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THE FUNCTIONAL AND ADAPTIVE MORPHOLOGY OF THE DEEP-SEA SPECIES OF THE FAMILY LIMOPSIDAE (BIVALVIA: ARCOIDA) FROM THE ATLANTIC

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CONTENTS

The functional and adaptive morphology of six species of the genus *Limopsis* from deep water of the Atlantic is investigated and the following species and subspecies are described:

L. aurita, *L. surinamensis* (new species), *L. tenella*, *L. minuta*, *L. cristata cristata*, *L. cristata affinis*, *L. cristata intermedia* (new subspeices), *L. cristata lanceolata* (new subspecies), *L. galathea*.

Species of the genus *Limopsis* are among the relatively few suspension-feeding bivalves of the deep sea. The genus is not represented in shelf faunas. It is byssate, but the species described here show a change in habit from the exobyssate to the endobyssate condition and a corresponding reduction in the number and coarseness of the byssus threads produced. While the morphology of the species is similar in all the species described, differences being restricted to minor variation in the gills and palps, the viscera are confined to a small dorsal portion of the mantle cavity. Thus, while small body size is related to the paucity of food, production of a large thick shell may require a relatively small proportion of the energy input and yet confer advantage possibly in protection and in feeding mechanism. Eggs are relatively few and of a size indicating that the larvae are planktonic but non-feeding.

The widely occurring species *L. tenella* shows differences in the shell characters of different populations. In *L. cristata* variation is such that it has been possible to describe subspecies.

INTRODUCTION

Previous studies have been directed towards two trophic groups, namely deposit feeders and carnivores (Allen 1971, 1978; Allen & Sanders 1966, 1973, 1980; Allen & Turner 1974; Allen & Morgan 1980; Sanders & Allen 1973, 1977). Deposit-feeding bivalves predominate in the deep sea (Sanders *et al.* 1965; Knudsen 1970). The genera considered in this study are epibenthic suspension-feeders and therefore contrast markedly with those deep-sea bivalves studied so far, and emphasis is placed on the relation of morphology to environment.

THE SUPERFAMILY LIMOPSACEA DALL 1895

The arcoid superfamily Limopsacea according to Newell (Moore 1969) comprises the following families: Limopsidae, Glycymerididae, Philobryidae and Manzanellidae. The last family has since been shown to belong to the Protobranchia (Allen & Sanders 1969).

Of these families the Limopsidae appears to be the only one with truly abyssal representatives. The family Limopsidae (Dall 1895) is defined as: shells small or moderately small, orbicular or subtrigonal, equilateral to strongly inequilateral, non-gaping, ligament short with central triangular resilifer, taxodont dentition, periostracum, thick, with bristles.

The definition of the genus *Limopsis* Sassi 1827 (type species *L. aurita* Brocchi by monotypy) is the same as that of the family.

Here we discuss the functional and adaptive morphology of species present in the deep waters of the Atlantic. One of us (G. O.) will separately later report on the taxonomy of the genus *Limopsis s.l.* on a world-wide basis.

Limopsis aurita (Brocchi 1814)

Type. *Arca aurita* Brocchi 1814. Location?.

Type locality. Tertiary fossil, Italy.

Synonymy.

1814	*Arca aurita*	Brocchi (2, p. 485; fig. 9*a*, *b*, pl. 11)
1836	*Pectunculus auritus*	Philippi (p. 63)
1862	*Limopsis aurita*	Jeffreys (p. 343)
1863	*Limopsis aurita*	Jeffreys (p. 161; fig. 3, pl. 4)
1927	*Limopsis aurita*	Dautzenberg (p. 284, parts)
1966	*Limopsis aurita*	Tebble (p. 33)

Station data.

ship	date	station no.	latitude	longitude	depth/m	number of specimens
Sarsia	19.07.64	8	48° 41.0′ N	09° 44.0′ W	270–310	11
	25.06.75	3	48° 40.0′ N	09° 43.0′ W	410	4
	08.07.75	22	46° 51.0′ N	05° 11.0′ W	270–250	16
Thalassa	22.10.73	Z397	47° 33.8′ N	07° 12.6′ W	511	16
Challenger	21.05.75	1	48° 41.0′ N	09° 41.0′ W	192	2
	21.05.75	2	48° 40.0′ N	09° 43.0′ W	300	300

Distribution. L. aurita has a continuous distribution from and including the Mediterranean, through the northwest Atlantic, to Norway. There are discontinuous records from the Canary Islands, the Azores, Iceland, Newfoundland, Bermuda and Virgin Islands. There is also a single record, but of valves only, from the Arctic at 75° N in the Wellington Channel.

The total recorded vertical range is from 20 to 1900 m, but records from over 1000 m are few and occur in areas where the shelf is narrow and the slope extended such as is found around many oceanic islands, e.g. Bermuda. In other areas, e.g. Bay of Biscay, *L. aurita* appears to be restricted to the continental margin zone at 200–600 m.

Description. Descriptions of the shell are given by Jeffreys (1863) and Tebble (1966) but neither take into account the great variability of the species. The maximum recorded size, measured along the largest dimension, is 15 mm. *L. aurita*, in common with most limopsids, changes shape with growth (figure 2). In specimens up to 2 mm, the shell is more or less circular in outline, but as the size increases there is a disproportionate increase in the posterior ventral direction, resulting in an oblique-oval or oblique-circular outline. The anterior margin remains rounded but the posterior margin becomes almost straight. The specific name reflects the presence of a projection at each end of the hinge plate, where it meets the anterior and posterior margins. These 'ears' are not prominent in all specimens and are not confined to this species and so should not be used in identification. The shell is equivalve, and is somewhat compressed, having a mean breadth to length ratio of 1:2.4 ± 0.2 (*Challenger*, sta. 2). The umbos are not prominent and the dorsal area between them is narrow and deeply cleft. Each valve is strong and moderately thick: 1.15 mm in a shell 15 mm in length.

The sculpture consists of low concentric ridges cut by fine radial striations which correspond to the lines of the periostracal bristles. In fresh unworn shells this results in a fine decussate sculpture, which is normally obscured by the periostracum. The shell is white and glossy in young specimens but becomes grey, dull and cracked with age.

The periostracum in the 1–2 mm size group is a smooth, transparent covering. Bristles are present on larger shells and these are arranged in radial lines, obvious in smaller animals but less so in older specimens, especially around the posterior ventral margin. The bristles are long and lie flat against the shell and form a thick fringe around the shell margin. The periostracum is yellowish in clean specimens and the bristles are almost white, but in old individuals they are both a dirty straw colour.

The hinge is typically taxodont, with the numerous teeth in two distinct series. Those of the anterior set number up to eight and form a series decreasing in size from anterior to posterior. Both sets are separated by a small edentulous space that lies just posterior to the ligament. The teeth of the posterior set number up to nine; the first few lie on a line parallel to the dorsal margin, but at the postero-dorsal angle they are turned parallel to the posterior margin. The

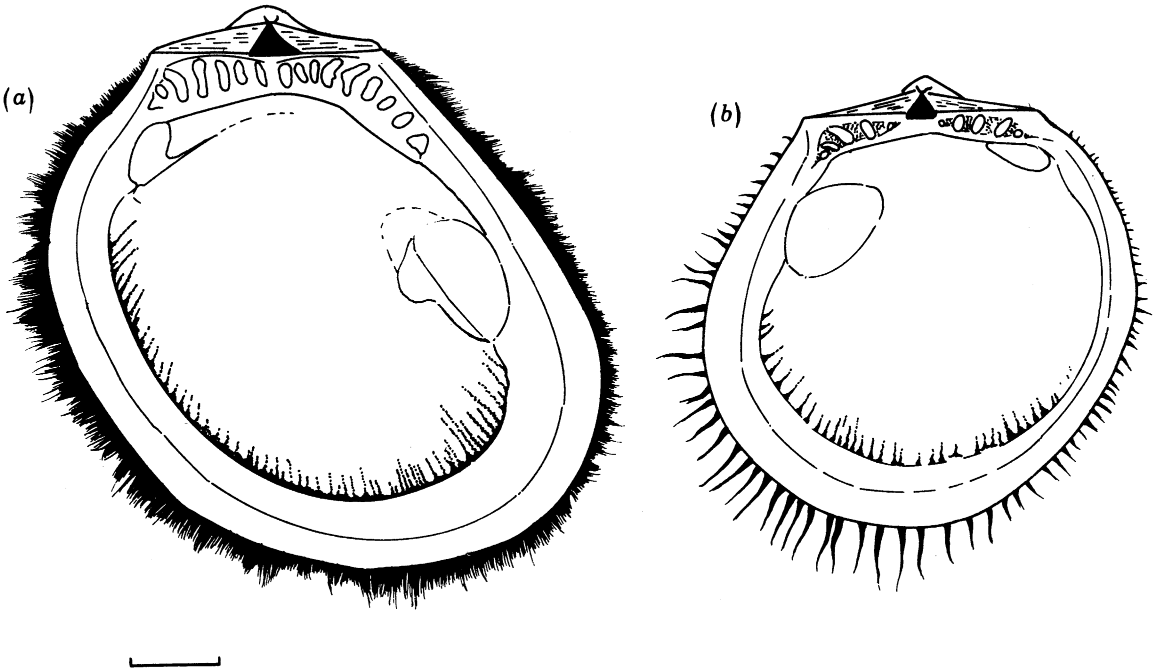

Figure 1. *Limopsis aurita.* Internal view of (*a*) right valve of a specimen from Bay of Biscay (300 m) and (*b*) left valve from St. Kitts (130 m). Scale bar, 2 mm.

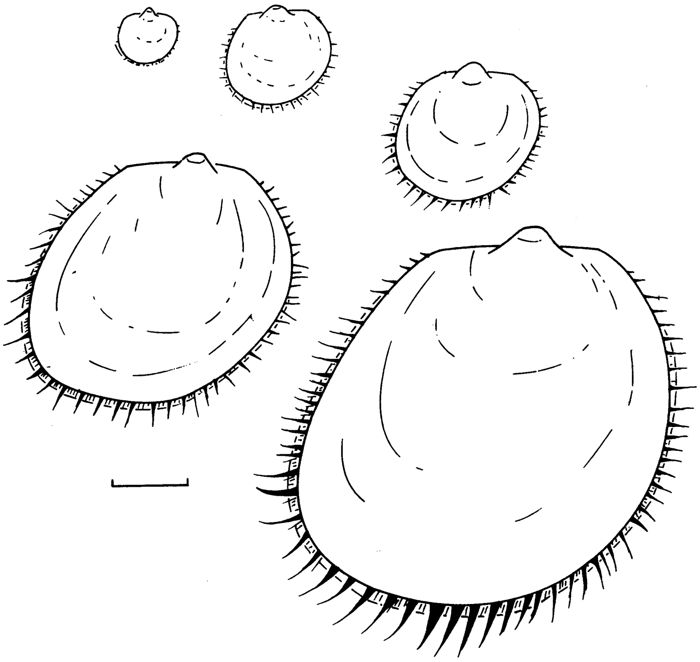

Figure 2. *Limopsis aurita.* Size series. Scale bar, 2 mm.

largest teeth are situated at the postero-dorsal angle. The two sets of teeth therefore form an arch that has its peak posterior to the ligament (figure 1). In some specimens, especially those from deeper water (1300 m), the teeth are smaller and lie almost parallel to the dorsal margin (figure 1). The ligament lies in a small triangular resilifer between the umbos.

Internally the shell is a dull greyish white colour. The pallial line and muscle scars are distinct. The heteromyarian condition is advanced; the posterior adductor scar, which lies opposite the midpoint of the posterior margin, is roughly twice the size of the anterior one, which lies beneath the anterior limit of the hinge plate. A distinct ridge runs from the ventral edge of the anterior adductor scar into the umbo. In some shells there are distinct but irregularly spaced radial striations inside the pallial line. These scars correspond to the radial pallial musculature and, contrary to Knudsen (1970), cannot be used as a specific character. The internal margin is broad, flat and completely smooth.

