rather than the *de facto* maximum depth occupied by this species. *M. abyssorum* has also been collected outside the Atlantic Ocean in the South Australian Basin of the Indian Ocean at a depth of 5020 m (Filatova & Shileika, 1981).

Malletia johnsoni Clarke, 1961

Malletia johnsoni Clarke, 1961: *Bull. Mus. Comp. Zool. Harv.* **125:** 370, pl. 2, fig. 6 TYPE LOCALITY. *Vema* Sta 22, Angola Basin, 175 miles W. of Banana, Zaire, 3065 m. TYPE SPECIMEN. Holotype, Mus. Comp. Zool. Harvard, 224961, paratypes Nat. Mus. Canada No. 4737.

Malletia estheriopsis Barnard, 1963: *Ann. S. Af. Mus.* **46:** 447, fig. 11b. TYPE LOCALITY. *Africana* Sta 317, Lat 33°55′S Long 16°30′E 2706 m—3036 m. TYPE SPECIMEN. Syntype, South Africa Mus. No. 9817.

DEPTH RANGE = 1100 m to 3834 m.

There has been considerable confusion between this species and *M. obtusa* G.O. Sars, 1878 (see p. 232). *M. obtusa* appears to be restricted to the biologically isolated Norwegian Basin and is found in more shallow water. The following records of *M. obtusa* are all of *M. johnsoni*: Jeffreys, 1879: 586; Verrill, 1884: 226 & 280; Smith, 1885: 245; Bush, 1893: 234; Locard, 1896: 202; Locard, 1898: 331: Verrill & Bush, 1898: 874, pl. 97, fig. 4; Thiele & Jaeckel, 1931: 49; Johnson, 1934: 19; Heath, 1937, fig. 62, 65; Clarke, 1962: 51.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
SIERRA LEONE BASIN							
Atlantis II	138	1976	3	10°36·0′N	17°52·0′W	ES	4.2.67
	141	2031	7	10°30·0′N	17°51·5′W	ES	5.2.67
	142	1796	4	10°30·0′N	17°51·5′W	ES	5.2.67
	143	2095	1	10°35·0′N	17°44·0′W	ES	5.2.67
	144	2204	3	10°36·0′N	17°49·0′W	ES	5.2.67
	145	2148	30	10°36·0′N	17°49·0′W	ES	6.2.67
	146	2867	2	10°39·5′N	17°44·5′W	ES	6.2.67
	147	2934	34	10°38·0′N	17°52·0′W	ES	6.2.67
ANGOLA BASIN							
Atlantis II	200	2754	1	9°29·0′S	11°34·0′E	ES	22.5.68
	201	2031	8	9°05·0′S	12°17·0′E	ES	23.5.68
CAPE BASIN							
Atlantis II	192	2154	3	23°02·0′S	12°19·0′E	ES	17.5.68
	194	2864	1	22°54·0′S	11°55·0′E	ES	17.5.68
Walda	DS06	2992	5	22°50·2′S	11°59·9′E	ES	11.6.71
	CY13	2044	195	12°03·7′S	12°22·3′E	T	.6.71
NORTH AMERICA BASIN							
Atlantis II	62	2496	140	39°26·0′N	70°33·0′W	ES	21.8.64
	64	2886	14	38°46·0′N	70°06·0′W	ES	21.8.64
	72	2864	53	38°16·0′N	71°47·0′W	ES	24.8.64
	73	1400	341	39°46·5′N	70°43·0′W	ES	25.8.64
Chain	76	2862	23	39°32·0′N	67°58·0′W	ES	29.6.65
	85	3834	2	37°59·0′N	69°26·0′W	ES	5.7.65
	87	1102	31	39°49·0′N	70°41·0′W	ES	6.7.65
	103	2022	185	39°44·0′N	70°37·0′W	ES	4.5.66
	115	2040	125	39°39·2′N	70°24·5′W	ES	16.8.66
Atlantis II	128	1388	19	39°46·5′N	70°45·2′W	ES	16.12.66
	131	2178	39	39°39·0′N	70°37·2′W	ES	18.12.66
Chain	210	2044	22	39°43·1′N	70°47·7′W	ES	22.2.69

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
WEST EUROPE BASIN							
Sarsia	S44	1739	14	43°41·0′N	3°35·0′W	ES	16.7.67
	S50	2379	13	43°47·0′N	3°38·0′W	ES	18.7.67
	S65	1922	50	46°15·0′N	4°50·0′W	ES	25.7.67
Chain	316	2191	109	50°58·7′N	13°01·6′W	ES	18.8.72
	318	2506	3	50°27·3′N	13°20·9′W	ES	19.8.72
Biogas I (La Perle)	DS11	2205	19	47°35·5′N	8°33·7′W	ES	8.8.72
	DS12	2180	1	47°28·5′N	8°35·5′W	ES	9.8.72
	CW03	1100	22	47°30·6′N	8°17·5′W	BT	5.8.72
	DS15	2246	8	47°35·2′N	8°40·1′W	ES	21.10.72
	DS18	2138	4	47°32·2′N	8°44·9′W	ES	22.10.72
	DS25	2096	5	44°08·2′N	4°15·7′W	ES	1.11.72
	CV09	2119	1	47°31·4′N	8°43·6′W	BT	22.6.72
Biogas II (J. Charcot)	DS32	2138	10	47°32·2′N	8°05·3′W	ES	19.8.73
Biogas III (J. Charcot)	DS35	2226	6	47°34·2′N	8°40·7′W	ES	24.8.73
	DS36	2147	2	47°32·7′N	8°36·5′W	ES	24.8.73
	DS37	2110	3	47°31·8′N	8°34·6′W	ES	24.8.73
	DS38	2138	8	47°32·5′N	8°35·8′W	ES	25.8.73
	DS49	1845	3	44°05·9′N	4°15·6′W	ES	1.9.73
Biogas IV (J. Charcot)	DS51	2430	10	44°11·3′N	4°15·4′W	ES	18.2.74
	DS52	2006	5	44°06·3′N	4°22·4′W	ES	18.2.74
	DS58	2775	1	47°34·1′N	9°08·2′W	ES	23.2.74
	DS61	2250	4	47°34·7′N	8°38·8′W	ES	25.2.74
	DS62	2175	19	47°32·8′N	8°40·9′W	ES	26.2.74
	DS64	2156	6	47°29·2′N	8°30·7′W	ES	26.2.74
	CP01	2315	1	47°34·6′N	8°38·8′W	FT	25.2.74
Biogas V (Cryos)	DS70	2150	2	44°08·8′N	4°17·4′W	ES	26.6.74
	CV39	2350	1	47°33·5′N	8°45·0′W	BT	14.6.74
	CP07	2170	8	44°09·8′N	4°16·4′W	FT	21.6.74
Biogas VI (J. Charcot)	CP08	2177	6	44°33·2′N	8°38·5′W	FT	20.10.74
	CP09	2171	2	47°33·0′N	8°44·1′W	FT	20.10.74
	DS71	2194	4	47°34·3′N	8°33·8′W	ES	20.10.74
	DS86	1950	3	44°04·8′N	4°18·7′W	ES	31.10.74

Shell description

Good descriptions of shell morphology have been given by Verrill & Bush (1898), Clarke (1961), Barnard (1963) and Knudsen (1970) and little needs to be added (Figs 10a & b). Maximum shell length 17·0 mm; prodissoconch length 410 μm.

Except for a very small resilium superficially inset onto the valves below the umbo the ligament is external and opisthodetic with a shorter component anterior to the umbo (Fig. 10a). The ligament in *M. johnsoni* is at its maximum development in terms of anterior and posterior extent both in the family and in the Order Nuculanoidea (Fig. 39). The resilium which represents the ligament of the prodissoconch or early post larva, comprises both inner and outer layers. It is extended posteriorly by both inner and outer layers with the outer layer extending posterior to the posterior limit of the inner layer. There is a further small posterior extension of the ligament by fused periostracum. Anteriorly the resilium is extended by anterior outer layer alone. As shell growth occurs the inner layer of the early resilium splits sagittally as the margins of what was the post larval valves open to 180° or more. The two halves of the inner layer are carried through the same angle, the split between them becoming filled with anterior outer layers. This was first observed in lamellibranchs (Allen, 1960) but had not been recorded in protobranchs no doubt because so few have a ligament so well developed as that in *M. johnsoni.*

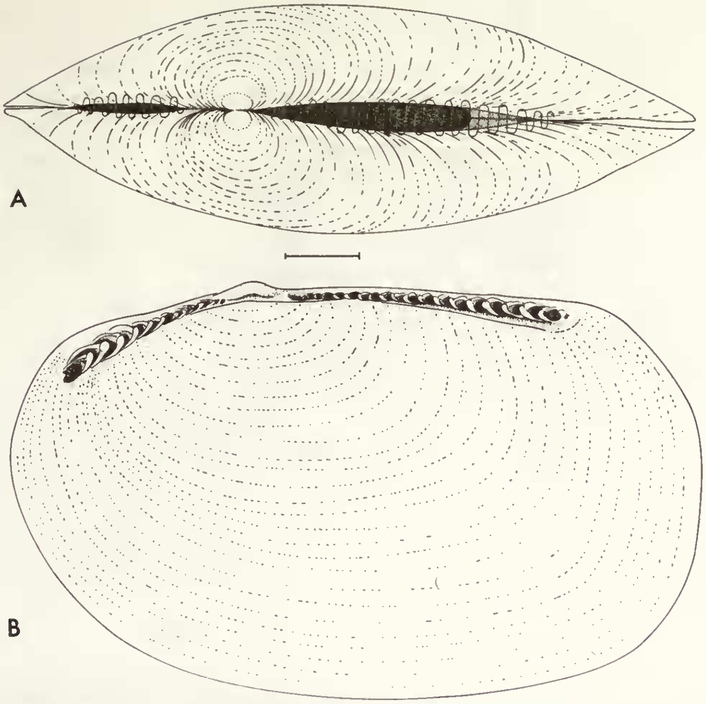

Fig. 10 *Malletia johnsoni.* (a) Dorsal view; (b) internal view of right valve of the shell of specimens from Stations 103 and 131 respectively. (North American Basin). Scale 1 mm.

Morphology

A few morphological details of *M. johnsoni* have been given by Verrill & Bush (1898) and Knudsen (1970) and some of the observations, particularly those on the siphons, are inaccurate. Verrill & Bush (1898) admit that their specimens were poorly preserved and from the small amount of detail given it must be assumed that those of Knudsen (1970) may also have been in poor condition.

Although there are relative differences the basic form of the anatomy is similar to that of *M. abyssorum* (Fig. 11). The adductor muscles are relatively large and oval in shape. The anterior sensory organ is well developed and so far anterior in position as to be slightly anterior to the anterior adductor. The feeding aperture is particularly well developed with an extensive inner glandular area (Fig. 11). The siphon is moderately long and can be completely retracted within a deep, narrow embayment. Whole mounts and sections show that the siphon is not permanently divided into inhalent and exhalent channels nor is there a pair of marked internal ridges of the type present in *M. abyssorum* which by aposition would divide the siphon into inhalent and exhalent portions (Fig. 12a). Nevertheless, there are few longitudinal muscle fibres ventrolaterally to each side of the siphon wall. These fibres connect with the gill axes but whether there is any effective division into incurrent or excurrent parts is very doubtful.

M. johnsoni is one of the few deep sea species that have been examined alive and muscular division of the siphonal aperture was not observed. Only outgoing currents, carrying faecal and pseudofaecal material were seen. The siphon was never extended far beyond the shell margins, but this may be but a reflection on the unnatural conditions under which these observations were made (in cool seawater in a glass dish at 1 atmosphere) and the inevitable lack of well-being of the animal. In contrast the single tentacle attached to the inner lower right wall of the mantle embayment was long, moderately developed, and extended some distance beyond the shell margins. The tentacle in cross section is composed of an outer epithelium tissue enclosing ten groups of longitudinal connective tissue and muscle fibres and a pair of small central longitudinal cavities.

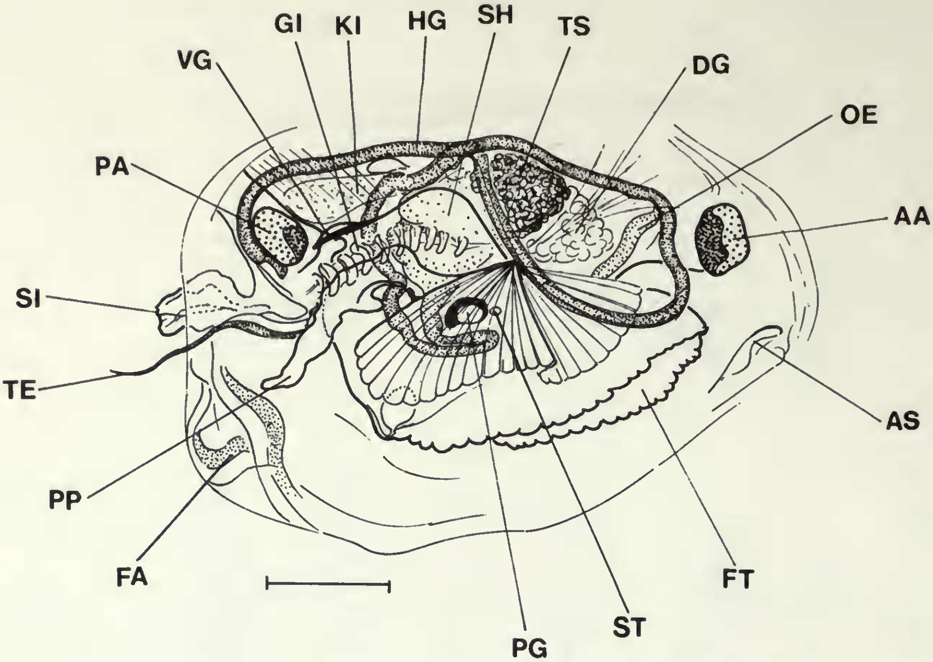

Fig. 11 *Malletia johnsoni.* Lateral view of the anatomy from the right side. For abbreviations see Appendix. Scale 1 mm.

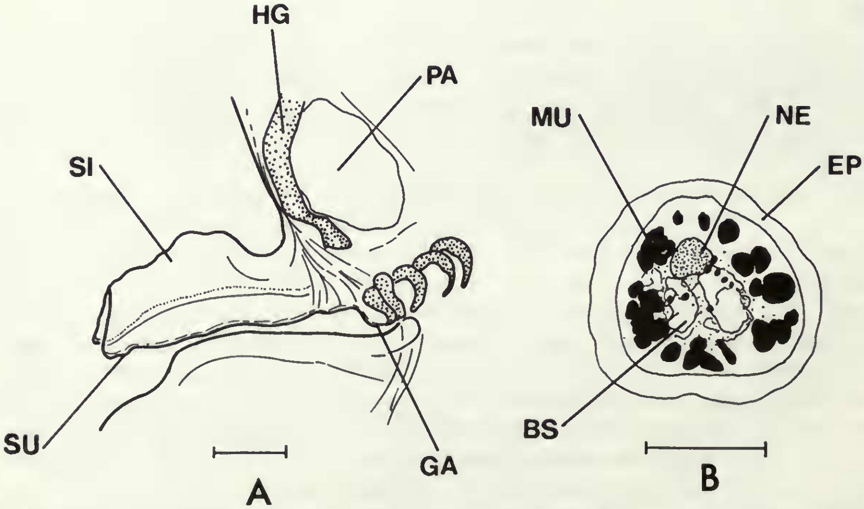

Fig. 12 *Malletia johnsoni.* (a) Lateral view of siphon (b) transverse section of siphonal tentacle. Scale 0·05 mm. Abbreviations see Appendix.