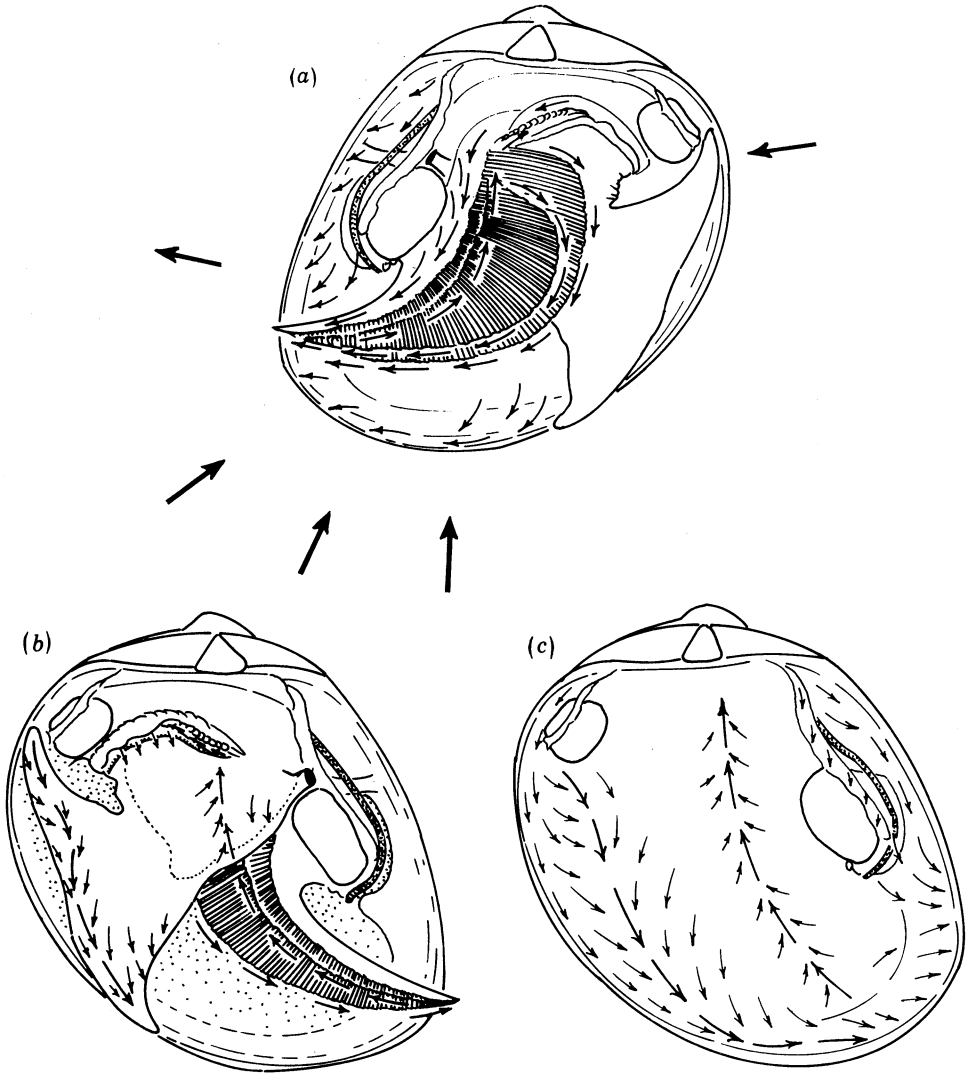

FIGURE 3. *Limopsis aurita*. Ciliary currents of the mantle foot and gills. (From an unpublished manuscript of the late Daphne Atkins.)

The mantle edges are free along their entire length. The edge is typical in having three folds, of which the inner muscular fold is the most prominent. The middle sensory fold is not well developed and there are no eyes or tentacles. The mantle itself is moderately thick, but unlike many arcids there are very few mucous glands present.

The gills (figure 3) are filibranchiate and suspended from a very muscular gill axis. The outer demibranch is slightly smaller than the inner and the ascending portions of the filaments are shorter than the descending portions. Ciliary junctions occur at the tips of the filaments and at the points of reflexion. The ciliation of the mantle organs (figure 3) is essentially the same as in *Arca tetragona* and *Glycymeris glycymeris* (Atkins 1936, and unpublished). The palps (figure 3) are small and little wider than the walls of the proximal oral groove running from the gills to the mouth. Up to seven ridges are present on each palp. Anteriorly the outer palp is somewhat broader than the inner and folds over the inner to form a tube leading to the mouth. The small size of the palps is related to the efficient sorting mechanism of the gills and they have become little more than a pathway from the gills to the mouth.

The route of the gut is similar to that described by Heath (1941) for the Arcidae and the Glycymeridae. The oesophagus runs close to the dorsal body margin and joins the stomach anteriorly. The stomach is also dorsal in position. The midgut and the style sac are combined and leave the stomach midventrally. The hindgut forms a single loop behind and to the right side of the stomach, and terminates with the anus projecting between the gill axes.

The oesophagus is long, slender and circular in cross section. The outer layer of muscle is very thin. The inner ciliated epithelium is thrown into folds, the number varying from four to ten.

The stomach (figure 4) is similar to those of *L. vaginatus* (Purchon 1957), *L. belcheri* (Dinamani 1967) and *Glycymeris glycymeris* (Reid 1965). The terminology used here follows Reid (1965), but analogous terms used by Dinamani (1967) are quoted where confusion may arise. The oesophagus enters the stomach high on the anterior face, into a prominent anterior chamber. On the dorsal surface of this chamber is a semitransparent area, which appears to be similar to the anterior–dorsal tract of Reid but that does not extend posteriorly to any great extent. The currents run from either end of this tract towards the centre, which corresponds with those described for the anterior–dorsal tract. Posterior to this and running posteriorly over the left roof of the stomach is a deep tract, strongly ciliated, which carries particles to, and ends in, the dorsal hood (hood tract). To the ventral side of this tract is a pad of tissue analogous to the 'buttress of stomach wall' of Reid (1965) and to the 'axial fold' of Dinamani (1967). This serves to separate the hood tract from the right duct tract. Dorsal and to the right side of the hood tract is a large ciliated area extending over and down the right side of the stomach to the ventral sorting area. The large gastric shield lies on the left posterior portion of the stomach wall, with one flange in the dorsal hood and another in the left pouch. The major sorting areas lie on the floor of the stomach and form a well defined area running from the right of the style sac forwards towards the oesophagus and then curving to the left and terminating below the axial fold. The portion nearest to the style sac is equivalent to Reid's posterior sorting area and the other end to Reid's right duct tract. The left pouch opens beneath the dorsal hood and is penetrated by a tongue of the major typhlosole. The major typhlosole runs on the left posterior side of the sorting area. The head of the minor typhlosole is very small and lies posterior to major typhlosole. The posterior portion of the stomach is not ciliated but is covered by a thin shining material, which in section appears homologous to shield material. This posterior wall is a very dark olive-brown. The digestive ducts open via eight apertures, two into the left pouch and six into the right anterior side of the sorting area.

The ciliary sorting mechanisms (figure 4) are essentially similar to those given by Reid (1965) for *Glycymeris*. Not having live material, neither Purchon (1957) nor Dinamani (1967) were able to study these mechanisms. The main circulatory currents are associated with the anterior face, hood tract and posterior right side and sorting area. Sorting occurs mainly in the ventral sorting area, where a 'type A' system operates (Reid 1965). The rejection tract runs along the edge of the major typhlosole, as in *Glycymeris*.

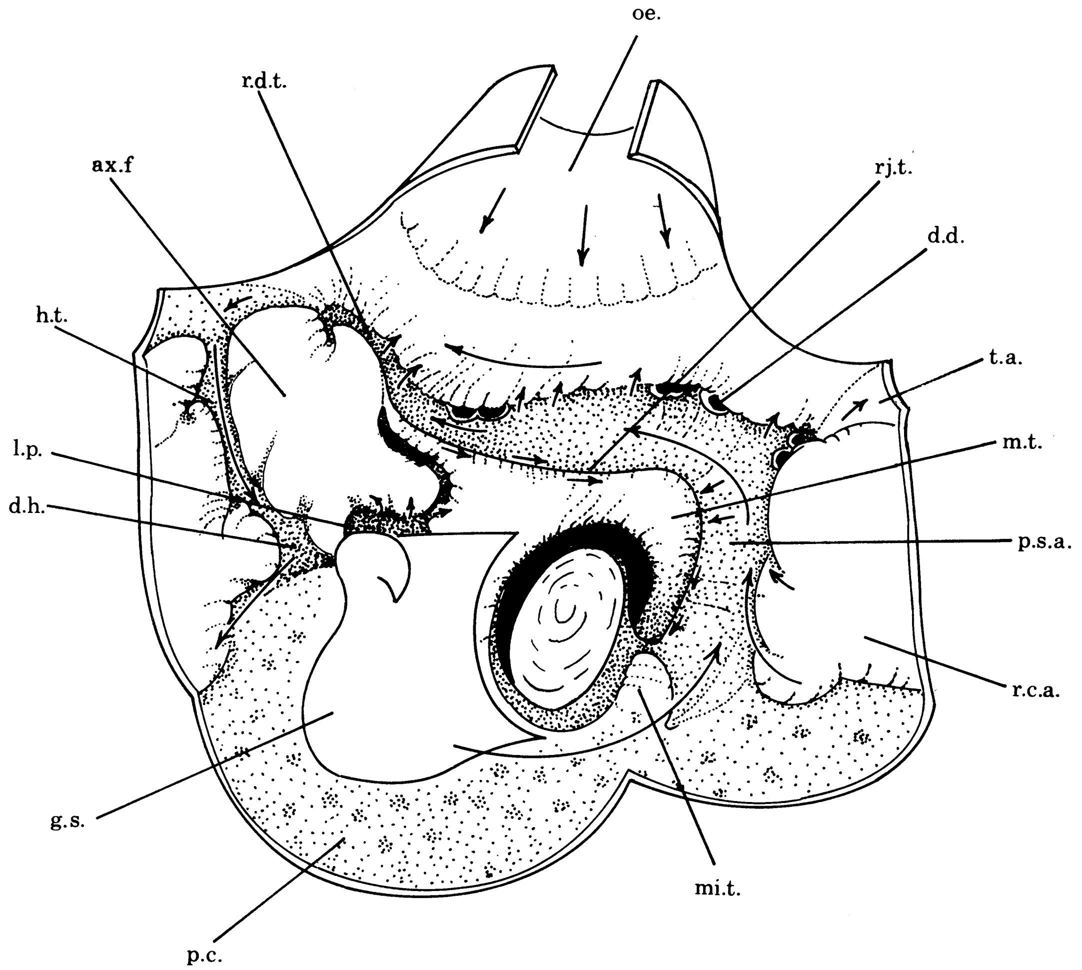

FIGURE 4. *Limopsis aurita*. Semidiagrammatic view of the stomach and its ciliary currents, as seen after a longitudinal incision dorsally on the right side. For explanation of abbreviations see key at end of paper.

The food particles in the stomach consist almost entirely of the tests of planktonic micro-organisms.

The digestive diverticula form a mass of greenish brown blind-ending tubules surrounding the stomach and part of the oesophagus. They do not extend far into the foot, reaching half-way down the midgut. Structurally and histologically they do not differ from described bivalve digestive diverticula (Owen 1972).

The kidneys are typical: paired and internally highly convoluted posteriorly but with a large anterior chamber. The floor of the anterior chamber is thrown into numerous folds increasing the functional area. The kidneys open ventrally via a pair of pores between the visceral mass and the gill axis.

Sexes are separate; the gonads occupy spaces in the viscera around the digestive gland and below it to the level of the pedal ganglion. In mature specimens the umbonal region of the body is swollen with gametes. The gametes are expelled via a duct joining the gonad to the renal pore. The eggs are 140 μm in diameter when ripe, and approximately 6000 are present in the largest specimens (15 mm). When live the eggs are bright orange and contrast with the testes, which are white. The testes initially develop as a lattice or network on the surface of the visceral mass.

The foot (figure 3) is moderate in size, muscular and highly mobile. It is laterally compressed and possesses a well developed heel and toe. The ventral margin usually lies parallel to the anterior margin of the shell. The musculature is typical, with outer circular, inner longitudinal and central transverse layers well developed. The anterior pedal retractors are small; the posterior retractors are much larger and are inserted above the posterior adductor. There is a ventral byssus slit and posteriorly a long byssus groove. Byssus glands are present but are not extensive; this is reflected by the byssus itself, which consists only of a single fine thread. The thread does not terminate with a disk as it does in *Mytilus*.