There is an acentric longitudinal nerve present (Fig. 12b). The flaps of the feeding aperture were also extended somewhat beyond the shell margins in living specimens, the palp proboscides being partially extended through the aperture. There is a main ventral rejection tract to the inside of the inner mantle fold, and particles are carried to the dorsal side of the feeding aperture. Particles on the mantle ventral and posterior to the palps are rejected via this tract.

Gills and palps are similar to those of *M. abyssorum*. The palps are moderately large with fine, numerous ridges. Rejected particles from each palp travel posteriorly to the posterior limit of the ventral palp margin from where they pass to the mantle and join the main rejection current. Observations on living gills indicate that particles on the frontal surface are passed to the ventral midline and then carried posteriorly to join either pseudofaecal material at the dorsal limit of the feeding aperture or pass through the siphon. No particles on the gills were seen to move anteriorly and be accepted by the palps or palp proboscides. Nevertheless, this has been seen to occur in some species of deep sea protobranchs.

The gut follows a similar course to that described in *M. abyssorum*. The stomach is very large taking up the posterior half of the visceral mass. Sorting areas are extensive with at least 16 ridges on the right hand wall of the stomach (Fig. 13). The gastric shield is also extensive with a large hooked tooth. Three apertures open to the digestive diverticula, the greatest proportion of which lies anterior to the stomach. The style sac is large and the gut extends ventral to the pedal ganglia. The hind gut has a single, poorly developed, typhlosole forming a fine ridge that is even less obvious than that of *M. abyssorum*.

The commissures and ganglia are large and prominent. The visceral ganglia abuts the anterior face of the posterior adductor muscle. There is a very large statocyst dorsal to each pedal ganglion.

The strong muscular, divided, foot is large with moderately fine papillae at the margins of the sole. The 'byssal' gland is large and spherical.

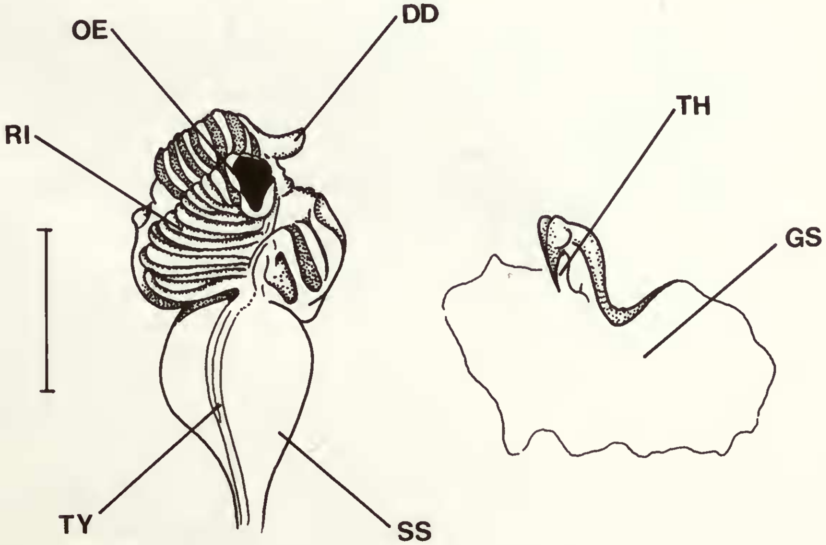

Fig. 13 *Malletia johnsoni*. Anterior view of stomach and style sac, with a gastric shield shown separately in whole mount. Scale 0·5 mm.

The gonads are similar in position to those of *M. abyssorum*. As in all deep sea protobranchs there are changes in shell shape as growth proceeds. In young specimens the umbos are posterior to the dorsal mid point of the shell (Fig. 14). The young shell is more oval in shape than it is when fully grown. With increasing size the height of the posterior part of the shell increases and in relation to length becomes more angular in outline. From the size frequency histograms which, unusually for a deep sea bivalve, are skewed markedly to the left, relatively fast growth is indicated (Fig. 15).

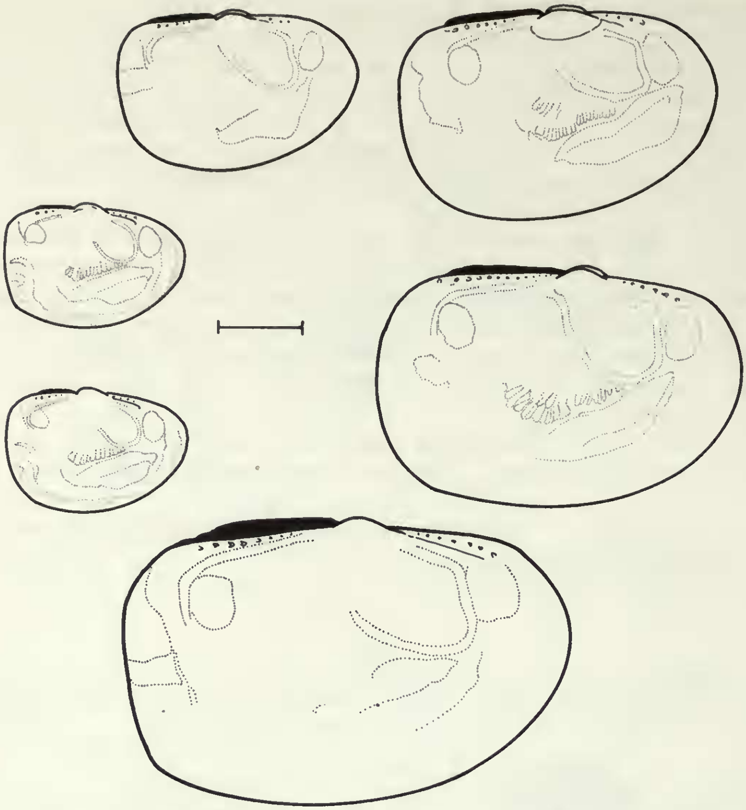

Fig. 14 *Malletia johnsoni.* Lateral view of a growth series showing variations in shape and relative positions of the umbo. Scale 1 mm.

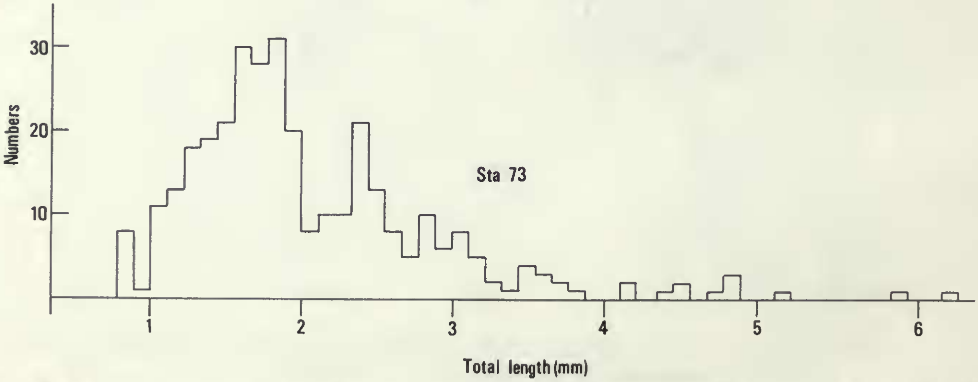

Fig. 15 *Malletia johnsoni.* Size frequency distribution of a sample from Station 73, North Atlantic Basin.

Malletia johnsoni is an inhabitant of the lower continental slope and upper abyssal rise. It has been collected from the Cape, Angola, Guinea, Sierra Leone, West Europe and North America Basins. On the assumption that *M. johnsoni* also occurs in those Eastern Atlantic Basins that were either not or superficially sampled (Cape Verde and Canaries Basins) and in the Newfoundland Basin in the Northwest Atlantic where analysed samples from the appropriate depths are lacking, we conclude that this species is continuously present at depths of from about 1000 m to 3000 m throught the entire Eastern Atlantic, across the North Atlantic and southwards in the Northwest Atlantic to at least the North America Basin. James (1972) reports an undescribed malletid similar if not identical to *Malletia johnsoni* from the Gulf of Mexico and Caribbean Basins with depth records which fall within the depth range found for *M. johnsoni*. It is occasionally collected from stations less than 1000 m and more than 3000 m but at the peripherals of its depth range where it is a minor numerical constituent of the protobranch fauna. For example, at its deepest recorded depth 3834 m (WHOI Sta 85, North America Basin), it comprised a mere 0·03% of the protobranch fauna.

Malletia grasslei (new species)

TYPE LOCALITY. *Knorr* Cruise 25, Sta 297, 523 m, Lat 7°45·3′N, Long 54°24′W, Guiana Basin.

TYPE SPECIMEN. Holotype, BM(NH) 1984058.

DEPTH RANGE = 523 m to 1022 m.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	295	1022	13	8°04·2′N	54°21·3′W	ES	28.2.72
	297	523	158	7°45·3′N	54°24·0′W	ES	28.2.72

Shell description

Shell slender, elongate, moderately fragile, fine concentric growth lines, maximum shell height at level of umbos; umbos fairly prominent, anterior to midline, anterior/posterior umbonal length ratio 5/9 in largest specimen, more central in small specimens; antero-dorsal margin gently slopes to form continuous curve with anterior margin, anterior limit of shell dorsal to horizontal midline of shell, postero-dorsal margin almost straight, slightly angled at posterior margin of hinge plate, posterior margin faintly angulate at two points dorsal to horizontal midline, ventral margin gently curved; hinge plate slender, slightly expanded posteriorly and anteriorly, numerous chevron teeth (up to 52), posterior series exceeding anterior in ratio of approximately 1·5/1, anterior and posterior series separated by edentulous space below umbos; ligament external and opisthodetic extended by fused periostracum, external except for small resilium inset at margin of edentulous space, short anterior external portion barely visible (Figs 16a, b & c). Maximum recorded shell length 17·9 mm; prodissoconch length 320 μm.

Morphology

The basic morphology of *M. grasslei* is similar to *M. johnsoni* (Fig. 17). Differences that occur can be related to the attenuated and slender form of this species. The anterior sense organ lies close to the anterior limit of the mantle margin. The posterior adductor muscle is elongate oval in shape but of similar area to the ovate anterior adductor muscle. The siphon is long. It differs from that described for *M. abyssorum* in that dorsal and ventral fusion forms an exhalent siphon but the ventral margins of the inhalent siphon are not fused but come together to form the inhalent channel. The gill axes connect with the ventrolateral edges of the exhalent siphon (Fig. 17b). The feeding aperture is relatively broad and moderately deep occupying about a third of the posterior ventral mantle margin. There is a single elongate tentacle on the right side and attached ventral to the base of the siphon. The gill axis is parallel to the antero-posterior axis. The palps are relatively short in preserved specimens and do not extend beyond the limits of the foot. There are 18 broad ridges in a specimen 5 mm in length.

In whole mount preparations a pair of small anterior palp retractor muscles can be seen attached to the shell posterior to the anterior adductor and to the palp at the point close to the mouth. The palp proboscides are very long and slender, a reflection of the small size of the palp and the posterior elongation of the body (Fig. 17a).

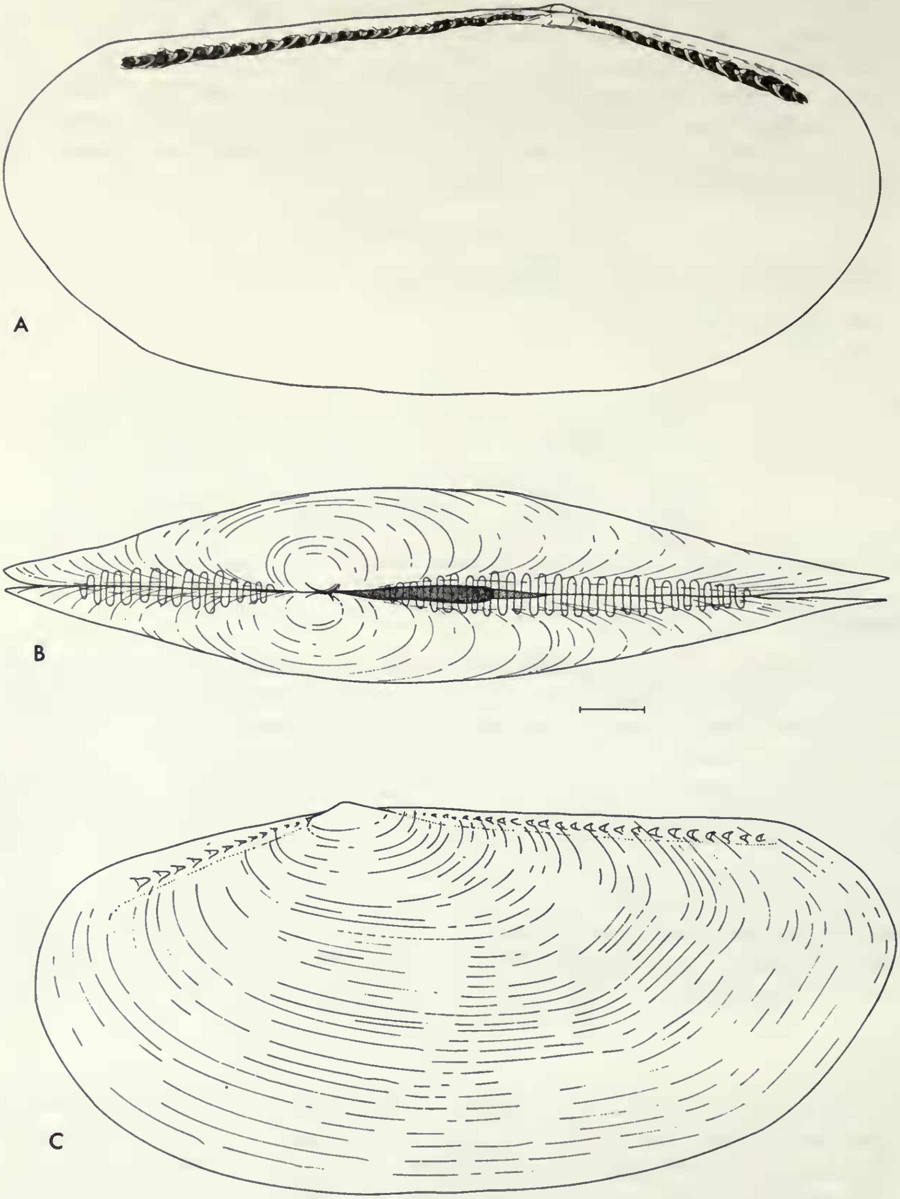

Fig. 16 *Malletia grasslei.* (a) Lateral view of left valve; (d) dorsal; (c) lateral view of the shell of the type specimen. Station 297, Guiana Basin, 7°45·3′N 54°24·0′W, 523 metres. Scale 1 mm.

Digestive and nervous systems are similar to those of *M. abyssorum* and *M. johnsoni.* The foot is elongate and points anteriorly, the margins are fringed with moderately fine papillae. The 'byssal' gland is exceptionally large. It is spherical, the sphere partially divided sagittally by an extension of the dorsal part of the peripheral epithelial cells. The cavity of the sphere appears to be filled with large cells, the contents of which cannot be made out. Peripheral nuclei can be seen only in the walls of the preparations (Allen & Chevis, in prep).

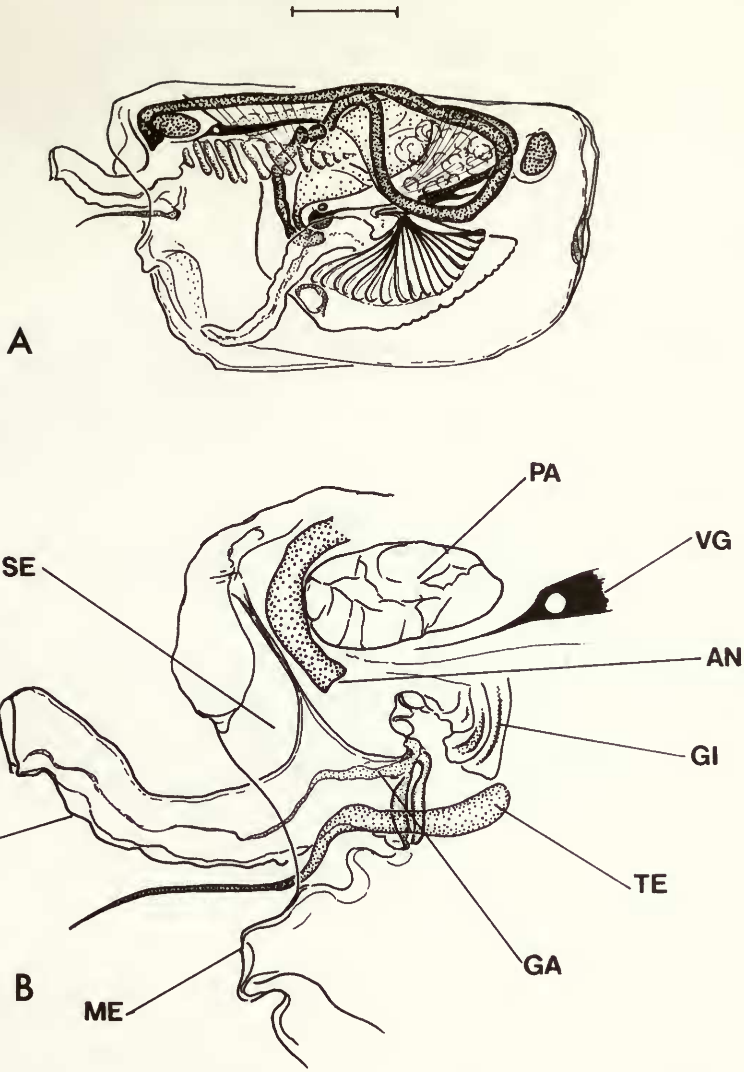

Fig. 17 *Malletia grasslei.* (a) Anatomy seen from the right side. Scale 1 mm (b) enlarged detail of siphonal region. For abbreviations see Appendix.

There is a very marked alteration in shell shape as growth proceeds. Specimens become more attenuated and there is a relative change in the height/length ratio which is accentuated by a corresponding relative increase in post umbonal shell length (Figs 18 & 19).

Malletia grasslei is present only at the two most shallow stations in the Guiana Basin from depths of 523 m and 1022 m, thus it has a remarkably narrow depth range and a very circumscribed zoogeographic distribution.

Malletia surinamensis (new species)

Type locality. *Knorr* Cruise 25, Sta 295, 1022 m, Lat 8°04·2′N Long 54°21·3′W, Guiana Basin.

Type specimen. Holotype, BM(NH) No. 1984059.

Depth range = 523 m to 1022 m.

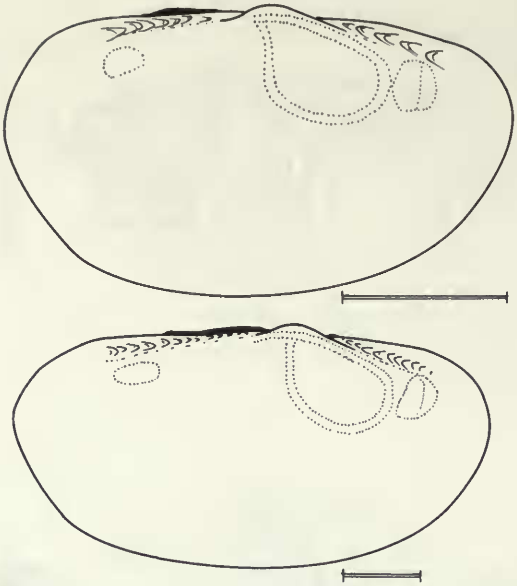

Fig. 18 *Malletia grasslei.* Comparison two shells in lateral view at different magnifications so that drawings are approximately the same overall length. Scale 1 mm. Station 295, Guiana Basin.

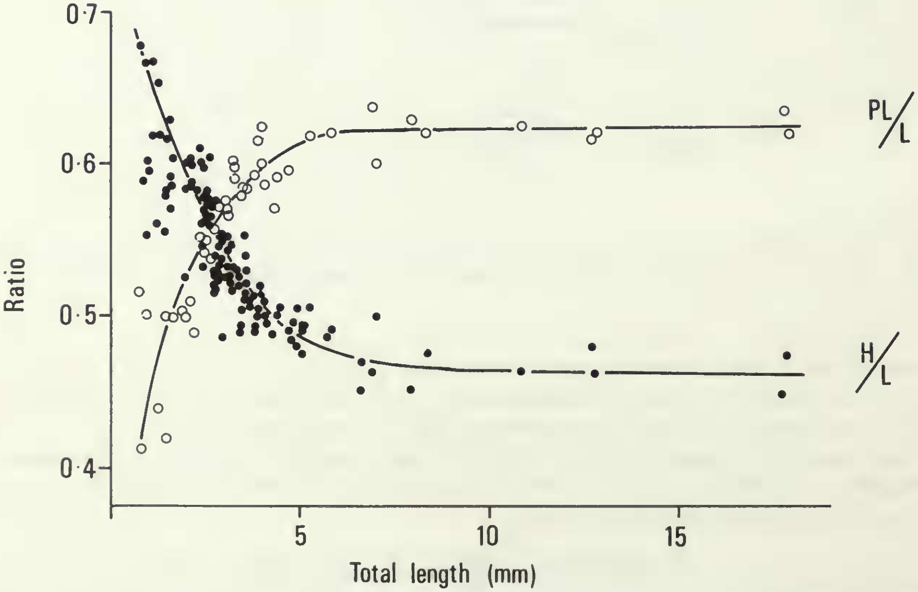

Fig. 19 *Malletia grasslei.* Analysis of shell proportions of sample taken from Station 297 showing changes with increasing size of the height/length ratio H/L and of the umbo to rostrum length/total length ratio PL/L.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	295	1022	40	8°04·2′N	54°21·3′W	ES	28.2.72
	297	523	9	7°45·3′N	54°24·0′W	ES	28.2.72

Shell description

Shell relatively short, moderately robust, with fine concentric lines, highest part of shell posterior to umbo; umbos prominent, anterior; anterior/posterior umbonal length ratio 2/3 in largest specimens, antero-dorsal margin almost straight, slopes gently to an anterior margin which it meets in a sharp curve dorsal to horizontal midline of shell, postero-dorsal margin almost

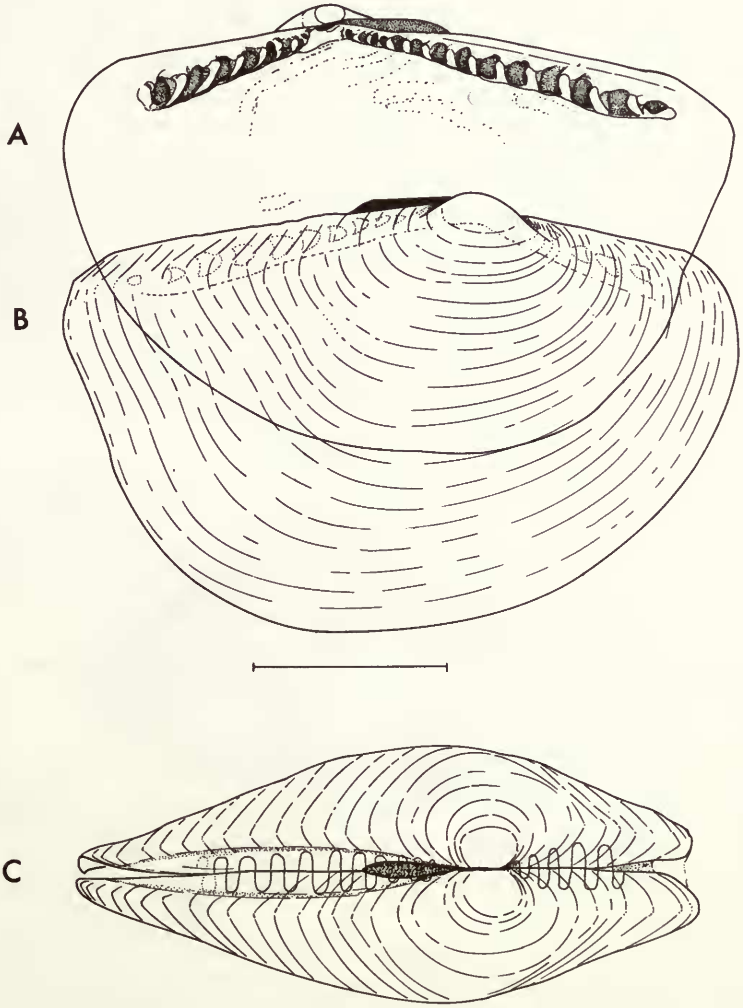

Fig. 20 *Malletia surinamensis.* (a) Lateral view of right valve; (b) lateral; (c) dorsal view of shell of type specimen from Station 295, Guiana Basin, 8°04·2′N 54°21·3′W, 1022 metres. Scale 1 mm.

straight, sharply angulate where it meets posterior margin, posterior margin deep, ventrally slightly sinuous where a very faint ridge meets margin, ventral margin moderately deeply curved; hinge plate moderately strong, well developed chevron teeth (up to 25), posterior series exceeding anterior by approximately 2/1, series separated by endentulous space below umbo; small elongate marginal resilium, relatively short opisthodetic, external, ligament, anterior outer layer very short, and due to curvature of the beaks may not be visible externally (Figs 20a, b & c; 39). Maximum shell length 4·9 mm; prodissoconch length *c.* 300 μm.

This species bears some resemblance to *Malletia dilatata* (Philippi, 1884) a specimen of which taken in 534 m off Moro Light, Havana, is illustrated in Figure 21. *M. surinamensis* does not have the upturned concave postero-dorsal margin which *M. dilatata* shares with the genus *Megayoldia*.

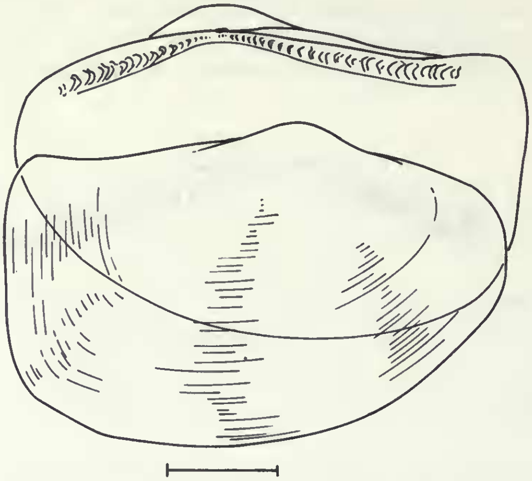

Fig. 21 *Malletia dilatata*. Internal and external lateral views of right valve of specimen, MCZ 7957, off Moro Light, Havana, 534 metres.

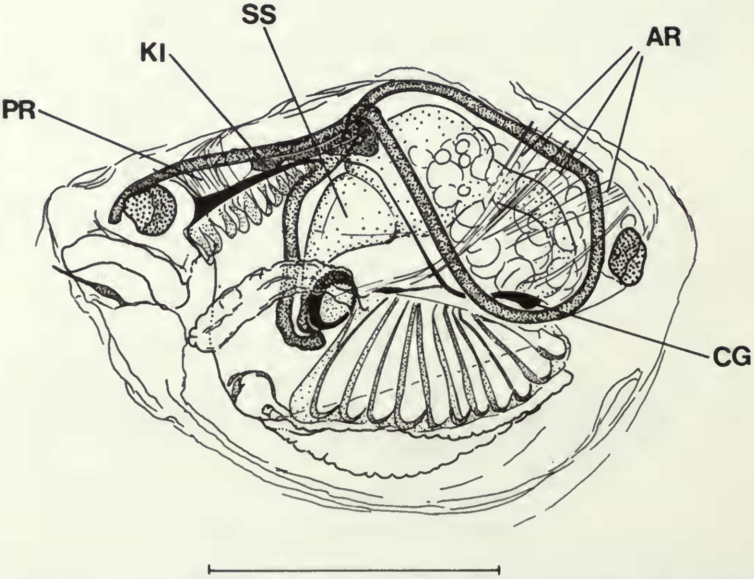

Fig. 22 *Malletia surinamensis*. Anatomy as seen from the right side. Scale 1 mm. Abbreviations see Appendix.

Although without the great development of a rostrum there is also some slight resemblance in shell shape to the genus *Spinula* (Allen & Sanders, 1982), however the ligaments is opisthodetic and not amphidetic, and the anatomy is typically malletiid in character. Thus, the hind gut is a single loop to the right of the body rather than multiple coils.

Morphology

The morphology of *M. surinamensis* is similar to that described for *M. abyssorum* (Fig. 22). The anterior mantle sense organ is situated ventral to the anterior adductor. The adductor muscles are large in comparison with other species of *Malletia.* The siphon is not permanently divided into inhalent and exhalent channels nor is there any clear internal ridging. As in *M. johnsoni* the gill axes attach ventrally and thus there is no clearly marked region that can be homologised with an inhalent siphon. The siphon is slender and ventral to it is an extensive feeding aperture. A pair of epithelial glandular ridges some seven cells deep occur to the inside of the inner mantle fold close to the siphonal embayment. The folds forming the feeding area are well supplied with mucous cells of two kinds. Glands are also present in the proximal ventral epithelium of the siphon. A tentacle is present on the right side ventral to the base of the siphon. The gill axes are at a slight angle to the anterior posterior axis of the body and in a specimen 2·0 mm total length there are 12 gill plates. The palp is relatively large with a small number of broad ridges. The palp proboscides are long and slender. The morphology of the foot and the nervous system is similar to that described for *M. abyssorum.* The hind gut is relatively slender. The digestive gland is clearly more extensive on the left side of the body but this reflects the space taken up on the right by the mid gut. The kidney extends far anterior to the level of the hind gut, posterior to the stomach. Microscopic examination of the contents of the stomach shows that there are more skeletal remains than are present in the mud trapped in the mantle, perhaps indicating that selective processes occur in the collection of food material.