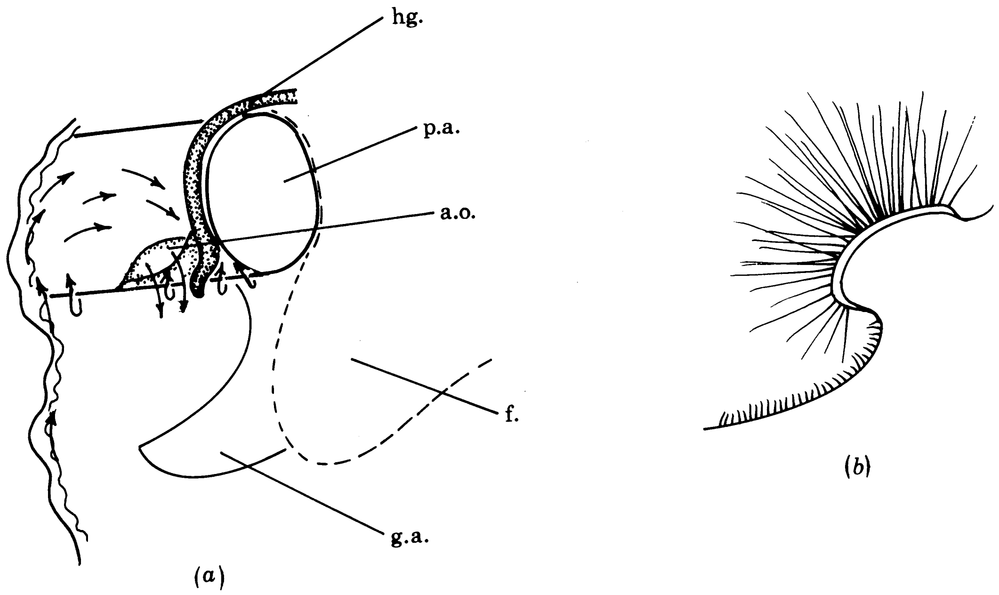

FIGURE 5. *Limopsis aurita*. Semidiagrammatic view of the left abdominal organ and its associated ciliary currents. For explanation of abbreviations see key at end of paper.

The nervous system is similar to that of other bivalves, with the cerebral ganglia lateral to the oesophagus, the visceral ganglia anterior to the posterior adductor and the pedal gangla situated somewhat anteriorly within the foot. Associated with the pedal ganglia is a pair of statocysts embedded in connective tissue.

So-called abdominal organs lie on either side of the anus and are attached to the ventral side of the posterior adductor muscle. Their structure has been described for a number of other genera and has been reviewed by Franc (1960). In *Limopsis* their construction is simple, each consisting of a low mound of connective tissue covered by an epithelium of large cells with large nuclei, which carry very long cilia (280 μm) (figure 5). A nerve connection was not found, but the organs overlie the anal nerves from the visceral ganglion. The abdominal organs are considered to be chemosensory, acting in a similar fashion to the osphradium. Observations on live animals show that the organs lie in the main exhalant flow and that they are frequently struck by particles and thus may act as tactile receptors and function as monitors of the amount of particulate material in the mantle cavity (figure 5).

Observations on living L. aurita. Approximately 300 specimens of *L. aurita* were collected from 300 m in the Bay of Biscay during the 1975 cruise of the *R.R.S. Challenger*. They were kept at 5 °C aboard the ship and then transported to the Dove Marine Laboratory, Cullercoats, where they were acclimatized to North Sea temperatures. The majority were alive over a year later, having been kept in a large tank without sediment. About 100 were kept in smaller tanks in sediments ranging through soft fine mud, sand, muddy gravel and gravel. The animals in each sediment type survived equally well and thus substantiated the many reports of this species occurring in bottoms of ooze to muddy gravel. Such a wide tolerance of bottom substrate is unusual. The behaviour of the animals in each sediment was similar but differences in the attitude of the shell were observed (figure 6).

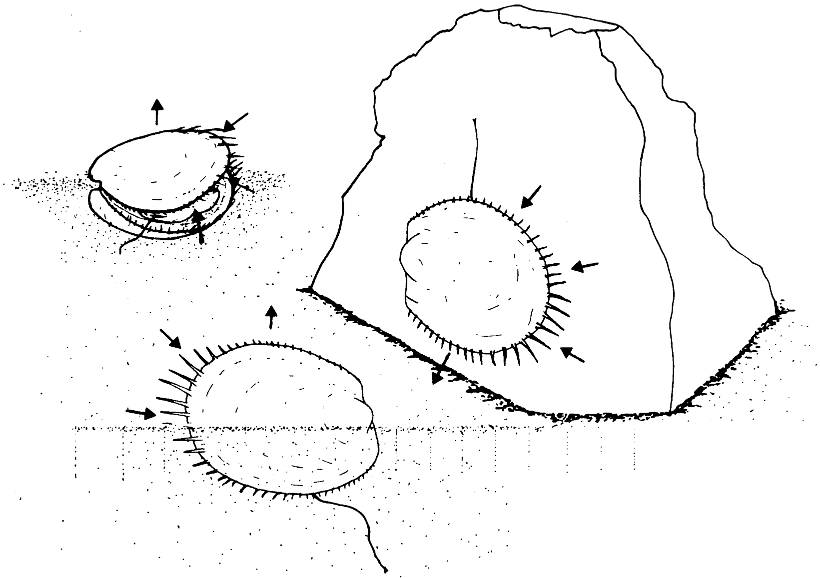

FIGURE 6. *Limopsis aurita*. Attitudes observed from living specimens.

Most animals remained in one place for long periods of time and would then move for a short distance. In motion over a hard, flat surface, the animal rights itself and crawls on the ventral portion of the foot, thereafter the animals fall on to one or the other of the valves. No preference for right or left was observed. Once the animal stops it normally secretes a byssus thread; thus in gravel the animals appear epibyssate. In softer sediments the compressed shell acts like a ploughshare and cuts into the sediment. In sand the animals leave a shallow groove but do not penetrate deep enough to remain in the upright position, while in mud the majority remain upright and some may be almost completely buried. In softer sediments the newly formed and unhardened byssus aggregates numerous particles and forms an effective anchor within the substrate. In soft sediments *L. aurita* can be said to be endobyssate. In all tanks some individuals crawled up the side of the tank and suspended themselves by their byssus.

The extent of the exhalant and inhalant apertures is controlled by the mantle edge, the tip of the gill axis and the degree of gaping, which in its turn affects the spacing between the periostracal bristles. With the valves shut it is not possible to open a live animal without damage. The fringing bristles, which normally lie with the curvature of the shell, abut each other and thus are forced outwards at the shell margin (figure 7). Initial opening allows the fringing bristles to lie with the curvature of the shell. Posteriorly, where the bristles are short and do not meet, a very small exhalant opening can be seen, the mantle edges having been drawn apart. In this second position (figure 7) a small current was observed leaving this opening and an anterior inhalant current was observed entering between the bristles. This appears to be a phase in which the environment is tested, for it is usually quickly followed by contraction or further relaxation until the tips of the bristles touch and no more. The opposing mantle edges are not in contact and an exhalant aperture is separated from the pedal gape by the positioning of the gill axes. The gill axes are muscular and highly mobile and protrude beyond the margin of the shell. In this fully extended position the foot usually lies along the anterior margin of the mantle edge, effectively sealing this area, and thus reduces the combined pedal and inhalant aperture. The fringing bristles act as a filtering device, preventing the entrance of large particles or large quantities of sediment into the mantle cavity. Further relaxation of the adductors may occur and the valves gape widely. Then the incurrent area extends from the tip of the gill axes to the anterior adductor and the excurrent aperture from the gill axes to the posterior adductor. Vigorous clapping of the valves was observed whenever large amounts of sediment entered the mantle cavity. This was also observed if the animals were artificially buried, in which case the clapping continued until the incurrent region was free of sediment. These frequent clapping movements are undoubtedly correlated with the large size of the quick portion of the posterior adductor. In soft sediments, sediment particles were often observed entering the mantle cavity and these were usually expelled as pseudofaeces; however, the possibility that some of the

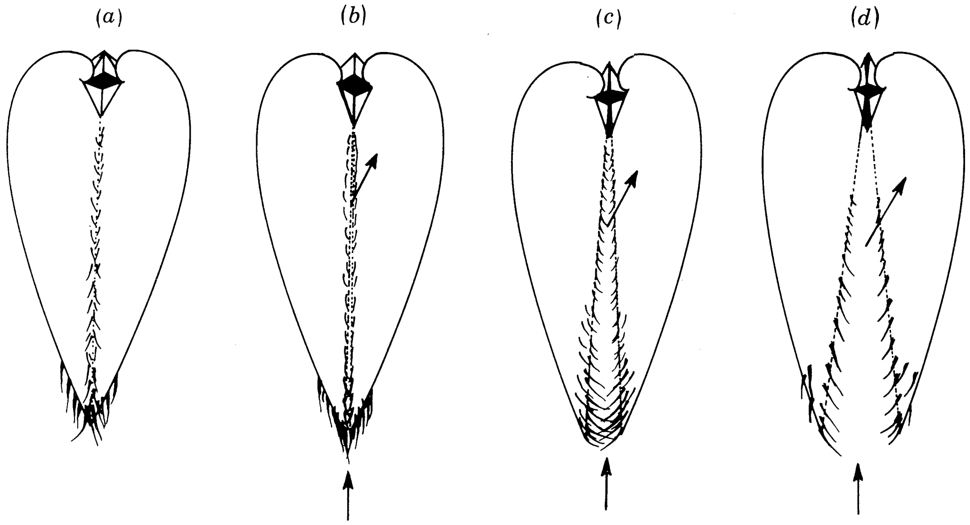

FIGURE 7. *Limopsis aurita*. To show four stages of increasing gape of the valves.

ingested material is benthic in origin cannot be discounted, although sediment particles were not frequently found in the stomach.

It appears that *L. aurita* is a true suspension feeder, which, because of periostracal bristles and behaviour, is able to survive in a wide range of bottom substrates.

Limopsis surinamensis new species

Type. *Limopsis surinamensis*. Location: Museum of Comparative Zoology, Harvard.

Type locality. *Knorr* cruise 25, station 297, off Surinam at 500 m.

Station data.

ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Knorr	25	28.02.72	297	07° 45.3′ N	54° 24.0′ W	500	418

Distribution. *L. surinamensis* has been recorded only from the above station off Surinam.

Description. Shell, thick, equivalve, inequilateral, compressed; shell shape varies with growth, small specimens circular, larger specimens oblique-circular; posterior margin slightly curved, anterior margin more strongly curved, dorsal margins variable in length, distance between them consistently narrow; no ear-like projections at junction of dorsal and lateral margins; umbos not prominent; ligament small; shell sculpture finely cancellate but obscured by periostracum; periostracal bristles, long, golden brown and lying flat against shell, arranged in closely spaced rows forming a broad fringe around shell margin; hinge plate well developed, teeth arranged in two series separated by small edentulous space; teeth number increases with size, there being seven to ten in each set in larger size classes; teeth arranged in arch that has its

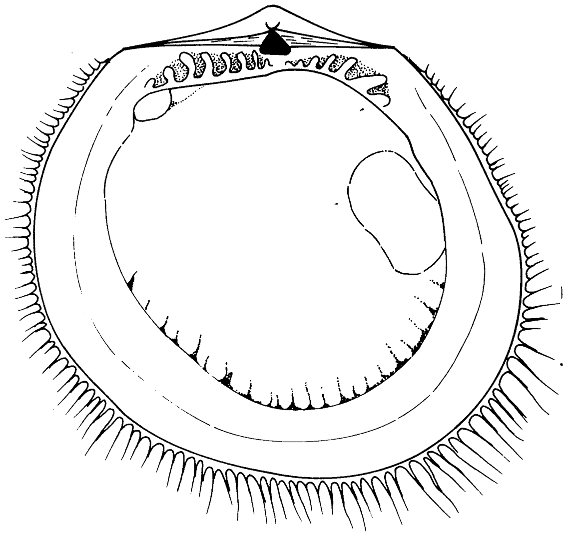

FIGURE 8. *Limopsis surinamensis*. Internal view of right valve.