Although likely, the present samples give no indication of a change in shape with the increasing size. This is because of the limited size range with 33 specimens out of 40 in the larger of the two samples under 2 mm total length and only two (3·6 mm and 4·9 mm) being larger than 3 mm.

Malletia surinamensis is limited to the same two shallow sampling sites as *M. grasslei,* i.e. depths of 523 m and 1022 m in the Guiana Basin.

Malletia malita (new species)

TYPE LOCALITY. *Knorr* Cruise 25, Sta 295, depth 1022 m, Lat 8°04·2′N, Long 54°21·3′W, Guiana Basin.

TYPE SPECIMEN. Holotype, BM(NH) No. 1984057.

DEPTH RANGE = 523 m to 1518 m.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	293	1518	2	8°58·0′N	54°04·3′W	ES	27.2.72
	295	1022	20	8°04·2′N	54°21·3′W	ES	28.2.72
	297	523	4	7°45·3′N	54°24·0′W	ES	28.2.72

Specific description

Shell ovate, moderately stout, with fine concentric growth lines, highest part of shell coincides with midline; umbos moderately prominent, slightly anterior to mid point of shell, in largest specimens posterior/anterior ratio 5/4; antero-dorsal shell margin more or less straight, inclined to form an even curve with anterior margin, postero-dorsal margin more or less straight, forms angle at posterior limits of hinge plate, posterior margin rostrate with moderately well defined ridge from umbo which meets posterior margin dorsal to horizontal midline from tip of blunt rostrum, very slight sinuosity ventral to rostrum, ventral margin smoothly and moderately deeply curved; lunule and escutcheon outlined by faint ridge; hinge plate moderately strong, expanded posteriorly and anteriorly, well-developed chevron teeth (up to 28), posterior series exceeding anterior in ratio approximately 5/3, series separated by edentulous plate below umbo, small marginal resilium; opisthodetic, external, ligament, short external anterior part (Figs 23a & b). Maximum shell length 7·8 mm; prodissoconch length 285 µm.

The form of the ligament is similar to other malletiids described here differing only in the extent of its parts. In *M. malita* the anterior outer layer extends over the proximal fifth of the anterior hinge plate while posteriorly the primary ligament extends to half the length of the hinge plate (Fig. 23a).

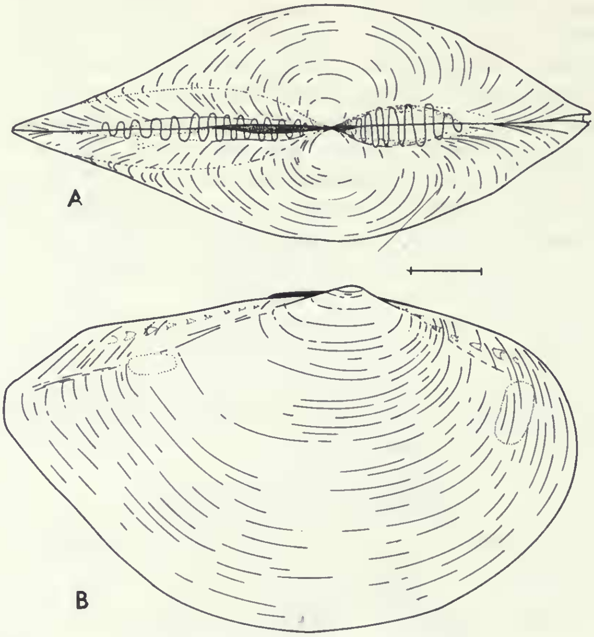

Fig. 23 *Malletia malita.* (a) Dorsal view; (b) lateral view of shell of type specimen from Station 295, Guiana Basin, 8° 04·2′N 54° 21·3′W, 1022 metres. Scale 1 mm.

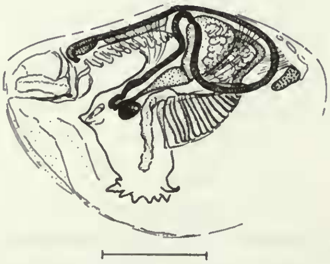

Fig. 24 *Malletia malita.* Anatomy seen from the right side. Scale 1 mm.

Morphology

The morphology of *M. malita* is essentially similar to that of other species described here (Fig. 24). The mantle differs somewhat from that of other species, in that the position of the anterior marginal sense organ is ventral and slightly anterior to the anterior adductor muscle. The adductor muscles are unequal in size, the posterior being the smaller, they also differ in shape, the anterior being broad and oval while the posterior is narrow, elongate and parallel to the dorsal shell margin. The siphons resemble those of *M. grasslei*. The feeding aperture occupies more than half of the ventro-posterior mantle margin but is relatively shallow. The gill axis lies parallel to the posterior dorsal shell margin and bears up to twelve plates. The palp is moderately large with up to eighteen ridges.

The morphology of the internal organs is similar to other malletiids described here. It may be noted that the hind gut is relatively narrow and the visceral ganglion lies short of the posterior adductor muscle. The commissures are slender. The foot is relatively small, fringing papillae being few in number. The 'byssal' gland is of moderate size.

No specimen is mature but in several, developing gonads can be seen at the anterior and ventral edge of the digestive gland.

Malletia malita is the third severely restricted malletiid species only to be found in the Guiana Basin. It co-occurs with *M. grasslei* and *M. surinamensis* at the two shallowest depths of 523 m and 1022 m but in this case is also present at the third shallowest depth of 1518 m.

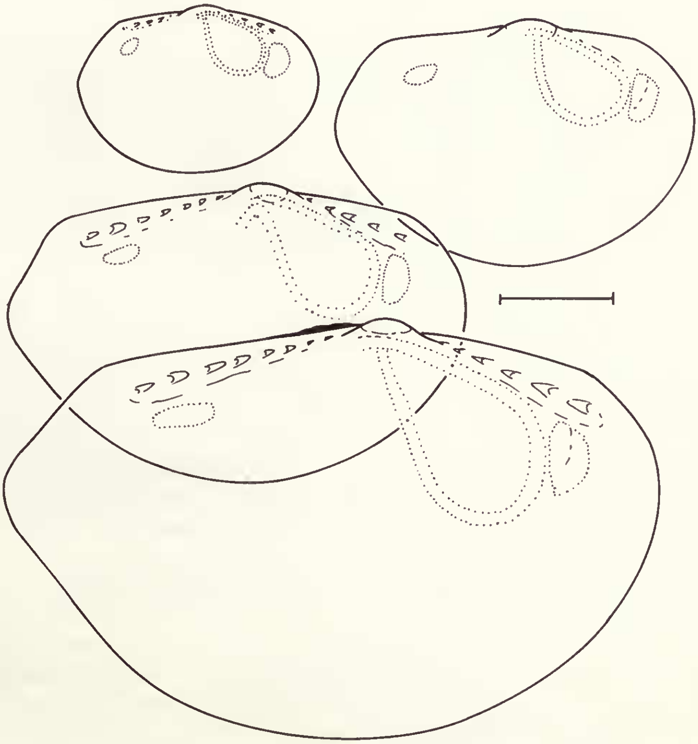

Fig. 25 *Malletia malita.* Lateral outlines of specimens to show change in shape with increasing size. Scale 1 mm.

As in the previous species, there are too few specimens to make any sure statement on change in shape with increasing size, but it is highly likely that the shell becomes more rostrate with age (Fig. 25).

Malletia pallida Smith, 1885

Malletia pallida Smith, 1885: *Chall. Rep.* **13:** 246, pl. 20, figs 8, 8a. TYPE LOCALITY. Challenger Sta 137, depth 4667 m, Lat 35°59·0′S, Long 01°34·0′E. TYPE SPECIMEN. Holotype, BM(NH) No. 1887.2.9.300 ba
Nuculana pallida Knudsen, 1970: *Galathea Rep.* **11,** figs 9 & 10.

DEPTH RANGE = 1261 m to 5280 m.

Knudsen (1970) gives no reason for transferring this species to the genus *Nuculana*. The species conforms to all the characters of genus *Malletia*.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
SIERRA LEONE BASIN							
Atlantis II	146	2891	1	10°39·5′N	17°44·5′W	ES	6.2.67
	147	2934	29	10°38·0′N	17°52·0′W	ES	6.2.67
	148	3828	6	10°37·0′N	18°14·0′W	ES	7.2.67
	149	3861	20	10°30·0′N	18°18·0′W	ES	7.2.67
GUINEA BASIN							
Walda (J. Charcot)	DS28/36	1261	4	4°21·2′N	4°35·2′E	ES	.6.71
ANGOLA BASIN							
Atlantis II	195	3797	58	14°40·0′S	9°54·0′E	ES	19.5.68
	197	4595	3	10°29·0′S	9°04·0′E	ES	21.5.68
	198	4566	7	10°24·0′S	9°09·0′E	ES	21.5.68
	199	3779	11	9°49·0′S	10°33·0′E	ES	22.5.68
	200	2754	5	9°43·5′S	10°57·0′E	ES	22.5.68
Walda (J. Charcot)	CY13/19	2044	228	12°03·7′S	12°22·3′E	T	.6.71
	DS05/06	2992	5	21°45·0′S	11°07·8′E	ES	11.6.71
CAPE BASIN							
Campagne Walvis I	DS02	5280	3	33°54·7′S	5°07·5′E	ES	25.12.78

Shell description

The original description by Smith (1885) and its later amplification by Knudsen (1970) is detailed and accurate. The species is closely related to *M. polita* of the North America Basin, to *M. polita* of the West Europe Basin and *M. cuneata* of the North Atlantic Ocean. Maximum shell length 16·5 mm; prodissoconch length 260 μm.

The morphologies of the species and varieties of the *pallida/polita/cuneata* complex are very similar. They possess the same basic malletiid form and only items of significance for identification need to be mentioned. The shell differences are subtle and not easily defined, but they are consistent and can be recognized by the experienced observer, and, thus, are best illustrated (Fig. 26a & b). In each case there is a change in shell shape with increasing size and undoubtedly the larger the specimen the more readily identifiable it becomes.

In the case of *M. pallida* the following may be mentioned: The umbos are small and anterior in position, the anterior/posterior umbonal length ratio is 5/8. The ligament is elongate, the anterior and posterior parts, not including extension by fused periostracum, occupy half the length of the dorsal shell margin (Figs 26a & 39). The shell is characteristically inflated in the central region lateral to the umbos and the maximum width coincides with the line of the maximum height measurement. A moderately strong hinge bears numerous close-set chevron teeth (50 in large specimens), the anterior and posterior series are in the ratio of 2/3.

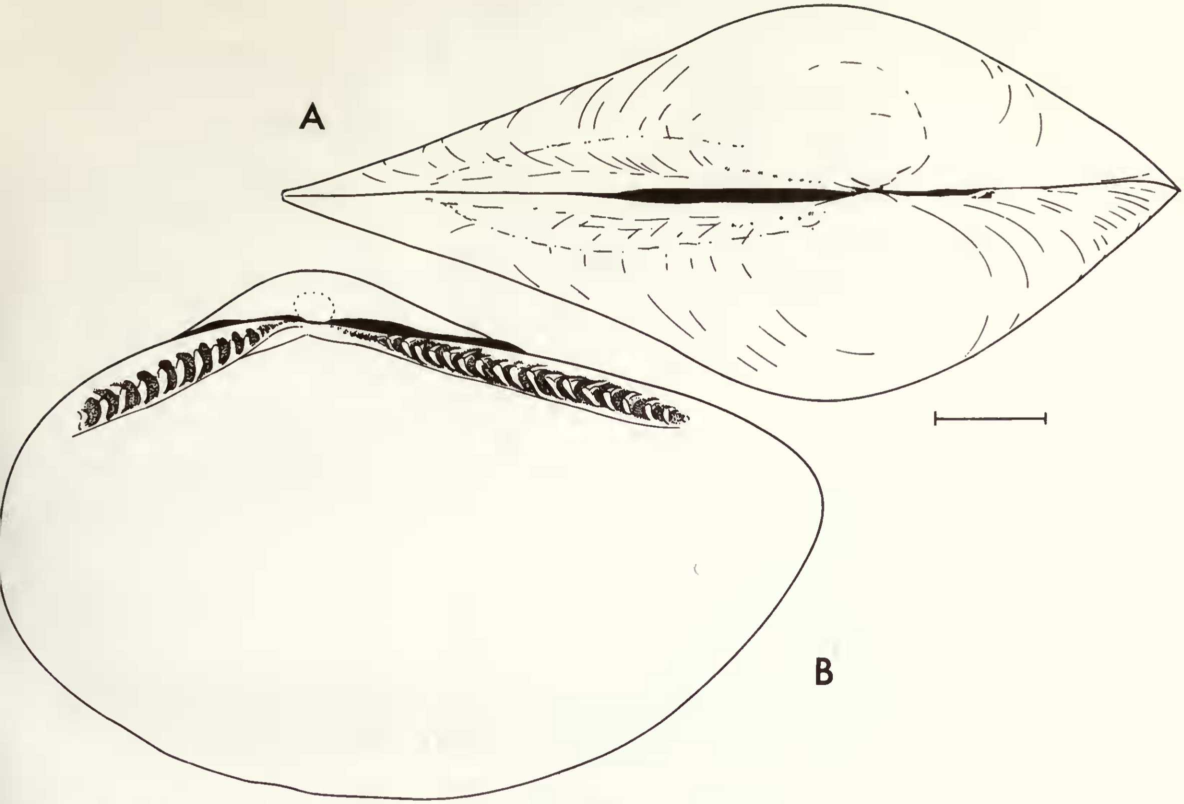

Fig. 26 *Malletia pallida.* (a) Dorsal view of shell; (b) internal lateral view of right valve from Station CY 13 Angola Basin 2044 metres. Scale 1 mm.

Morphology

The strength of the malletiid hinge is related to the size of the adductor muscles. In *M. pallida* these are relatively small and unequal in size. The posterior adductor is an elongate oval in the horizontal plane, the anterior adductor is somewhat larger in cross section and broadly oval. The siphons and feeding aperture are similar to those described for *M. grasslei.* The 'byssal' gland is very large. The cerebral and visceral ganglia and the connecting commissures are particularly stout. Other features are best compared by reference to Figures 27, 31 & 37.

Growth with age follows a similar course to that described for *M. abyssorum* with large specimens more elongate and rostrate than smaller (Fig. 28). *M. pallida* collected in the Sierra Leone, Guinea, Angola and Cape basins, is confined to tropical and southern regions of the East Atlantic. It has a remarkably wide depth distribution that extends from 1261 m to 5280 m.

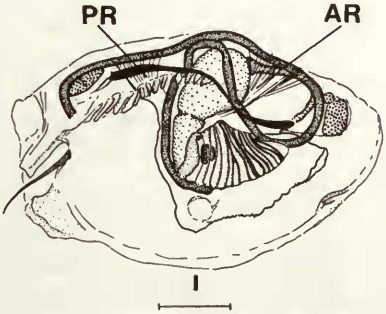

Fig. 27 *Malletia pallida.* Anatomy as seen from the right side. Scale 1 mm.

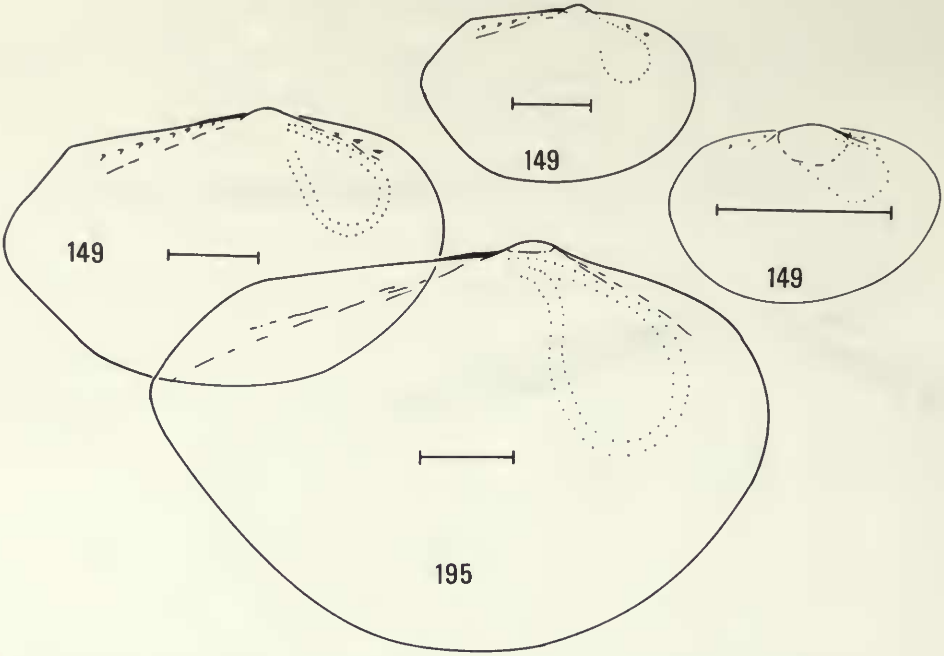

Fig. 28 *Malletia pallida.* Lateral outlines of specimens to show change in shape with increasing size. Note smallest specimen is magnified × 2 and largest specimen is from a different Station (195) to the others (149) and shows a difference in ventral curvature between the two populations. Scale 1 mm.

Malletia polita Verrill & Bush, 1898

Malletia polita Verrill & Bush, 1898: *Proc. U.S. natl. Mus.* **20:** 876, pl. 82, fig. 10. Type locality. US Fish. Commission, Sta 2718, Lat 38°24·0′N, Long 71°51·0′W. 2871 m. Type specimen. Holotype, U.S. Natl Mus. No. 78972.

Malletia bermudensis Haas, 1949; *Butl. Inst. Catalana d'Hist. Nat.* **37:** 71. Type locality. Lat 32°82.0′N, Long 64°33.0′W, 1700 fathoms deep off Bermuda coast. Type specimen. Holotype. Field Mus. Natl Hist., Chicago, No. 31658.

Depth range Variety **A** = 2871 to 5867 m.

Depth range Variety **B**—4521 to 4825 m.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Variety **A**							
North america basin							
Chain	80	4970	71	34°50·0′N	66°34·0′W	ES	2.7.65
	84	4749	6	36°24·0′N	67°56·0′W	ES	4.7.65
	85	3834	2	37°59·0′N	69°26·0′W	ES	5.7.83
Atlantis II	93	5007	51	34°39·0′N	66°26·0′W	ES	14.12.65
	121	4800	7	35°50·0′N	65°11·0′W	ES	21.8.66
	122	4833	2	35°52·0′N	64°58·0′W	ES	21.8.66
	123	4853	3	37°29·0′N	64°14·0′W	ES	22.8.66
	124	4862	3	37°58·0′N	63°58·0′W	ES	22.8.66
	125	4825	20	37°26·0′N	65°50·0′W	ES	23.8.66
	175	4693	5	36°36·0′N	68°31·0′W	ES	29.11.67
Oceanus	605	4986		35°11·0′N	67°20·0′W	ST*	27.4.76

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
GUIANA BASIN							
Knorr	287	4980	180	13°16·0′N	54°52·0′W	ES	24.2.72
	288	4429	71	11°04·0′N	58°05·0′W	ES	15.2.72
	307	3862	1	12°41·0′N	59°09·0′W	ES	3.3.72
Biovema (J. Charcot)							
	DS01	5097	1	10°57·2′N	45°07·6′W	ES	14.11.77
	DS03	5150	22	10°47·1′N	42°40·7′W	ES	16.11.77
	DS04	5100	49	10°46·3′N	42°41·4′W	ES	17.11.77
	DS05	5100	24	10°46·0′N	42°40·3′W	ES	18.11.77
	DS11	5867	63	11°37·5′N	32°53·8′W	ES	26.11.77
Variety **B**							
WEST EUROPE BASIN							
Polygas	CV15	4700	1	46°32·2′N	10°28·4′W	BT	27.10.72
(J. Charcot)							
	DS23	4721	3	46°32·8′N	10°21·0′W	ES	26.10.72
Biogas III	DS46	4521	1	46°28·6′N	10°23·0′W	ES	29.8.73
Biogas IV	DS59	4659	1	46°31·1′N	10°29·2′W	ES	19.2.74
Biogas VI	CP16	4706	16	46°27·3′N	10°25·8′W	FT	25.10.74
	CP17	4825	39	46°30·8′N	10°19·5′W	FT	26.10.74
	DS78	4706	8	46°31·2′N	10°23·8′W	ES	25.10.74
	DS79	4715	12	46°30·4′N	10°27·1′W	ES	26.10.74
	DS80	4720	3	46°29·5′N	10°29·5′W	ES	27.10.74
	DS81	4715	2	46°28·3′N	10°24·6′W	ES	27.10.74

*41 foot Gulf of Mexico Shrimp Trawl

Shell description

The original description (Verrill & Bush, 1898) was based on a single damaged valve, however, for the most part this description is both detailed and accurate. The description by Haas (1949) of what he thought was a new species of *Malletia* is based on three valves which are much less damaged than the type. The description is modest and in no great detail, but is supported by a photograph. Both descriptions are of shells from the Western Atlantic North America Basin and correspond to Variety **A.**

Despite the existing descriptions the following shell features should be mentioned (Figs 29a & b). Shell robust, inflated with clear concentric ornamentations; umbos prominent, anterior/posterior umbonal length ratio being 2/3; antero-dorsal, anterior and ventral margins in continuous curve, posterior margin somewhat rostrate dorsally with postero-dorsal margin angled at posterior limit of hinge plate, faint indication of a rostral ridge, no lunule, escutcheon barley visible, hinge plate moderately strong, many short chevron teeth (*c.* 40 in large specimens) anterior and posterior series in ratio 3/5, series separated by relatively short edentulous space below umbo; resilium small, inset at margin of edentulous space, external ligament prominent anterior and posterior to umbo, posterior ligament extends along half posterior hinge plate and is three times length of anterior external ligament. With increasing size, the shell becomes posteriorly elongate and more clearly rostrate (Fig. 30).

Although sample numbers are small, population histograms show a typical deep-sea pattern without a marked skew in numbers to the left, indicative of low mortality of the younger specimens. Maximum shell length 24·5 mm; prodissoconch length 340 µm.

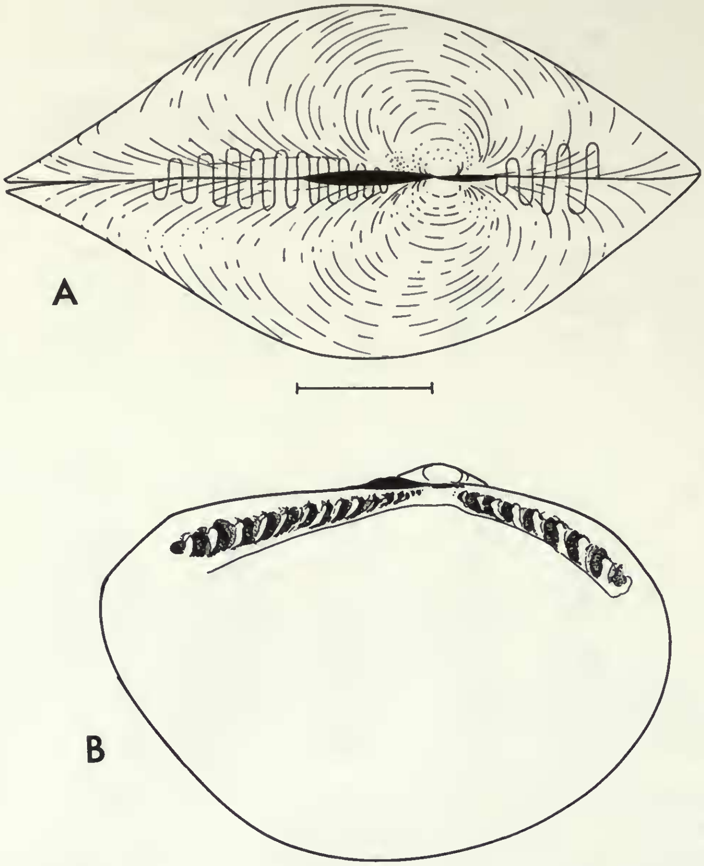

Fig. 29 *Malletia polita*. Variety A. (a) dorsal view of shell; (b) lateral view of inner left valve from Station 125, North America Basin, 4825 metres. Scale 1 mm.

Morphology

The morphology is similar to the previous species (Fig. 31a & b). The adductor muscles are elongate, oval and relatively small. The mouth lies some distance posterior to the anterior adductor, the stomach lies in the body and the hind gut is large in diameter with a well defined typhlosole. The palps are relatively large with elongate slender proboscides, the palp ridges are broad. The gills are elongate with relatively few broad plates. The gills are not joined in the midline behind the foot. The axes are connected to the fused ventral margin of the exhalent siphon. There is no clearly defined inhalent siphon although in some preserved specimens there is a suggestion of a short, ventrally open, channel, which extends about half way along the proximal ventral margin of the exhalent siphon. A narrow feeding aperture is ventral to the siphon. The centro-visceral commissures are stout. The above description relates to Variety **A** which is restricted to the Western Atlantic.

Variety **B**

Specimens from the West Europe Basin are, to the practised eye, subtly distinct and have been designated Variety **B**. The differences are not so clearly obvious as to define a different species. This is a state of affairs that is common to many species of deep sea bivalves from the Atlantic and must relate to the relative isolation of the basins as the ocean enlarged and to the slowness of gene flow, which in turn presumably is related to reproductive strategy and the extent of larval dispersion.

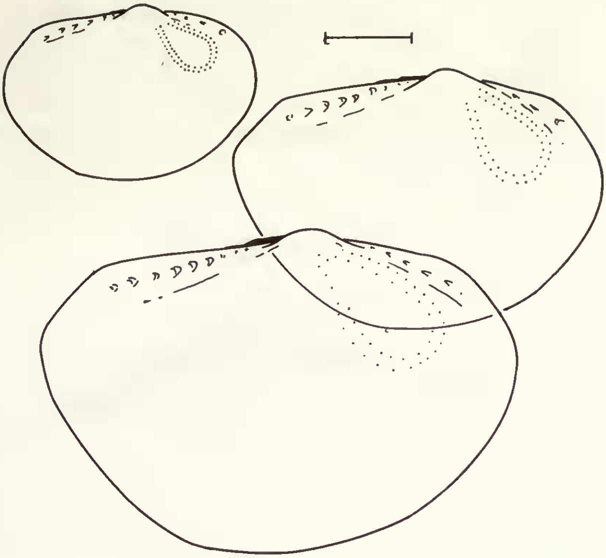

Fig. 30 *Malletia polita.* Variety A. Lateral outlines of specimens to change in shape with increasing size. Scale 1 mm.

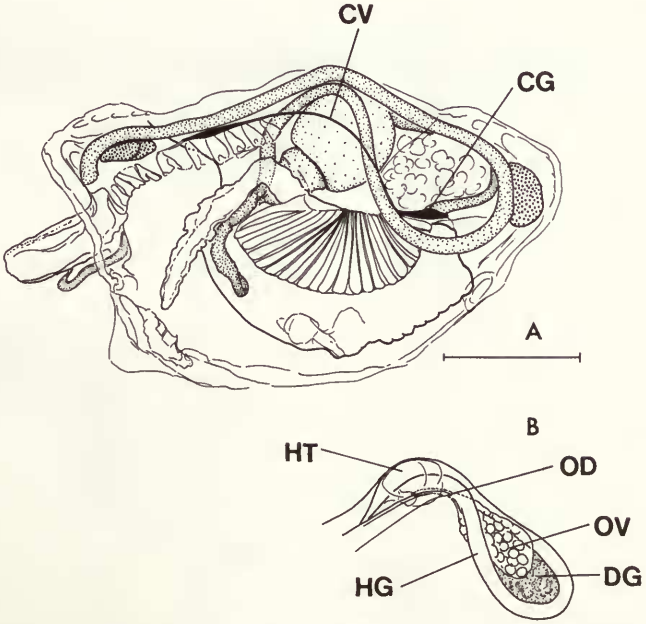

Fig. 31 *Malletia polita.* Variety A. (a) Anatomy as seen from the right side; (b) detail of developing ovary and oviduct as seen dorso-laterally. Scale 1 mm. Abbreviations see Appendix.

The shell differs from Variety **A** in that it is slightly more posteriorly elongate (Figs 32a & b) with the rostral ridge and escutcheon slightly more defined; the ventral margin is not so deep and round. The ligament of Variety **A** is longer than that of Variety **B** and extends further anterior (Fig. 39). Maximum shell length 19·0 mm; prodissoconch length 340 µm.