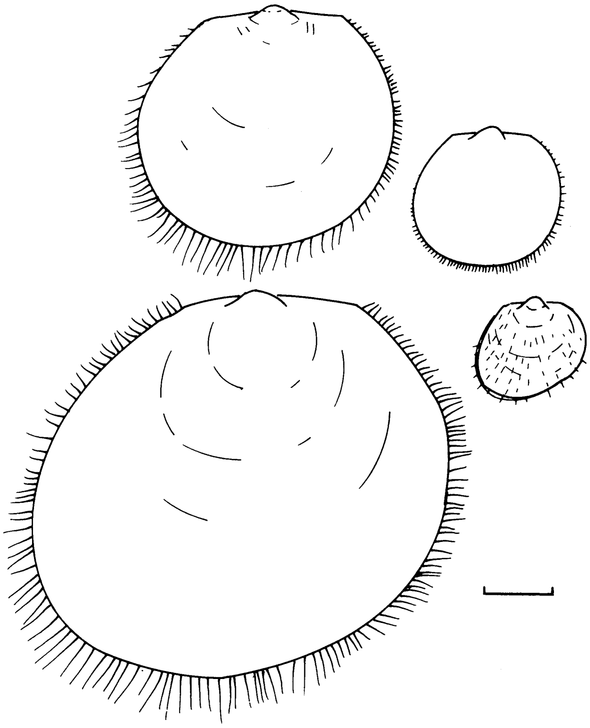

FIGURE 9. *Limopsis surinamensis*. Size series. Scale bar, 2 mm.

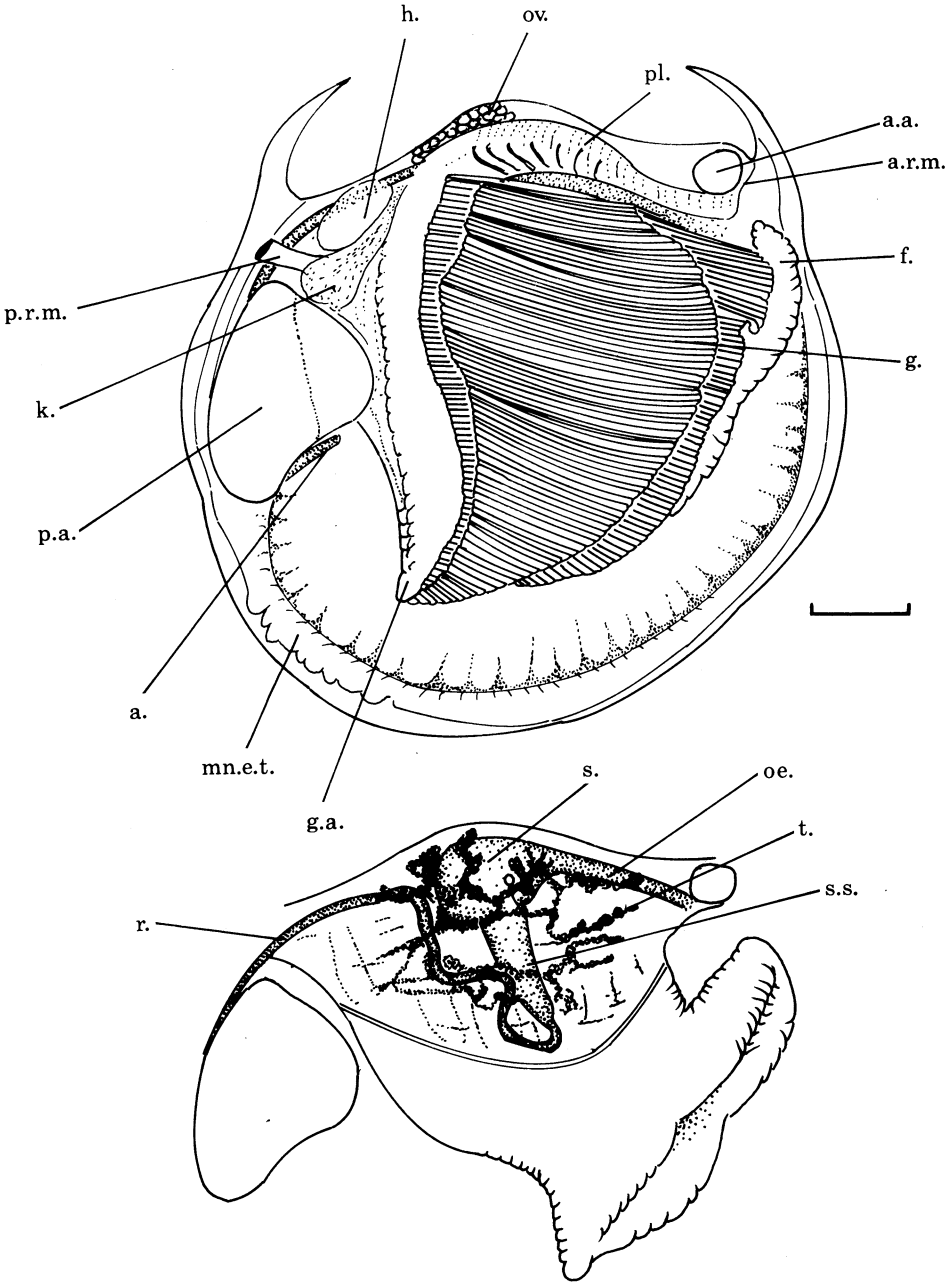

Figure 10. *Limopsis surinamensis*. Anatomy as seen from the left side. Lower figure shows the visceral organs, following removal of part of the body wall. For explanation of abbreviations see key at end of paper. Scale bar, 1 mm.

peak posterior to the ligament; adductor scars distinct, posterior scar much larger than anterior, ridge present from anterior adductor to umbo; inner shell margin broad, flat, completely smooth; radial pallial striations present inside distinct pallial line. First prodissoconch measures 175–180 μm. Maximum shell length, 15 mm.

This species does not fall within the limits of the variations exhibited by the other species of

Limopsis known from the equatorial regions of the Atlantic Ocean. Thus, while *L. aurita* has been recorded from the Lesser Antilles it differs from *L. surinamensis* in having pale periostracal bristles and in being consistently more oblique in outline. *L. janeiroensis* Smith (1915) has been recorded once from off Brazil and, like *L. aurita*, it has a strong oblique shape. Unfortunately the type material of *L. janeiroensis* consists of worn shells without bristles and therefore this character cannot be compared. Because *L. janeiroensis* is a large species, reaching 25 mm, the difference in shape is not completely conclusive for distinguishing the two species and it may well be that when further examples are obtained *L. surinamensis* and *L. janeiroensis* will be synonymized.

Gross morphology is close to that of *L. aurita* and a full description is not necessary (figures 8–10). Of note is the large size of the very thin-walled heart. Stomach contents include a large proportion of fine sediment, together with diatoms and green cells. Byssus threads were not observed despite the presence of a well developed byssus slit in the toe of the foot.

Limopsis tenella Jeffreys 1876

Type. *Limopsis tenella* Jeffreys 1876. Location: British Museum (Natural History).

Type locality. *Valorous* expedition, station 12, 56° 11′ N, 37° 41′ W, (2650 m).

Synonymy.

1876	*Limopsis tenella*	Jeffreys (p. 434–5; not figured)
1885	*Limopsis pelagica*	Smith (p. 254; figs 3, 3A, pl. 18)
1888	*Limopsis pelagica*	Pelseneer (p. 12; fig. 1, pl. 2)
1893	*Limopsis plana*	Bush (p. 240; figs 19, 20, pl. 2)
1898	*Limopsis plana*	Verrill & Bush (p. 846; fig. 5, pl. 75)
1898	*Limopsis profundicola*	Verrill & Bush (p. 847, fig. 4, pl. 75; fig. 4, pl. 83)
1898	*Limopsis transversa*	Locard (pl. 326; figs 11–14, pl. 15)
1906	*Limopsis indica*	Smith (p. 254, parts)
1927	*Limopsis pelagica*	Dautzenberg (p. 286)
1927	*Limopsis aurita*	Dautzenberg (p. 284, parts)
1931	*Limopsis guinensis*	Thiele (Thiele & Jaeckel 1931, p. 25; fig. 17, pl. 1)
1967	*Limopsis pelagica*	Knudsen (p. 265; figs 12–15, pl. 1)
1970	*Limopsis pelagica*	Knudsen (p. 83; figs 11, 12, pl. 9; figs 1–11, pl. 10; figs 1–3, pl. 11)

Station data.

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Gay Head–Bermuda transect	*Atlantis II*	12	21.08.64	64	38° 46.0′ N	70° 06.0′ W	2886	3
	Chain	50	29.06.65	76	39° 08.3′ N	67° 57.8′ W	2862	2
			30.06.65	77	38° 00.7′ N	69° 16.0′ W	3806	56
			30.06.65	78	38° 00.8′ N	69° 18.7′ W	3828	15
			05.07.65	85	37° 59.2′ N	69° 26.2′ W	3834	53
	Atlantis II	24	24.08.66	126	39° 37.0′ N	66° 47.0′ W	3806	42
					39° 37.5′ N	66° 44.0′ W		
Dakar–Recife	*Atlantis II*	31	07.02.66	148	10° 37.0′ N	18° 14.0′ W	3814–3828	10
			07.02.66	149	10° 30.0′ N	18° 18.0′ W	3961	22
			13.02.67	155	00° 03.0′ S	27° 48.0′ W	3730–3783	24
			14.02.67	156	00° 46.0′ S	29° 28.0′ W	3459	5
					00° 46.5′ S	29° 24.0′ W		
southwest Africa	*Atlantis II*	42	17.05.68	194	22° 54.0′ S	11° 55.0′ E	2864	12
					14° 49.0′ S	09° 56.0′ E		
			19.05.68	195	14° 40.0′ S	09° 54.0′ E	3797	40
					10° 29.0′ S	09° 03.0′ E		
			21.05.68	197	10° 29.0′ S	09° 04.0′ E	3865–4595	2

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
southwest Africa (*cont.*)	*Walda*	71	21.05.68	CY05	21° 58.8′ S	09° 19.7′ E	2953	1
				CY07	22° 53.3′ S	11° 56.2′ E	2840	158
				CY12	14° 31.8′ S	09° 46.0′ E	3975	381
				CY14	12° 21.4′ S	11° 02.7′ E	3431	300
				DS13	14° 21.5′ S	09° 46.2′ E	3985	14
				DS17	09° 12.0′ S	10° 29.0′ E	4223	1
				DS18	06° 3.40′ S	08° 18.2′ E	4079	1
				DS21	02° 38.2′ S	05° 40.0′ E	4019	1
				DS22	00° 35.6′ S	06° 49.4′ E	3025	3

Distribution. L. tenella has a continuous distribution throughout the N. Atlantic, S. Atlantic and Indian oceans. A subspecies *L.t. dalli* (Knudsen 1970), is confined to the Pacific Ocean adjacent to central America. It is abyssal and is restricted to depths between 2000 and 5000 m.

Because of its wide geographical range and variability of shell form, *L. tenella* has a complicated taxonomic history. Knudsen (1967, 1970) clarified the situation considerably but only limited museum material from the North Atlantic was available. Knudsen could not locate the type of *L. tenella* and therefore synonymized his material under *L. pelagica* Smith 1885. The type material in the British Museum (Natural History) is doubtful as no locality is given, but United States National Museum lot no. 62834 probably contains syntypes. This lot carries the label: '*Limopsis tenella* sp.n. Jeffreys. st 12. 1450 fms Valorous Ex', which is identical to the locality given by Jeffreys (1876) in his type description. A comparison of *L. tenella* and *L. pelagica* is shown in figures 11 and 12. Both shells are approximately the same size, 6.1 and 5.8 mm respectively, there is little difference in outline, the muscle scars are identical and the number and orientation of the teeth are the same. The flat smooth inner margin is also common to both. The concentric sculpture is similar but the radial marks produced by the insertion of the bristles is more pronounced in *L. tenella*. *L. tenella* has a thinner shell and a weaker hinge is associated with this. Both shells have a prodissoconch measuring 238 μm. The variation between the two is entirely consistent with that found within the present sample and therefore *L. pelagica*

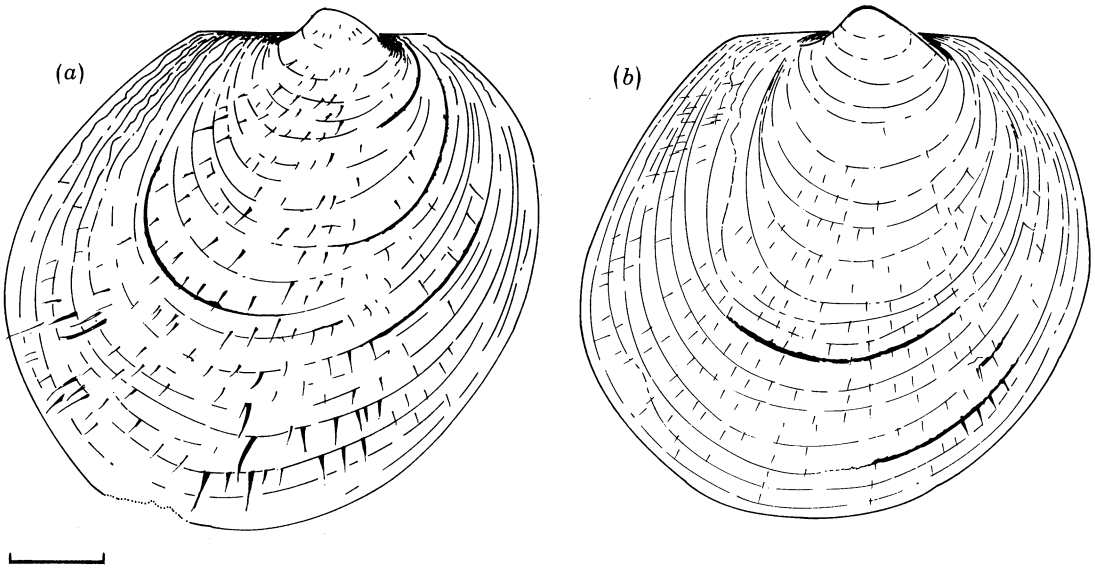

Figure 11. Comparison of the right valves of *Limopsis pelagica* and *L. tenella*. Scale bar, 1 mm.