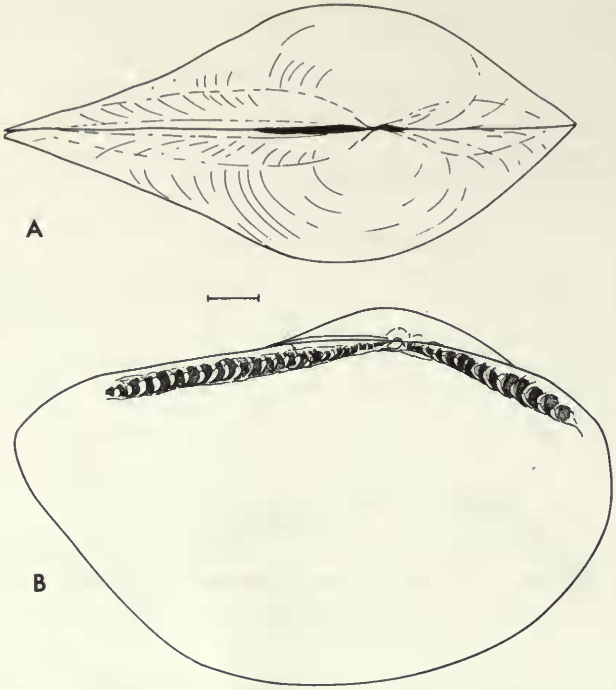

Fig. 32 *Malletia polita.* Variety B. (a) Dorsal view of shell; (b) lateral view of inner left valve from Station BG VI CP 16, West European Basin, 4825 metres. Scale 1 mm.

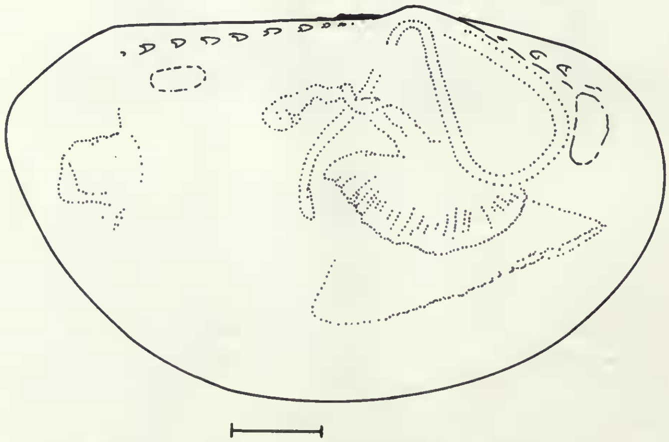

Fig. 33 *Malletia polita.* Variety B. Lateral view of shell from the right side with outline of hind gut, foot, palp and adductor muscles seen through the partially transparent shell. Scale 1 mm.

Anatomically **B** differs little from **A,** but the gut appears to be not so large in diameter and the loop of the hind gut not so deep. (*cf.* Fig. 31 & Fig. 33). The overall impression of the European specimens is that they are less robust than their West Atlantic counterparts. This is a subjective opinion, which may possibly be quantified in the future by genetical and computer analysis of larger collections. At present it rests on an almost indefinable overall comparative appreciation.

Two varieties of *Malletia polita* are found only at deeper abyssal depths. Variety **A**, the Western Atlantic form, was collected from the North America Basin and Guiana Basin. Excepting polar seas it occurs over a depth range of 3834 m to 5867 m however, if the two shallowest records are excluded and which form a mere trace of the protobranch fauna present (0·74%, 0·03%) then the depth range narrows to 4429 m to 5867 m. *M. polita* variety **B**, the Eastern Atlantic form, was taken only from the West Europe Basin, is similarly confined to great depths which range from 4521 m to 4706 m.

Malletia cuneata Jeffreys, 1876

Malletia cuneata Jeffreys, 1876: *Ann. mag. nat. Hist.* (18)**4:** 435 (*non Solenella cuneata* Jeffreys, 1874: *Rep. Brit. Ass.*, 1873, *nomen nudum*). TYPE LOCALITY. *Valorous* Expedition, Sta 9, 59°10.0′N, Long 50°25.0′E, 3150 m. TYPE SPECIMEN. Lectotype. BM(NH) No. 1877–11.28.34.

Portlandia kolthoffi Hägg, 1904: *Ark. Zool.* 2: 12, pl. 1, figs 1–3. TYPE LOCALITY. Swedish Zoological Polar Expedition 1900. Lat 72°1′N Long 08°33′W, 2400 m. TYPE SPECIMEN. Not recorded.

Malletia pellucida Thiele, 1912: *Dt. Südpol. exped.* **13:** 254, pl. 17, fig. 23. TYPE LOCALITY. Deutsch Südpolar Expedition. North West of Gauss-Station, 2916 and 3423 m. TYPE SPECIMEN. Zoological Museum Berlin.

Malletia (Neilo) fiora Dall, 1916: *Proc. U.S. natn. Mus.* **52:** 400. TYPE LOCALITY. U.S. Fisheries Steamer *Albatross* Sta 2859 SW of Stika Bay, Alaska, 2860 m. TYPE SPECIMEN. U.S. Natl Mus. No. 207251.

Neilonella kolthoffi Gurbunov, 1946: *Trudy drief. Eksped. 'G. Sedov'* 1937–40. **3:** 312, fig. 4, pl. 3, figs 2a–c.

Neilonella cuneata Soot-Ryen, 1966: *Sarsia* **24:** 3.

Katadesmia kolthoffi Bouchet & Waren, 1979; *Sarsia* 64: 214, figs 2a–c, 21 & 22.

non Malletia cuneata Smith, 1888: *Chall. Rep.* **13:** 247, pl. XX, figs 10–10a.

Material

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Variety **A**							
NORTH AMERICA BASIN							
Atlantis II	64	2886	6	38°46·0′N	70°06·0′W	ES	21.8.64
	70	4680	8	36°23·0′N	67°58·0′W	ES	23.8.64
	72	2864	1	38°16·0′N	71°47·0′W	ES	24.8.64
Chain	77	3806	1	38°07·0′N	69°16·0′W	ES	30.6.65
	78	3828	64	38°08·0′N	69°18·7′W	ES	30.6.65
	84	4749	3	36°24·4′N	67°56·0′W	ES	4.7.65
	85	3834	787	37°59·2′N	69°26·2′W	ES	5.7.65
Atlantis II	92	4694	2	36°20·0′N	67°56·0′W	ES	13.12.65
	175	4693	4	36°36·0′N	68°31·0′W	ES	2.12.67
Chain	340	3356	43	38°17·6′N	70°22·8′W	ES	24.11.73
WEST EUROPE BASIN							
Sarsia	50	2379	4	43°46·7′N	03°38·0′W	ES	18.7.67
Chain	321	2890	3	50°12·3′N	13°35·8′W	ES	20.8.72
	323	3356	8	50°08·3′N	13°53·7′W	ES	21.8.72
	326	3859	85	50°04·9′N	14°23·8′W	ES	22.8.72
	328	4435	1	50°04·7′N	15°44·8′W	ES	23.8.72
Polygas (J. Charcot)	DS20	4226	25	47°33·0′N	09°36·7′W	ES	24.10.72
	DS21	4190	24	47°31·5′N	09°40·7′W	ES	24.10.72
	DS22	4144	20	47°34·1′N	09°38·4′W	ES	25.10.72
	DS23	4734	6	46°32·8′N	10°21·0′W	ES	26.10.72
Biogas II (J. Charcot)	DS30	4106	1	47°38·3′N	09°33·9′W	ES	18.4.73
	CV18	4120	1	47°32·2′N	09°36·5′W	BT	18.4.73

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Biogas III	DS41	3548	2	47°28.3′N	09°07·2′W	ES	26.8.73
	DS42	4104	2	47°32·1′N	09°35·6′W	ES	27.8.73
	DS44	3992	2	47°33·2′N	09°42·0′W	ES	27.8.73
	DS45	4260	3	47°33·9′N	09°38·4′W	ES	27.8.73
	CV27	4023	4	47°34·2′N	09°32·4′W	BT	28.8.73
	CV30	4518	2	46°32·8′N	10°20·0′W	BT	29.8.73
Biogas IV	DS54	4659	7	46°31·1′N	10°29·2′W	ES	21.2.74
	DS55	4125	109	47°34·9′N	09°40·9′W	ES	22.2.74
	DS56	4050	2	47°32·7′N	09°28·2′W	ES	23.2.74
	DS57	2906	1	47°30·8′N	09°07·6′W	ES	23.2.74
	DS58	2775	3	47°34·1′N	09°08·2′W	ES	23.2.74
	DS60	3742	10	47°26·8′N	09°07·2′W	ES	24.2.74
	DS61	2250	1	47°34·7′N	08°38·8′W	ES	25.2.74
Biogas V	CV36	4209	1	47°34·1′N	09°38·5′W	BT	22.2.74
(Cryos)	DS66	3480	18	47°28·2′N	09°00·0′W	ES	16.6.74
	DS67	4150	7	47°31·0′N	09°35·0′W	ES	17.6.74
Biogas VI (J. Charcot)	CP13	4134	12	47°34·4′N	09°38·0′W	HT	23.10.74
	CP14	4237	9	47°32·0′N	09°35·9′W	HT	23.10.74
	CP15	4715	25	46°32·2′N	10°28·5′W	HT	23.10.74
	CP17	4706	2	46°30·8′N	10°19·5′W	HT	26.10.74
	DS75	3250	1	47°28·1′N	09°07·8′W	ES	22.10.74
	DS76	4228	198	47°34·8′N	09°33·3′W	ES	23.10.76
	DS77	4240	34	47°31·8′N	09°34·6′W	ES	24.10.74
	DS78	4706	21	46°31·2′N	10°23·8′W	ES	25.10.74
	DS79	4715	58	46°30·4′N	10°27·1′W	ES	26.10.74
	DS80	4720	17	46°29·5′N	10°29·5′W	ES	27.6.74
	DS82	4462	3	44°25·4′N	04°52·8′W	ES	29.10.74
	DS84	4466	1	44°30·0′N	04°53·8′W	ES	29.10.74
CANARIES BASIN							
Discovery	6696	1780	2	28°06·0′N	13°28·0′W	ES	15.3.68
	6711	2988	5	27°14·9′N	15°36·3′W	ES	19.3.68
	6714	3301	1	27°13·0′N	15°41·0′W	ES	20.3.68
GUINEA BASIN							
Walda (J. Charcot)	DS30/38	3109	7	04°04·1′N	03°42·0′E	ES	.6.71
Variety **B**							
ARGENTINE BASIN							
Atlantis II	242	4402	15	38°16·9′S	51°56·1′W	ES	13.3.71
	245	2707	62	36°55·7′S	53°01·4′W	ES	14.3.71
	256	3917	353	37°40·9′S	52°19·3′W	ES	24.3.71
	259	3317	106	37°13·3′S	52°45·0′W	ES	26.3.71
	262	2480	231	36°05·2′S	52°17·9′W	ES	27.3.71

Malletia cuneata is one of the few cosmopolitan protobranch species of the abyss. As would be expected, as we confirm, populations from the various oceans and basins show variations in shell form which, in our experience, overlap to an extent that we would be unwilling at this stage to define as species. Because it is one of the more common and larger bivalve species present in the deep sea it has been collected frequently during the past hundred years of exploration. As a result there is a long and confused literature. This is indicated by the list of synonymies. The most recent nomenclatural debate is by Bouchet & Warén (1979) when they discuss the population from the Norwegian Sea and they separate *M. cuneata* from *Katadesmia kolthoffi*. Bouchet & Warén (1979, Figs 21–24) compare, photographically, a specimen from the Norwegian Sea and one of the original specimens of *M. cuneata* taken by Jeffreys. They clearly differ in shape and in fact illustrate extremes of the range of variation that exist in the Atlantic populations. Bouchet & Warén claim that Soot-Ryen also recognised *M. kolthoffi* as differing from *M. cuneata,* in fact Soot-Ryen (1966: 3) states 'in my opinion *M. cuneata* is a northern deep water species identical to *Portlandia kolthoffi*' and then goes on to say 'the outline of *cuneata* is somewhat variable'. Soot-Ryen (1966) however does doubt whether the more southern forms from the tropics and the Mediterranean can be referred to *M. cuneata.* We confirm that specimens from the Sierra Leone Basin are distinct (see M. *pallida* p. 220). Unfortunately Soot-Ryen had so little material to consider that it is little wonder that he was perplexed by the range in form. Knudsen (1970) also covers similar ground and, with similar debate, concludes that *M. kolthoffi* and *M. cuneta* are one of the same species. In this we agree.

Shell description

There are numerous descriptions of both shell and animal, here we will emphasize only those features of Variety A that are of comparative importance.

Shell, moderately fragile, fine concentric growth lines; umbos moderately prominent, anterior, anterior/posterior umbonal length ratio *ca.* 3/5 (see below); postero-dorsal shell margin almost straight, angled at posterior limit of hinge plate, posterior margin angulate, dorsal to horizontal mid-line of shell, an ill-defined posterior umbonal ridge follows line of hinge plate, but does not meet posterior angle to form a rostral ridge, antero-dorsal and antero-ventral margins smoothly curved, ventral margin curvature varies with size and population, thus may be curved or, centrally, almost straight; hinge plate moderately broad, numerous short chevron teeth (*c.* 35 in large specimens), small edentulous space between tooth series; anterior and posterior series ratio 1/2; resilium small, relatively deep set, resilifer extending to half depth of hinge plate below umbo, external ligament, opisthodetic, shortest ligament of all species described here, less than half length of posterior hinge plate, anterior external ligament very short (Figs 34a & b; 35a & b; 39). Maximum shell length 10·0 mm; prodissoconch length 325 μm.

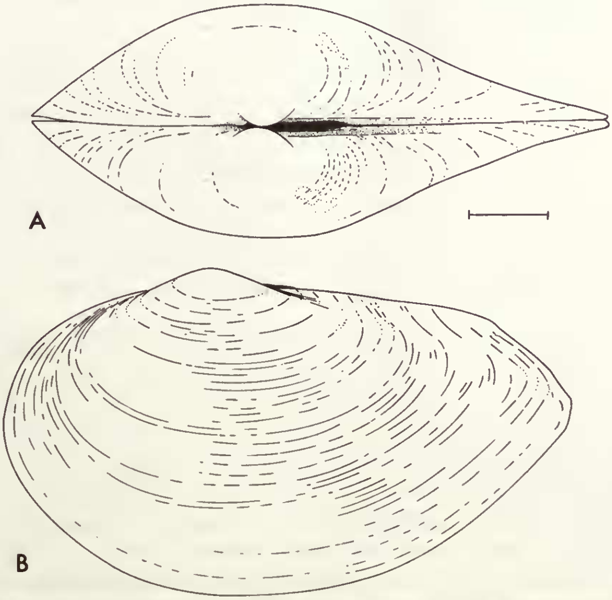

Fig. 34 *Malletia cuneata.* Variety A. (a) Dorsal; (b) lateral view of the shell of a specimen from Station 85, North America Basin, 3834 metres. Scale 1 mm.