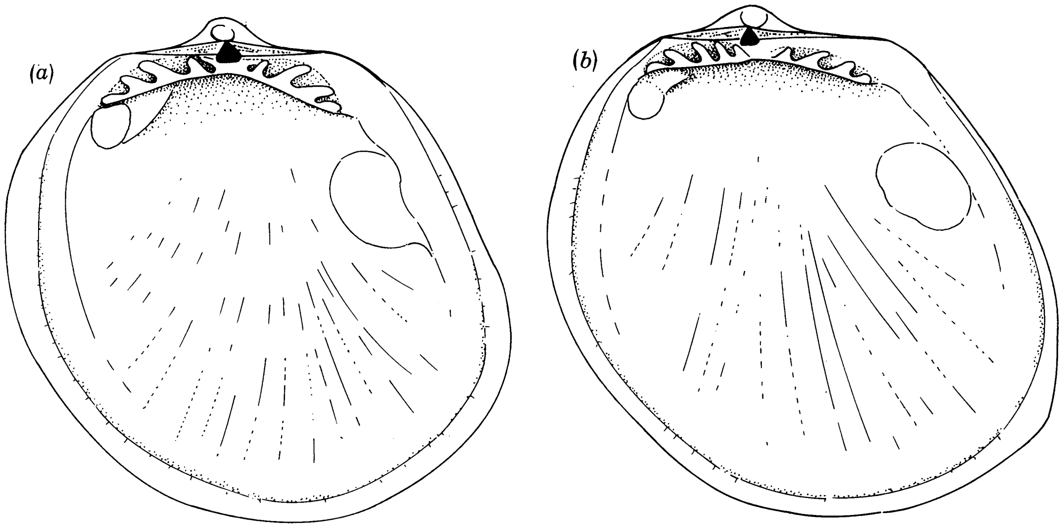

FIGURE 12. Comparison of the internal views of the right valves of *Limopsis pelagica* and *L. tenella*.

has been synonymized under *L. tenella*. It is also confirmed that *L. profundicola* Verrill and Bush 1898 and *L. plana* Verrill 1885 are identical to *L. tenella* (see below).

Description. This large limopsid (maximum length 35 mm) is very variable and consequently requires careful description. The following account is based on material from the North and South Atlantic oceans. Specimens from the Indian Ocean described by Knudsen and those in the British Museum (Natural History) all fall within the limits of variation described below.

Very small shells (1.5 mm, figure 13). These are almost circular in outline. The posterior margin is only slightly less rounded than the anterior. The umbos are prominent and the ends of the hinge plate are noticeable. The sculpture consists of concentric lines only, radial sculpture is not yet apparent. The lack of radial sculpture is probably associated with the absence of periostracal bristles at this stage. The periostracum is present as a thin, smooth, transparent covering that extends beyond the shell margin. Teeth are few; usually there is only one on each side, the remainder of the hinge plate being dominated by the larval hinge. Muscle scars are not apparent.

By means of the above characters it is very difficult to separate this species from similar-sized

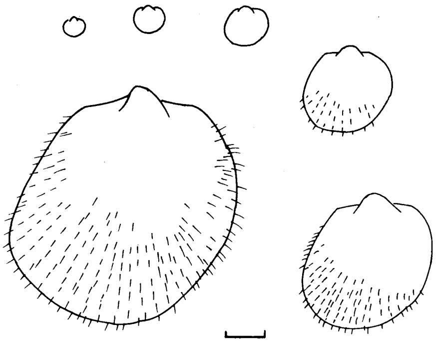

FIGURE 13. *Limopsis tenella*. Size series. Scale bar, 1 mm.

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specimens of *L. aurita*, except that the first prodissoconch is larger in *L. tenella* (240 μm) than in *L. aurita* (170 μm).

Shells 1.5–3.5 mm (figure 13). Oblique growth, characteristic of the species, becomes apparent at this stage. The posterior margin is straighter whereas the anterior margin remains strongly curved. Periostracal bristles are visible when the shell is 3 mm long but the sculpture remains predominantly concentric. Although the number of teeth increases, the larval hinge is still observable.

Shells 3.5 mm and larger (figure 13) Oblique growth continues but the degree of posterior ventral extension is variable and there is variation in the degree of curvature of the posterior margin. The angle at which the anterior and posterior margins meet the dorsal margins is also variable, some specimens having a smooth curved junction, others being sharply angled. The latter possess eared structures similar to those described for *L. aurita*. The umbos are relatively less prominent in the larger individuals. The shell is compressed to a greater degree than in *L. aurita* but there is variation and a degree of interspecific overlap. The variation in shell width appears to be related to the interumbonal growth rather than to variation in the curvature of the valves; thus the dorsal area is variable in width and depth (figure 14). The thickness of the shell is also variable, some shells being twice as thick as others of the same length and this is most obvious in shells from different samples. Sculpture consists of concentric lines and irregular low ridges cut by numerous fine radial striations. The decussation is more noticeable than that of *L. aurita*. Periostracal bristles are long and fine and arranged in numerous closely spaced rows. In the unworn shell the bristles are so numerous that the linear arrangement is obscured.

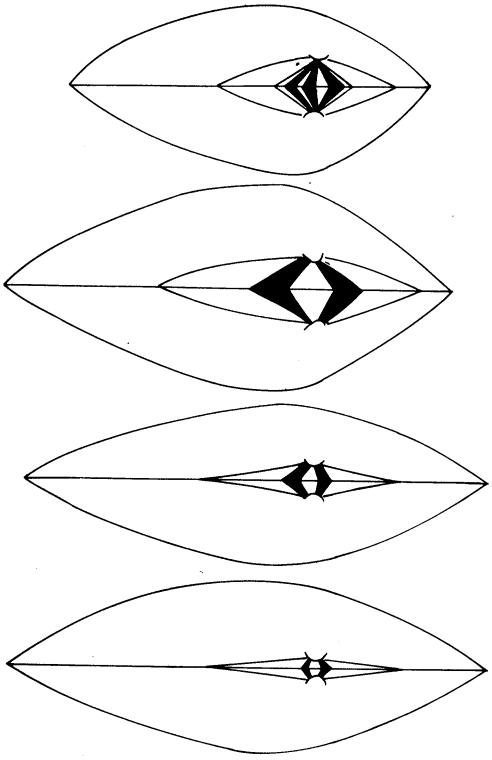

FIGURE 14. *Limopsis tenella*. Variation in interumbonal growth.

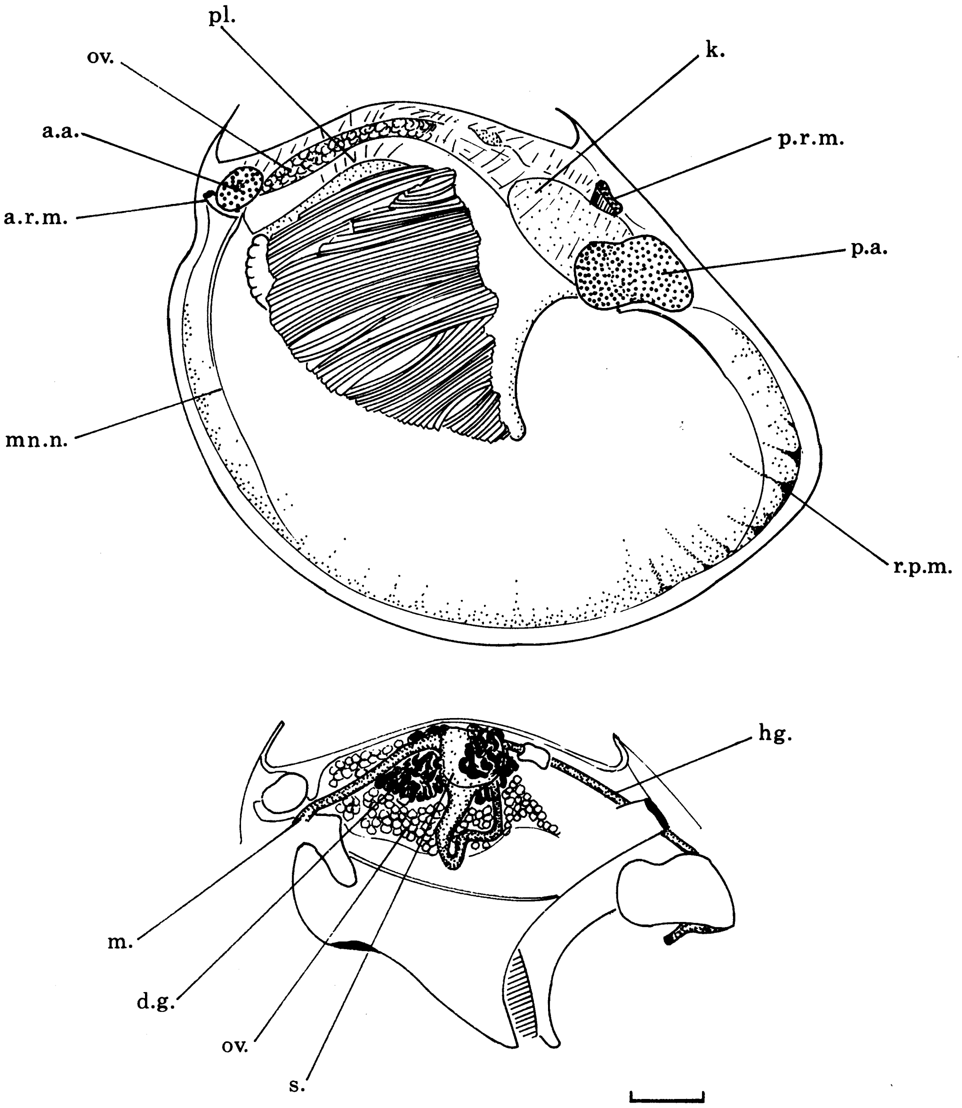

FIGURE 15. *Limopsis tenella*. Anatomy as seen from the left side. Lower figure shows the visceral organs following removal of part of the body wall. For explanation of abbreviations see key at end of paper. Scale bar, 2 mm.

In worn shells bristles may remain around the margin while in others no bristles are present. The periostracum can be straw-coloured, brown or olive, but the bristles are consistently a deep golden brown and somewhat translucent in appearance.

Variation in the thickness of the shell affects the strength of the hinge plate and both it and the teeth are stronger in the thicker shells. The teeth are arranged in two series, numbering up to eleven on each side. Both sets lie along a line more or less parallel to the dorsal edge. The edentulous space between the two sets of teeth may occupy up to 50% of the hinge plate. In thin shells muscle scars are faint, only those of the adductors being noticeable, and of these the posterior scar is characteristically raised. In thick shells the adductor scars are obvious and impressed, a pallial line is visible and occasionally radial pallial scars can be seen. A low ridge from anterior adductor to umbo is present. The internal margin varies in width but is always smooth.