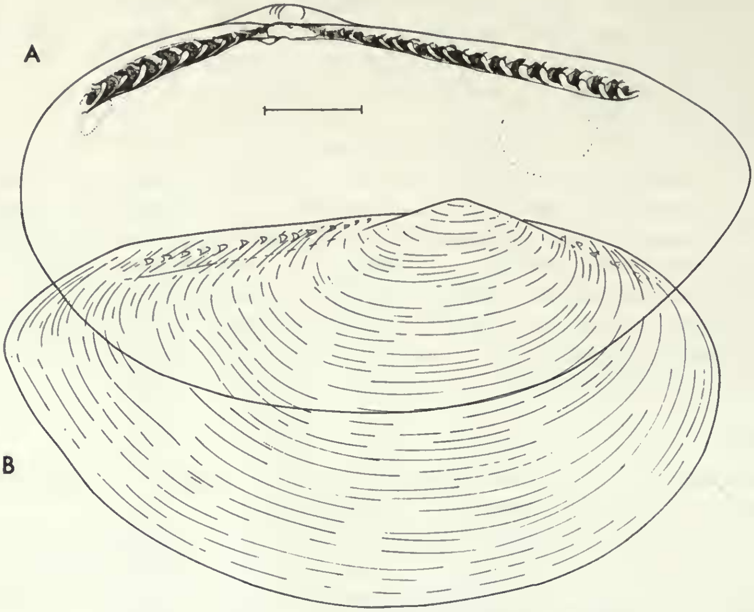

Fig. 35 *Malletia cuneata.* Variety A. (a) Internal lateral view of right valve; (b) lateral view of shell of specimen from Station BG II CV 18 West European Basin, 4120 metres. Scale 1 mm.

Morphology

With increasing size the shell becomes posteriorly more elongate and angulate. In older specimens the central portion of the ventral margin tends to become straighter (Fig. 36).

The morphology of the animal is similar to the other species described here (Fig. 37). The adductor muscles are oval, the anterior being more than twice as large as the posterior. The mouth is distant from the anterior adductor. The palps are relatively large with numerous ridges (*c.* 30), the foot and gills are large and robust in comparison with other species. The hind gut follows a similar course to other species of *Malletia* with a single loop on the right side of the body. There is a well marked typhlosole and the gut is relatively large in diameter. The ganglia and commissures are not particularly robust. Both inhalent and exhalent channels of the siphons are clearly demarcated, the exhalent siphon is entire, the ventral margins of the inhalent siphon are not fused. The feeding aperture ventral to the inhalent siphon is extensive and occupies most of the postero-ventral mantle margin, but the mantle folds themselves are not excessively well developed. The anterior mantle sense organ is well defined and lies ventral to the anterior adductor.

The above description relates to Variety **A.** Variety **B** occurring in the Argentine Basin is sufficiently consistent in its differences to warrant separate treatment, and indeed, it may be possible to erect a new species to include it. However, at our present limited state of knowledge we prefer to retain this form within *M. cuneata.*

The shell of Variety **B** differs from that of Variety **A** in that the umbo is slightly more anterior in position, anterior/posterior umbonal length ratio being 1/2, the marginal angle at the posterior limit of the hinge plate is less acute and the angle of the posterior margin relatively more distal in position (*cf.* Figs. 38a & b; 39). The proportion and numbers of anterior and posterior hinge teeth are not significantly different in the two varieties. The external ligament is significantly longer than in Variety **A,** both anteriorly and posteriorly. This is the only clear difference between the two varieties. Maximum shell length 9·5 mm; prodissoconch length 322 μm.

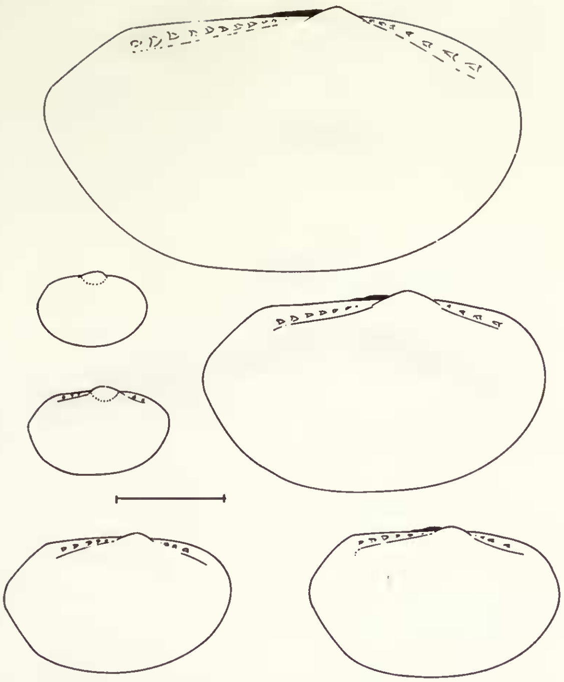

Fig. 36 *Malletia cuneata.* Variety A. Lateral outlines of specimens to show change in shape with increasing age. Station 326, West European Basin, 3859 metres. Scale 1 mm.

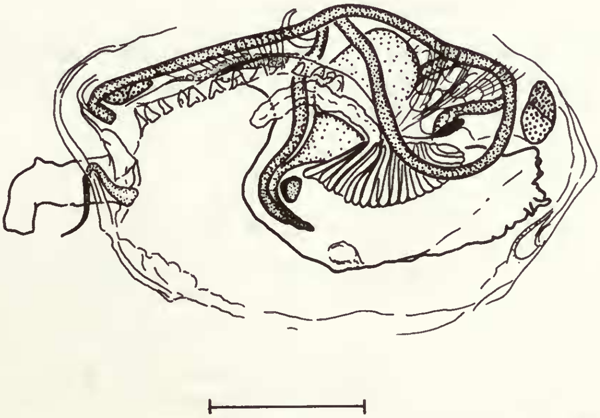

Fig. 37 *Malletia cuneata.* Variety B. Anatomy as seen from the right side. Scale 1 mm.

Very few differences can be seen in the morphology of the varieties. The general impression of Variety **B** is that the anatomy is less robust. For example the gut is marginally smaller in diameter, and foot, palp and gills are also smaller. Unfortunately these subjective differences are not easy to quantify in preserved material. Based entirely on those samples that we have personally examined, the depth range of *Malletia cuneata* in the Atlantic Ocean ranges from 1780 m to 4797 m. *M. cuneata* variety **A** includes all specimens collected from the North America, West Europe, Canaries and Guinea Basins and encompasses the entire depth range of 1780–4749 m. The large concentrations of *M. cuneata* variety **A** appears to be aggregated between 3000 m and

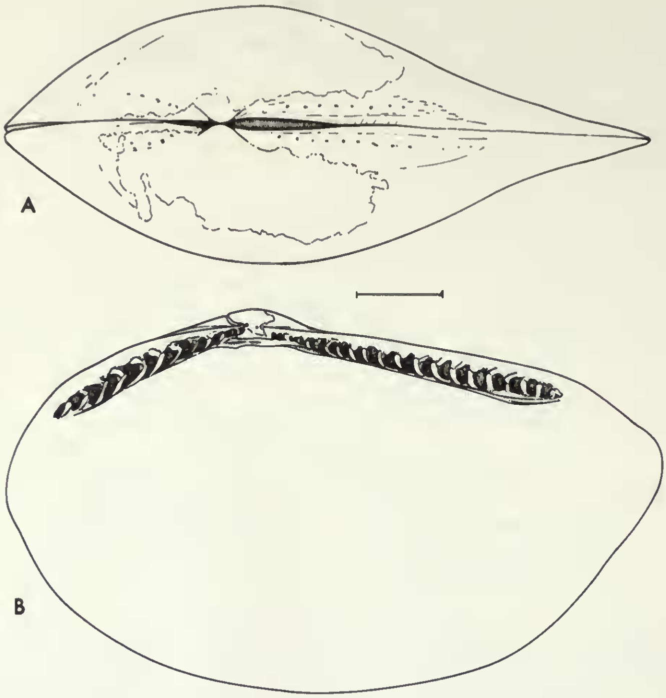

Fig. 38 *Malletia cuneata*. Variety B. (a) Dorsal view of shell; (b) internal lateral view of right valve of a specimen from Station 265, Argentine Basin, 3908 metres. Scale 1 mm.

4500 m. *M. cuneata* variety **B** was obtained from the Argentine Basin at all depths between 2480 m and 4402 m. At each of the five stations where it was recorded it was the numerically dominant constituent of the protobranch fauna.

Malletia obtusa G. O. Sars, 1878

Malletia obtusa G.O. Sars, 1878: *Moll. reg. arct. Norv.* p. 41, pl. 19, figs 3a & b. Type locality. Off west coast of Norway, South of Lofoten Isles, exact locality not recorded. Type specimen. Not recorded. Depth range = 350 m to 2941 m.

[Although Michael Sars recorded the name of *Malletia obtusa* in 1872 in *Bidrag til Kundskab om Christiania fjordens* Fauna I–III (1868–73) he gave no adequate description of the species. An earlier species *Yoldia abyssicola* recorded by Michael Sars in 1858 is also unacceptable (Sars, G. O., 1878)]

Specimens were obtained from Korsfjorden 50 km south of Bergen, Norway.

This species appears to be restricted to the Norwegian Basin and all records of *M. obtusa* from outside this area have in all probability been mis-identified and are of *M. johnsoni* (see p. 205).

This is the best known of all species of the genus and is well described both in terms of its shell characters (Sars, 1878) and in terms of its functional morphology (Yonge, 1939).

Morphology

Although the morphology is similar to *M. johnsoni* (Figs 40 & 41) certain characters should be mentioned for comparative purposes. Thus, the anterior sense organ is far anterior, more so than any other species. The siphons are well developed, broad and elongate, and the inhalent and exhalent channels are entire. There is a single tentacle attached to the base of the inhalent siphon

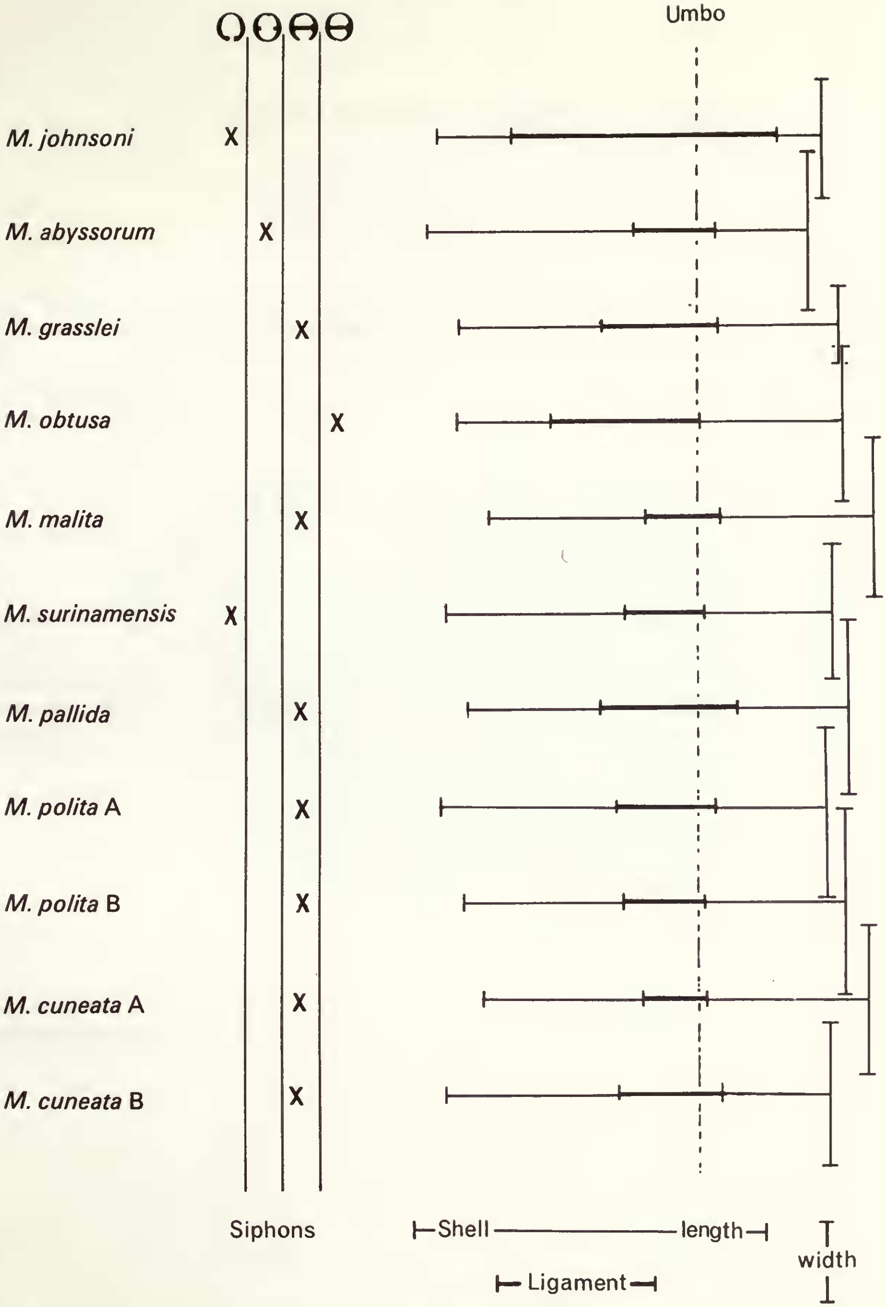

Fig. 39 The comparison of siphonal morphology, and dimensional ratios of shell features of live species of *Malletia*.

ventrally on the right hand side. The feeding aperture is relatively circumscribed, no more than 1/4 of the post mantle margin in extent. The palp is large and with numerous ridges. The foot is also large, but not the pedal ganglion, in comparison with other species. The visceral ganglion abuts the posterior adductor yet it and the commissures are not large.

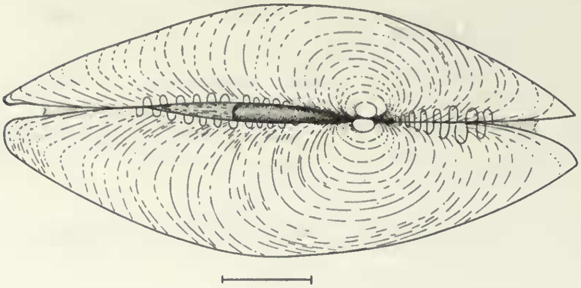

Fig. 40 *Malletia obtusa.* Dorsal view of shell, from Korsfjorden, Norway. Scale 1 mm.