The anatomy (figure 15) of *L. tenella* is similar to that of *L. aurita*. As in the latter species, the mantle edge is at its most muscular at the posterior ventral margin. The gill axes are also muscular to a similar degree and the gills are of similar form. The palps have up to seven ridges, the same number as in *L. aurita*, although in animals twice the size. The ridges are often indistinct but this may be due to poor fixation. The gut follows the same route as in other limopsids and there are no observable differences in the relative length of the various parts. The longitudinal ridges of the oesophagus are indistinct and the structure of the stomach is similar to that of *L. aurita*. The kidney differs in that the ventral convolutions are less developed and the lumen appears larger. The reproductive system is less extensive in this species, the eggs being larger than those of *L. aurita* (140 µm in diameter in specimens preserved in alcohol, which is equivalent to about 196 µm when fresh). Byssus glands open via a slit in the toe but in only two small (10 mm) specimens was a byssus thread observed.

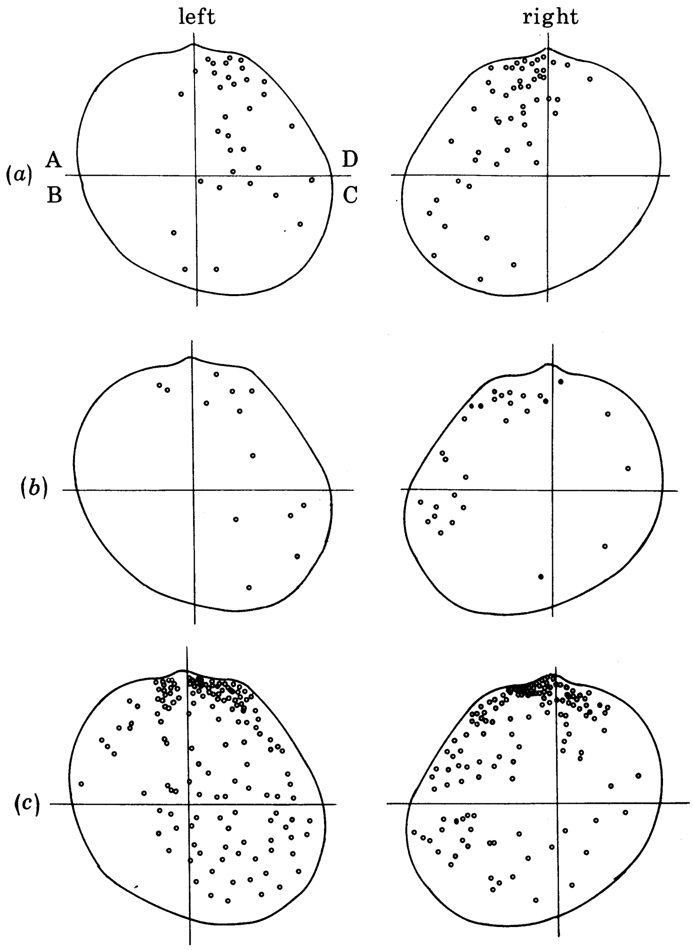

FIGURE 16. *Limopsis tenella*. Distribution of the epifauna on the left and right valves: (*a*) *Waldheimia*; (*b*) *Atlantodiscus*; (*c*) *Bentharca*.

L. tenella was not observed alive and circumstantial evidence had to be used to build a picture of the habits of the animal. Of all the samples available, those from southwest Africa were most heavily infested with an epifauna. Thus the sample from station CY12 had present the bivalve

Table 1. The numerical distribution of epifauna on the left and right valves of *L. tenella*

station CY14	left	right
Waldheimia sp. (Brachiopoda)		
whole animals	18	30
peduncle only	14	24
total	32	54
$X^2\ \frac{(Q-E)^2}{E}$ total	5.68 (applies between 0.02 and 0.01)	
Pelagodiscus atlanticus (Brachiopoda)		
whole animals	14	29
X^2	5.24 (applies between 0.05 and 0.02)	
station CY12		
Bentharca asperula (Bivalvia)		
byssus stalks	190	175
X^2	0.06 (applies between 0.9 and 0.8)	

Table 2. The numerical distribution of epifauna on the anterior and posterior halves of the shell of *L. tenella*

	left		right	
station CY14				
Waldheimia sp.	AB	CD	AB	CD
	3	28	5	45
	X^2 total 22.1 $p < 0.001$		X^2 total 32 $p < 0.001$	
Pelagodiscus atlanticus	AB	CD	AB	CD
	2	12	4	24
	X^2 total 7.1 $p < 0.01$		X^2 total 14.3 $p < 0.001$	
station CY12				
Bentharca nodulosa	AB	CD	AB	CD
	56	138	42	134
	X^2 total 34.6 $p < 0.001$		X^2 total 48.1 $p < 0.001$	

Bentharca asperula and a few specimens of *Pelagodiscus atlanticus* (Brachiopoda). Specimens from station CY14 had *P. atlanticus* and another brachiopod of the genus *Waldheimia* attached. The distribution of these three species on the shell is plotted in figure 16. In *Bentharca* the distribution is similar for both right and left valves but in the brachiopods there appears to be a bias in favour of the right valve (table 1). There is a significant difference between the distribution on the anterior and posterior portions of the shell (table 2) (denoted by the diagonal line in figure 16). This pattern is common to all three epifaunal species. There are no morphological differences between the two valves, that would account for the preferential settlement of epifauna on the right valve. There are also shells that have, or have had, epifauna on both valves. All would indicate that the limopsid does not lie on one valve for any length of time and that the anterior area is not available for settlement. Thus there is evidence that *L. tenella* spends much of its time in an upright position, with only the posterior area above the sediment. From the infrequent occurrence of byssus threads it might be suspected that *L. tenella* may be the more active than *L. aurita*. Less probably, this species may lie deeper in the sediment, making the byssus attachment redundant. The somewhat greater compression of the shell also points to a more infaunal existence. Thus *L. tenella* is probably a semi-infaunal species that at times may lie on one side, especially when a large epifauna is present.

Limopsis minuta (Philippi 1836)

Type. *Pectunculus minutus* Philippi 1836. Location?

Type locality. Tertiary fossil. Sicily.

Synonymy.

1836	*Pectunculus minutus*	Philippi (vol. 1: p. 63; fig. 3, pl. 5)
1862	*Limopsis abyssicola*	Adams (p. 230; not figured)
1876	*Limopsis minuta*	Jeffreys (p. 434)
1883	*Limopsis minuta*	Jeffreys (p. 392)
1927	*Limopsis minuta*	Dautzenberg (p. 285)
1931	*Limopsis anceps*	Thiele (p. 184; fig. 20, pl. 6)
1964	*Limopsis anceps*	Barnard (p. 384; fig. 4*a*)

Station data.

region	ship	date	station no.	latitude	longitude	depth/m	number of specimens
Canary Islands	*Discovery*	19.03.68	6711	27° 14.9′ N	15° 36.3′ W	2938	3
Bay of Biscay	*Sarsia*	24.07.67	61	46° 20.1′ N	04° 36.0′ W	952	9
	Thalassa	21.10.73	Z392	47° 34.9′ N	07° 01.2′ W	390	3
		22.10.73	Z397	47° 33.8′ N	07° 12.6′ W	511	62
			Z398	47° 36.0′ N	07° 16.8′ W	398	2
			Z399	47° 34.8′ N	07° 18.1′ W	825	1
			Z402	47° 39.5′ N	07° 28.5′ W	450	3
		23.10.73	X409	47° 43.1′ N 47° 42.9′ N	08° 04.0′ W 08° 00.9′ W	1035–1080	13
		24.10.73	Z413	48° 03.1′ N	08° 29.4′ W	805	2
			Z414	48° 05.0′ N	08° 29.8′ W	650	56
			Z415	48° 07.1′ N	08° 26.2′ W	380	6
			Z417	48° 12.0′ N	09° 09.5′ W	865	2
			Z421	48° 22.5′ N	09° 33.5′ W	950	3
			Z435	48° 39.7′ N	09° 53.2′ W	1050	4
			Z437	48° 35.0′ N	10° 23.7′ W	610	8

Distribution. *L. minuta* has been recorded from many localities off both east and west coasts of the N. Atlantic and also from the Caribbean, the Gulf of Mexico, the Canaries, the Azores, off Iceland and off the south of Greenland. The bathymetric range is very wide, 20–3500 m. However, as with *L. aurita*, the range in a single geographical area is much narrower (e.g. Bay of Biscay, approximately 400–1000 m). It is not clear how many abyssal records are of dead shells or are misidentifications. Despite this the present Canaries record from 2938 m confirms the great range. It is interesting to note that *L. minuta* is usually taken with *Bentharca nodulosa* in the Bay of Biscay and that both species appear at great depths off the Canaries, suggesting equatorial submergence or that the area off the Canaries is environmentally unusual and the depth range is extended accordingly.

Synonomy. Although there are no specimens of this species from the South Atlantic in the present collections, there are examples in the British Museum (Natural History), from Cape of Good Hope. These latter are labelled '*L. abyssicola* (A. Adams)' and are Adams's types, but they are identical to *L. minuta*. Barnard (1964) also noted the similarity of *L. abyssicola* and *L. anceps* Thiele (1931), and although *L. anceps* has not been examined it seems probable that it should be synonymized with *L. minuta*.

Description. Shell equivalve, inequilateral with prominent umbos; adult shape markedly oblique and characteristically inflated (B/L ratios of 1:1.9); posterior margin more or less straight, anterior margin often with short, straight, upper edge giving whole margin an angled appearance; smaller specimens less oblique with more rounded margins and resembling young *L. aurita*; shape almost circular in smallest size groups (in mixed samples equivalent-sized *L. aurita* are less oblique than *L. minuta*); dorsal margins short; interumbonal distance wide, especially in large specimens; in unworn shells sculpture typically decussate, occasionally raised radial ribs present on dorsal posterior region; periostracum may be absent except at shell margins; bristles finer than those of *L. aurita* and more closely spaced; bristles, pale straw colour except in old specimens, where they are dirty and darker; teeth arranged in an arch with peak beneath ligament; up to five teeth in each set, the anterior set being orientated vertically to the dorsal edge, the posterior set oblique; internally, shell is white with prominent adductor scars and pallial line; heteromyarian condition extreme, the anterior adductor muscle being one-seventh of the cross section of the posterior; a ridge is present from umbone to anterior adductor scar; the inner margin of shell is crenulated to a varying degree: in minute shells the

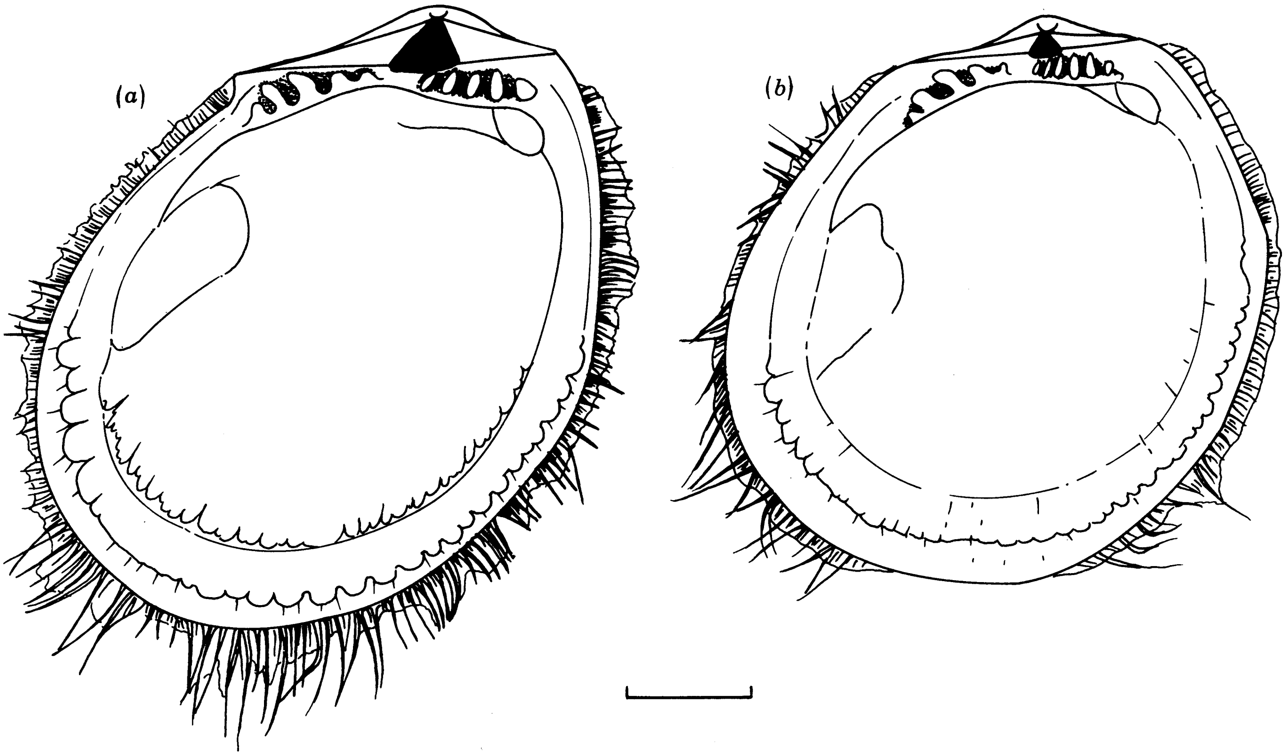

FIGURE 17. *Limopsis minuta*. Internal views of the left valves of (*a*) inflated and (*b*) compressed specimens. Scale bar, 2 mm.

crenulations are barely visible; they are clear in midsize classes; while in large shells the crenulations are reduced to a few (usually 3), large, posterior ventral swellings (figure 17). Maximum length 9 mm.