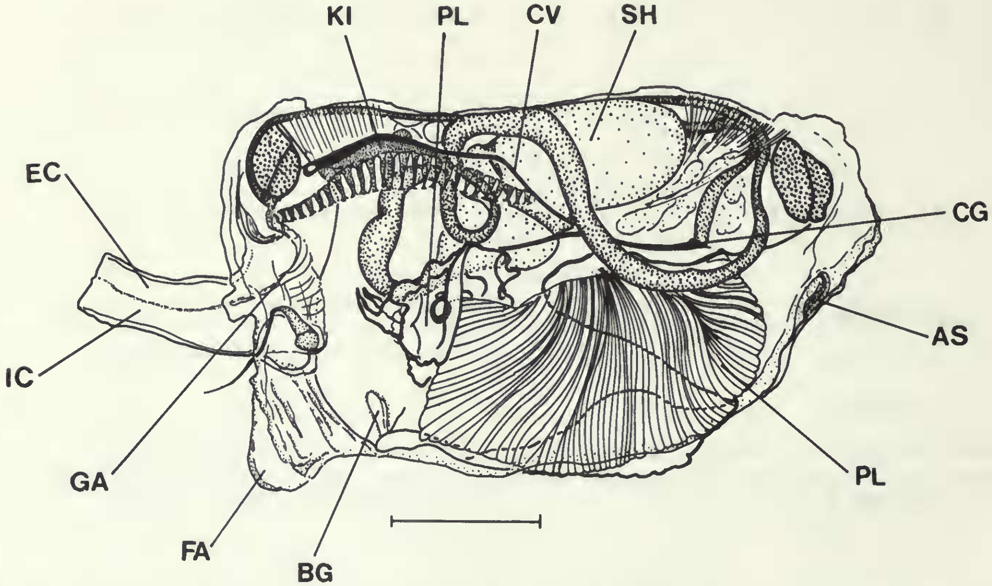

Fig. 41 *Malletia obtusa.* Anatomy as seen from the right side. Scale 1 mm. Abbreviations see Appendix.

Other species: previously identified as malletiids

In the course of these studies we have examined two species which have previously been identified as members of the family Malletiidae, namely, *M. aeoleta* Dall, 1980 and *M. agatheda* Dall, 1890. Both heavy rostrate shells with a prominent external amphidetic ligament. Their internal morphology differs greatly from the species described here, in particular both have multiple coiled hind guts. They belong to the genus *Tindariopsis* that is to be included in the subfamily Ledellinae (Allen & Hannah, in prep).

Discussion

Assessment of shell shape in terms of lateral outline, obesity and attenuation of the posterior region and of morphological features including the position of anterior sense organ and the length of siphons indicates that there are two major trends in form. On the one hand there are the elongate species with dorso-ventrally parallel shells, exceptionally long posterior external ligaments and with the mantle sense organ far anterior (eg. *M. johnsoni* and *M. obtusa*) and on the other hand there are species with cuneate, rostrate, ventrally curved shells, shorter ligaments, and with the anterior sense organ more ventral in position (eg. *M. polita, M. pallida, M. cuneata* and other species described here).

One can argue differences in probable behaviour and we speculate that the *johnsoni/obtusa* group is positioned vertical to the sediment surface and the *polita/pallida/cuneata* group at an angle to it. The latter group of species changes shape dramatically with increasing size becoming more obese centrally and posteriorly more rostrate. Although the siphons of the *polita/pallida/cuneata* group are relatively well developed, suggesting an infaunal habit at least they must appear at the surface at times because some large specimens have Foraminifera and hydroids attached to them. The more obese shape must functionally make rapid and efficient burrowing more difficult and result in a more sedentary mode of life. In contrast, the large specimens of *M. johnsoni* and *M. obtusa* do not have an attached fauna and they may well burrow deeper than the species of the other group.

The malletiid species are extremely conservative in their anatomy and shell morphology. Young specimens of the *polita/pallida/cuneata* groups in particular are extremely difficult to tell apart even though larger specimens clearly differ. The change in form of the species with increasing size presents considerable taxonomic difficulties, particularly to the observer with few specimens at hand.

The morphologies of the nine species are remarkably similar and for the most part differ only in minor ways (see Fig. 39). The most variable feature is the structure of the siphons. Within the Atlantic species of *Malletia* there are all the protobranch variations that Yonge (1939) described and two other besides. The variation involves the degree of separation of the lumena of inhalent and exhalent siphons and whether the enclosing siphonal wall is entire or not. As best developed the lumena are separate and formed by entire but conjoined siphons (*M. obtusa* and *M. cuneata*). Other morphologies are:

—separate lumena but the ventral wall of the inhalent siphon are not entire but, in life, the edges are apposed in the ventral mid-line (*M. grasslei* and *M. polita*).

—The inhalent siphon may be shorter than the exhalent siphons in which the lumena are not separate but there is a pair of mid lateral ridges, that may or may not be apposed in life to form functionally separate lumena but which certainly act as ventral guides to the extended faecal rod (*M. abyssorum*).

—Siphons in which the lumena are not separate and without mid lateral ridges marking the ventral and dorsal limits respectively of the inhalent and exhalent channels (*M. johnsoni* and *M. surinamensis*). In this case the gill axes are attached lateroventrally and therefore the inhalent siphon and ventral section must be considered to be functionally absent—although the ventral floor of the siphon may be the remnant of the wall of the inhalent siphon.

In the variety of its form the malletiid siphon differs little from some other deep water nuculanoid families and subfamilies, eg. Yoldiellidae (Allen, Hannah & Sanders, in prep). The reason for the variation lies in the fact that the nuculanoid protobranchs possess a feeding aperture from which the palp proboscides extend.

In deep water species with gills reduced in size and having specialized respiratory surfaces and mechanisms that are least developed, there is probably sufficient inflow of water in the feeding process to satisfy the animal's needs. The exhalent aperture remains functional for the passage of the faeces. If the faecal rods are large in diameter, then the use of the combined inhalent and exhalent lumena is advantageous.

Thus the picture of protobranch siphon evolution that Yonge (1939) described and which involved successive fusion of the posterior mantle to form totally enclosed apertures may have to be extended further to involve secondary loss of siphonal walls with the lumena combined that probably relate in part to reduced respiratory needs satisfied by another point of inflow and in part to accommodate an enlarged faecal rod.

Other noteworthy aspects of the morphology are the robustness of the nervous system and size of the foot and statocysts (eg. Fig. 41). The anterior sense organ and the byssal gland are also extremely well developed. All would indicate that *Malletia* is an active burrowing genus. Whether the well developed external ligament is also related to this is debatable, but the analogy with the shallow water, fast burrowing deposit feeding Tellinacea is obvious.

The malletiids have retained the primitive form of the hind gut—a single loop to the right of the body. However it is lengthened and in all species extends to the inner face of the anterior adductor. The diameter of the hind gut although varying from species to species is either large or very large. All have a typhlosole. The stomach is also very voluminous and all points to the consumption and processing of great quantities of particulate matter.

Malletiids are of unusually large size in comparison with other deep sea protobranchs and this may be a reflection of their ability to process considerable quantities of sediment with commensurate energy gain.

Observations on the digestive system indicate that selection of particles occurs. The number of skeletal remains within the gut is significantly greater than those present in the general sediment.

The recent recognition (Gooday pers. comm.) of rich infaunal populations of undescribed species of foraminifera, xenophyophores and komoki that live within frustules and other foraminiferan exoskeletions and have differing depth ranges within the substrata appear to provide answers to the ecological problem of why many nuculanoid species (→ 15) are able to live together and appear to ingest the same deposits. Niche separation, by living in different depth horizons was always postulated (Allen, 1978) but is now immeasurably strengthened by the knowledge of differing cryptic meiofaunal communities at differing depths of abyssal sediments.

A universal feature of all deep sea protobranchs is the solid packing of the gut with ingested fine deposits. However, it is not clear how this material is transported posterior to the stomach. Probably the pedal retractor muscles play a role. They lie close to all parts of the gut (eg. Figs 22, 27 & 37). Anteriorly there are four pairs of pedal retractors lying lateral to the oesophagus. The anterior retractors cradle the anterior ventral side of the stomach while the posterior retractor muscles lie close to the mid and hind gut posterior to the style sac. Since the gut wall is not muscular, it is difficult to imagine that cilia are the sole means of moving the solid rod of sediment through the hind gut, although it will play an important role in movement of the contents of oesophagus and stomach.

The Argentine and Guinea Basins both show endemism, a feature of many protobranch groups. Elsewhere the situation is one of slight east to west Atlantic population differences. This suggests some gene flow but there is insufficient evidence for us to speculate that we are seeing the first stages in emergent species. Further south on the eastern Atlantic there is clearly more discontinuity with our recognition of the sibling species *M. pallida,* from the more cosmopolitan *M. cuneata*.

Apart from holotypes of new species, specimens (including paratypes) listed in this paper presently remain in the possession of the authors. When the analysis of the protobranch bivalves of the Atlantic is completed specimens will be lodged in the British Museum, the Smithsonian Museum and the Paris Museum depending on the country origin of the collections.

References

Allen, J. A. 1960. The ligament of the Lucinacea (Eulamellibranchia). *Quarterly Journal of Microscopical Science* **101:** 25–36.

—— 1978. Evolution of the deep sea protobranch bivalves. *Philosophical Transactions of the Royal Society of London* B **284:** 387–401.

—— **& Sanders, H. L.** 1973. Studies on deep-sea Protobranchia: The families Siliculidae and Lametilidae. *Bulletin of the Museum of Comparative Zoology Harvard* **145:** 263–310.

—— —— 1982. Studies on the deep-sea Protobranchia: the subfamily Spinulinae (family Nuculanidae). *Bulletin of the Museum of Comparative Zoology Harvard* **150:** 1–30.

Barnard, K. H. 1963. Deep-sea Mollusca from West of Cape Point, South Africa. *Annals of the South Africa Museum* **46:** 407–452.

Bouchet, P. & Warén, A. 1979. The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. *Sarsia* **64:** 211–243.

Bush, K. J. 1893. Report on the Mollusca dredged by the 'Blake' in 1880, including descriptions of several new species. *Bulletin of the Museum of Comparative Zoology Havard* **23:** 199–242.

Clarke, A. H. Jr. 1961. Abyssal mollusks from the South Atlantic Ocean. *Bulletin of the Museum of Comparative Zoology Harvard* **125:** 345–387.

—— 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. *Bulletin of the National Museum of Canada* **181:** 1–114.

Dall, W. H. 1898. Contributions to the Tertiary fauna of Florida, with special reference to the silex-beds of Tampa, and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated and of their American Tertiary species. *Transactions of the Wagner Free Institute of Science Philadelphia* **3:** 569–916.

—— 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer 'Albatross' during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding... The Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology Harvard* **43:** 205–487.

Filatova, Z. A. & Shileiko, A. A. 1981. Structure and ecology of the deep-sea species *Clencharia diaphana* (Clarke, 1961) (Bivalvia: Protobranchia). *Byulleten Moskovskogo Obstichestra Ispytateler Prirody* **87:** 53–62.

Heath, H. 1937. The anatomy of some protobranch mollusks. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* **10** (2): 1–26.

Johnson, C. W. 1934. List of marine Mollusca of the Atlantic coast from Labrador to Texas. *Proceedings of the Boston Natural History Society* **40:** 1–203.

Jeffreys, J. G. 1879. On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions 1869–1870. Pt. II. *Proceedings of the Zoological Society of London* 553–588.

Knudsen, J. 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Report* **11:** 7–241.

Locard, A. 1896. Resultats scientifiques de la Campagne du 'Candan' dans le Golfe de Gascoigne, aout-septembre 1895. Mollusques testacés et Brachiopodes. *Annales de l'Université de Lyon* 129–242.

—— 1898. Mollusques testacés. *Exped. Sci. Travailleur 'Talisman'.* **2:** 1–515.

McAlester, A. L 1964. Preliminary suggestions for a classification of nuculoid bivalves. *Journal of Paleontology* **38:** 397–400.

McAlester, A. L. 1969. *In* Moore, R. C. *Treatise on Invertebrate Palaeontology, Pt N, 1, Mollusca 6, Bivalvia:* N1-N489. Geol. Soc. Inc., Kansas and University of Kansas.

Moulins, C. des 1832. Description d'une nouveau genre de coquille vivante, bivalve, des mers du Chile. *Actes de la Société Linneean de Bordeaux* **5:** 83–92.

Philippi, R. A. 1844. *Enumeratio Molluscorum Siciliae cum viventium, tum in tellure tertiaria fossilium quae in itinere suo observavit auctor.* **2:** 1–304.

Sanders, H. L. & Allen, J. A. 1973. Studies on deep-sea Protobranchia (Bivalvia): prologue and the Pristiglomidae. *Bulletin of the Museum of Comparative Zoology Harvard* **145;** 237–262.

—— ——1977. Studies on the deep-sea Protobranchia (Bivalvia), the family Tindariidae and the genus *Pseudotindaria. Bulletin of the Museum of Comparative Zoology Harvard* **148:** 23–59.

Sars, G. O. 1878. *Bidrag til Kundskaben om Norges arktiske Fauna. 1. Mollusca regionis arcticae Norvegiae:* 466 pp. Christiania.

Smith, E. A. 1885. Report on the Lamellibranchiata collected by HMS Challenger during the years 1873–76. *Report of the Scientific Results of the Exploring Voyage of HMS Challenger 1873–76* **13:** 1–341.

Soot-Ryen, T. 1957. Preliminary diagnoses of new Genera and species of pelecypods from Chile. *Astarte* **1** (16): 1–5.

—— 1966. Revision of the pelecypods from the Michael Sars North Atlantic Deep-Sea Expedition 1910 with notes on the family Verticordiidae and other interesting species. *Sarsia* **24:** 1–31.

Thiele, J. & Jaeckel, S. 1931. Muscheln der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdiva'* **21:** 1–110.

Verrill, A. E. 1884. Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Science* **6:** 139–294.

—— & Bush, J. J. 1897. Revision of the genera of Ledidae and Nuculidae of the Atlantic coast of the United States. *American Journal of Science* **3:** 51–63.

—— —— 1898. Revision of the deep-water Mollusca of the Atlantic coast of North America with descriptions of new genera and species. Pt. 1. Bivalvia. *Proceedings of the United States National Museum* **20:** 775–901.

Vokes, H. E. 1967. Genera of the Bivalvia: a systematic and bibliographic catalogue. *Bulletin of American Paleontology* **51:** 111–394.

Yonge, C. M. 1939. The protobranchiate Mollusca; a functional interpretation of their structure and evolution. *Philosophical Transactions of the Royal Society of London* **230:** 79–147.

The authors wish to acknowledge the care and assistance of the referees, particularly in respect of matters of nomenclature.

Manuscript accepted for publication 17 December 1984

Appendix

Abbreviations to text figures

AA	Anterior adductor	NE	Nerve
AN	Anus	OD	Oviduct
AR	Anterior pedal retractor muscles	OE	Oesophagus
AS	Anterior sense organ	OV	Ovary
BG	'Byssal' gland	PA	Posterior adductor
BS	Blood space	PG	Pedal ganglion
CG	Cerebral ganglion	PL	Palp
CV	Cerebro-visceral commisure	PP	Palp proboscis
DD	Digestive duct	PR	Posterior pedal retractor muscles
DG	Digestive gland	RI	Ridges
EC	Excurrent canal	SE	Siphonal embayment
EP	Epidermis	SH	Stomach
FA	Feeding aperture	SI	Siphon
FT	Foot	SR	Siphonal ridge
GA	Gill axis	SS	Style sac
GL	Gill	SR	Statocyst
GS	Gastric shield	SU	Unfused siphon
HG	Hindgut	TE	Siphonal tentacle
HT	Heart	TH	Tooth
IC	Incurrent canal	TS	Testis
KI	Kidney	TY	Typhlosole
ME	Mantle edge	VD	Vas deferens
MU	Muscle	VG	Visceral ganglion