Except for the form of the foot and its associated musculature, the anatomy of this species is very similar to that of *L. aurita* (figure 18).

The foot is somewhat bulbous, with a reduced heel and a short toe. The toe is inflated, with a wide oval byssus aperture on its sole. The toe is placed below the anterior adductor, high on the anterior shell margin. The pedal retractor muscles are well developed. One posterior pedal retractor is attached to the shell; the other is embedded in the posterior adductor and acts as a powerful byssal retractor. The byssus is well developed; it secretes around a central stalk the sheath of a strong byssus which, distally, splits into a few (up to five) short wide threads (figure 19). This is the strongest byssus observed within the present genus.

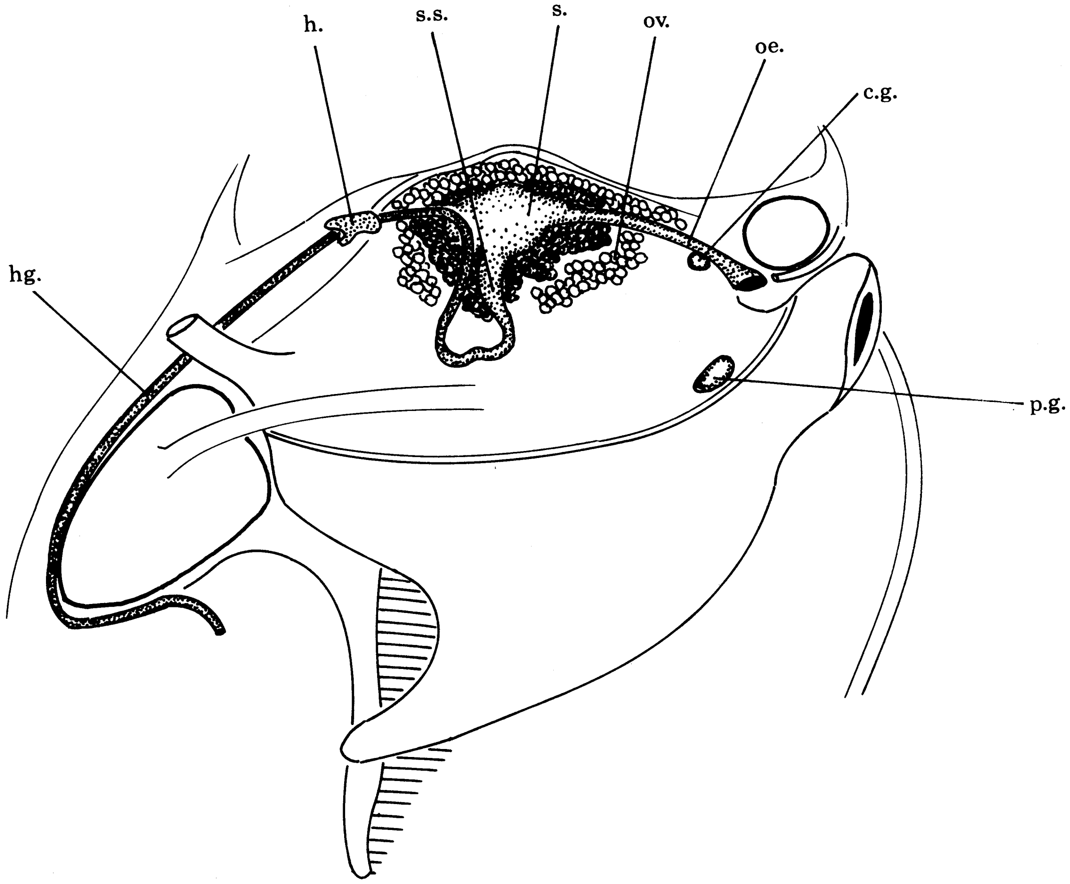

FIGURE 18. *Limopsis minuta*. Viscera as seen following the removal of the right demibranchs and part of the body wall. For explanation of abbreviations see key at end of paper.

Other significant differences in gross morphology from *L. aurita* are as follows:

(*a*) The stomach, although similar, has a thinner and less ridged inner epithelium. The contents consist of diatom and radiolarian skeletons together with an occasional piece of crustacean exoskeleton.

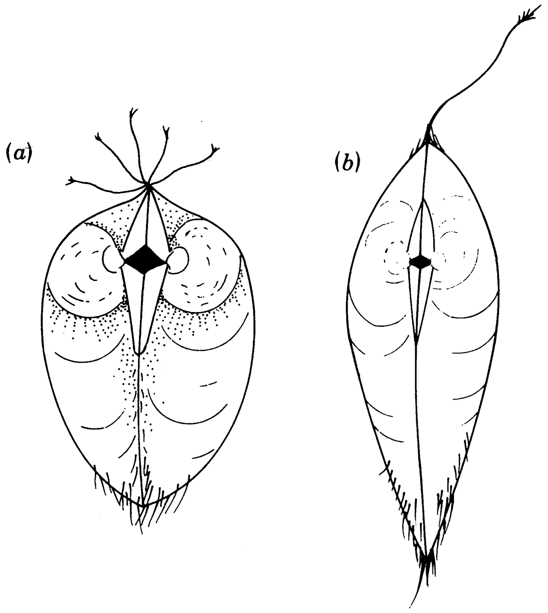

FIGURE 19. Dorsal views of (*a*) *Limopsis minuta* and (*b*) *L. aurita.*

(*b*) The convolutions of the kidney epithelium are slightly less.
(*c*) The mantle edge is not greatly thickened along the posterior ventral margin.

Habitat and mode of life. Station data of the Bay of Biscay samples indicate that *L. minuta* was collected either from the deep water coral zone or the gravel substrates below that zone.

The strong short byssus and oblique inflated shape suggest that this species is epibyssate and attached to the surface of the gravel or just within the surface layer of the sediment (figure 20). This may represent the first stage of an evolutionary trend to a truly epifaunal habit, which can give rise, through extreme heteromyarianism, to a mytilid form of bivalve and to the loss of the anterior adductor, e.g. in *Philobrya munita* (Morton 1978).

Limopsis cristata agg. Jeffreys 1876

At present the systematics of this species complex cannot be clarified with complete certainty. The material at hand from the North and South Atlantic comprises four forms, which, although

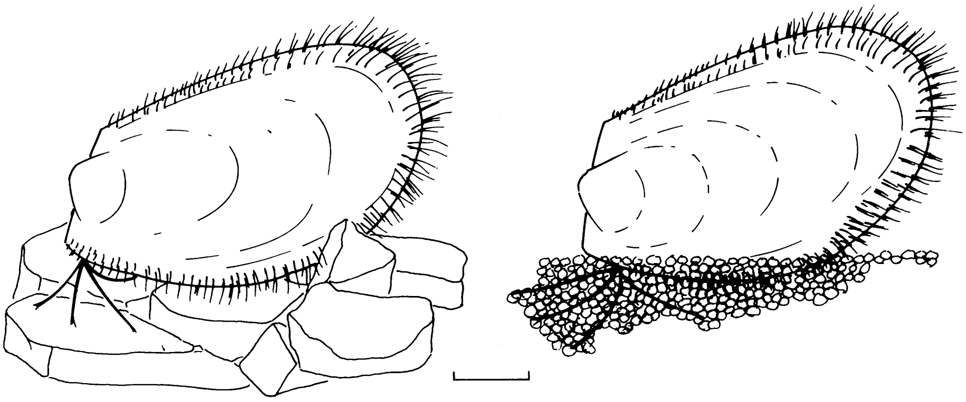

FIGURE 20. *Limopsis minuta.* Orientation of living specimens. Scale bar, 2 mm.

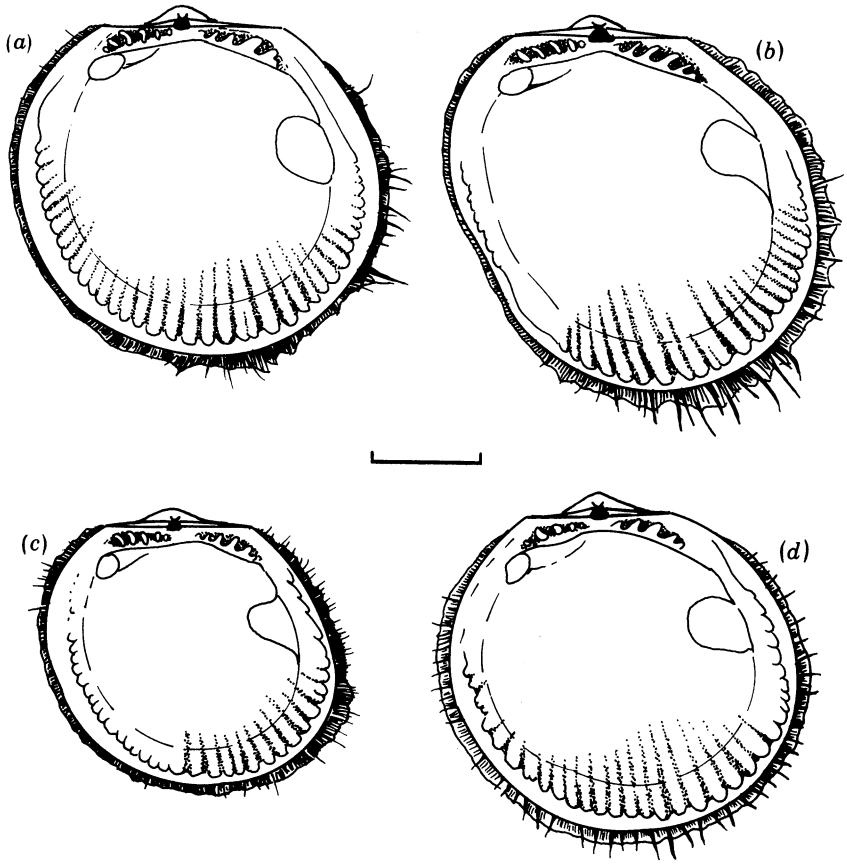

FIGURE 21. *Limopsis cristata*. Internal view of the right valves of (*a*) *L.c. cristata*, (*b*) *L.c. affinis*, (*c*) *L.c. intermedia* and (*d*) *L.c. lanceolata*. Scale bar, 2 mm.

distinct, are obviously very similar (figure 21). The four are widely separated geographically and may represent either localized sibling species or parts of a geographical cline. Because distinct forms are at present recognizable, subspecific names have been given.

L.c. cristata Jeffreys 1876

Type. *Limopsis cristata* Jeffreys 1876. Location: British Museum (Natural History).

Type locality. West of Ireland. *Porcupine* (1869), station 13, 1263 m.

Synonymy.

1876	*Limopsis cristata*	Jeffreys (p. 434)
1879	*Limopsis cristata*	Jeffreys (p. 585; fig. 8, pl. 56)

Station data.

ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Discovery		15.03.68	6697	27° 57.0′ N	13° 46.2′ W	1564	1
Chain	106	17.09.72	313	51° 32.2′ N	12° 35.9′ W	1500–1491	1842
Biogas VI (*Jean Charcot*)		01.11.74	D587	44° 05.2′ N	04° 19.4′ W	1931	1

Distribution. L. cristata cristata has been recorded from both east and west sectors of the North Atlantic, but it may be that the western records are of one of the other subspecies. The present specimens of *L.c. cristata* are restricted to the eastern North Atlantic from the Canary Islands to the Shetland Islands. Depth range: 500–1931 m.

Jeffreys (1879) considered *L.c. cristata* to be close to *L. minuta* and in his paper he figures both species. The similarity is striking, but the figure of *L. cristata* is not much like that described by him originally nor like the *Porcupine* material. Dall (1886) and Locard (1898) also commented on the similarity of the two species. There was widespread difficulty in separating them and this casts doubt on the accuracy of many records. The description of *L.c. cristata* given here emphasizes the differences between this subspecies and other small deep-water forms.

Description. L.c. cristata: shell small, reaching a maximum length of 8 mm; equivalve, inequilateral and somewhat compressed; change of shell outline from circular when small to obliquely oval when full sized; in contrast with *L. minuta*, not higher than long; posterior and anterior margins rounded, dorsal margins long, interumbonal distance narrow; umbos not prominent; ligament small; shell thin, but not brittle, sculpture cancellate but usually obscured by a characteristic periostracum; bristles sparse but visible in smallest specimens, arranged in distinct rows, in large animals bristles long, stout, more or less erect and arranged in rows, with larger bristles in roughly alternating rows, bristles less erect and most stout at posterior ventral margin; overall periostracum coarser than in *L. minuta*; hinge plate narrow, weak, valves easily separated; teeth small, up to five in each of two sets, arranged in arch with peak below ligament, small edentulous space between sets, posterior teeth orientated somewhat obliquely but less obliquely than in *L. minuta;* adductor scars distinct, anterior scar very small compared to posterior, ridge between anterior adductor scar and umbo; inner shell margin evenly crenulate with small nodules that coincide with radial thickenings within the shell.

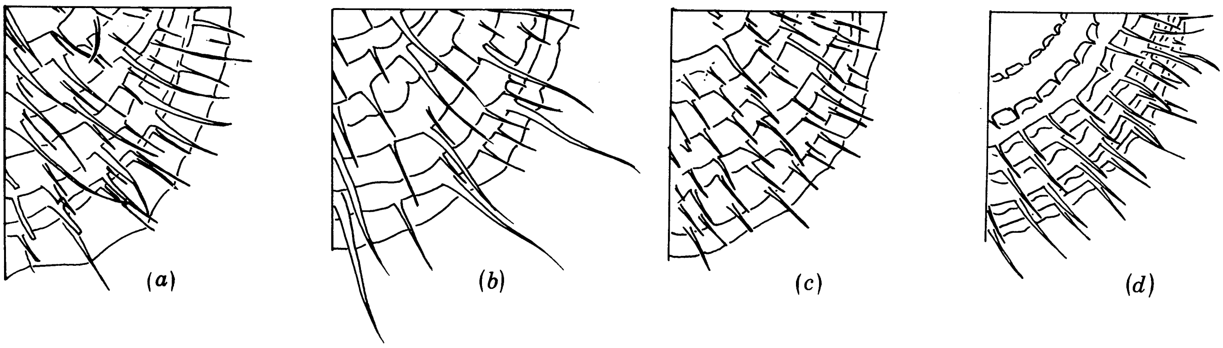

FIGURE 22. *Limopsis cristata.* Periostracal bristles of (*a*) *L.c. cristata*, (*b*) *L.c. affinis*, (*c*) *L.c. intermedia* and (*d*) *L.c. lanceolata.*

L.c. affinis Verrill 1885

Type. *Limopsis affinis* Verrill. Location: no. 44829, United States National Museum.

Type locality. Off New England, *Albatross*, station 2092, 358 m.

Synonymy.

1885	*Limopsis affinis*	Verrill (p. 442)
1898	*Limopsis affinis*	Verrill & Bush (p. 846; fig. 2, pl. 75)

Station data.

ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Atlantis	277	23.05.62	DH1	39° 54.5′ N	70° 35.0′ W	508	7
Atlantis II	12	12.09.64	73	39° 46.5′ N	70° 43.3′ W	1470–1330	297
Chain	50	06.07.65	87	39° 48.7′ N	70° 40.8′ W	1102	171
Chain	58	04.05.66	103G	39° 43.6′ N	70° 37.4′ W	2022	189
Atlantis II	30	30.12.66	131	39° 38.5′ N 39° 39.0′ N	70° 36.5′ W 70° 37.1′ W	2178	14
Chain	88	21.02.69	207	39° 51.3′ N 39° 51.0′ N	70° 54.3′ W 70° 51.5′ W	805–811	11

Distribution. *L.c. affinis* is restricted to the northwestern Atlantic. Depth range: 400–2200 m.

Description. Similar to *L.c. cristata* but differs in that the maximum size reached is 11 mm. Large specimens (6–11 mm) have an almost straight anterior margin and appear very oblique in outline. The periostracal bristles in *L.c. affinis* are more stout and longer, and the radial rows are more obvious (figure 22). Smaller specimens are virtually indistinguishable from *L.c. cristata.*

L.c. intermedia new subspecies

Type. *Limopsis cristata intermedia.* Location: Museum of Comparative Zoology, Harvard.

Type locality. Off Surinam, *Knorr,* station 295, 1000–1022 m.

Station data.

ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Knorr	25	27.02.72	293	08° 58.0′ N	54° 04.3′ W	1456–1518	44
Knorr	25	28.02.72	295	08° 04.2′ N	54° 21.3′ W	1000–1022	37

Distribution. The subspecies is recorded only from the continental slope off Surinam, South America. Depth range: 1000–1518 m.

Description. This subspecies differs from *L.c. cristata* in being slightly inflated, with shorter and more slender periostracal bristles (figure 22). The periostracum appears to be more dense and the radial arrangement of the bristles is not so obvious. The maximum size is less (7 mm) (figure 21).

L.c. lanceolata new subspecies

Type. *Limopsis cristata lanceolata.* Location: Museum of Comparative Zoology, Harvard.

Type locality. Off Angola, *Atlantis II,* station 189, 1007–1014 m.

Station data.

ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Atlantis II	42	16.05.68	189	23° 00.0′ S	12° 45.0′ E	1007–1014	275
		17.05.68	190	23° 05.0′ S	12° 45.0′ E	974–979	2
		17.05.68	191	23° 05.0′ S	12° 31.5′ E	1546–1559	2
Walda	71		DS10	18° 40.0′ S	10° 56.3′ E	1432	2
			DS14	10° 57.8′ S	12° 54.3′ E	1537	1

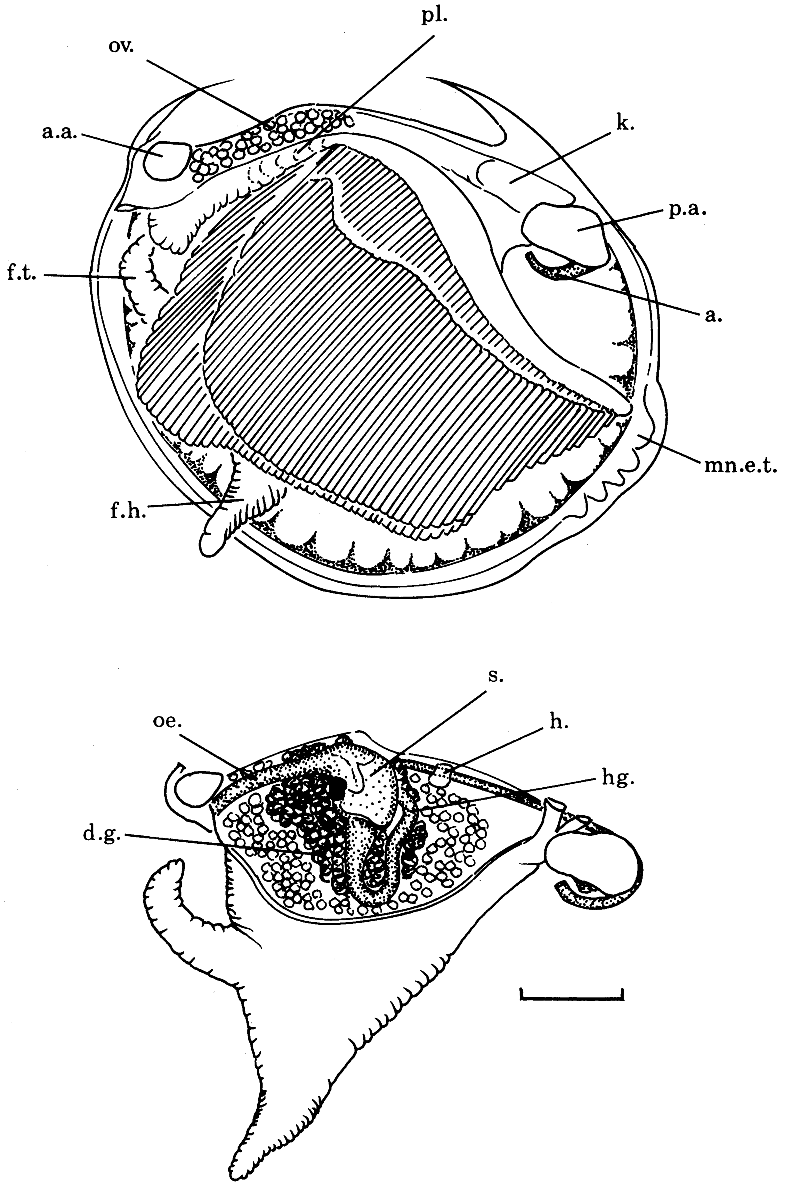

FIGURE 23. *Limopsis cristata cristata*. Anatomy as seen from the left side. Lower figure shows the visceral organs, following the removal of part of the body wall. For explanation of abbreviations see key at end of paper. Scale bar, 1 mm.

Distribution. *L.c. lanceolata* has been recorded only from the slope off southwest Africa and Angola. Depth range: 1432–1559 m.

Description. *L.c. lanceolata* is similar in shape to *L.c. cristata*; however, the form and distribution of the bristles is distinctive. The bristles are of equal size, rather slender, needle-shaped and arranged in very regular radial rows.

Morphology of L. cristata agg.

The gross morphology of the four subspecies is so similar that separate description is unnecessary (figure 23).

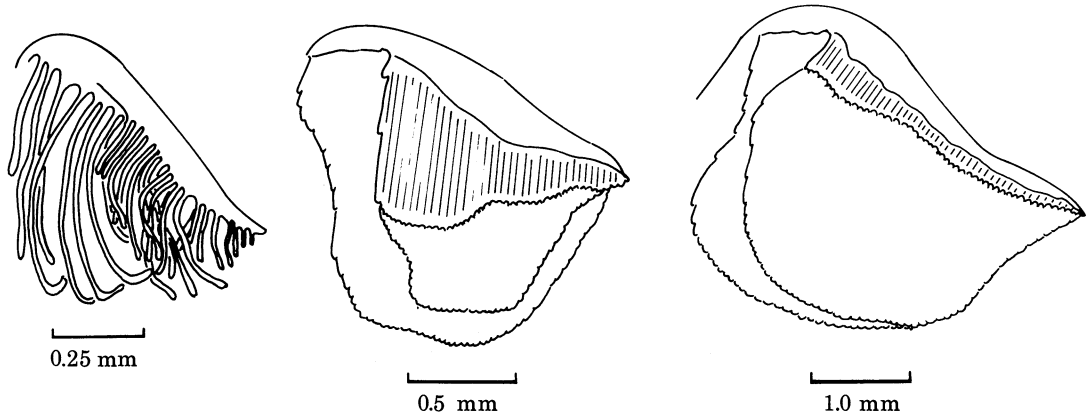

FIGURE 24. *Limopsis cristata cristata*. Stages in the reflexion of the gill filaments.

The main differences between the subspecies and those species described previously are as follows. The posterior ventral thickening and folding of the mantle edge is more marked than in any of the other species described here (figure 23). The gills are large; the filaments remain joined only at the tips and the points of reflexion. The degree of reflexion of the gill varies with size; thus in a specimen 2 mm in length there is little reflexion and the gills resemble those of *L. galathea* (p. 106). At 4 mm the gills are half reflexed and only when the animal is fully grown is the gill fully reflected (figure 24). The gill axis is muscular. The palps have six or seven well developed ridges.

The overall form of the gut is similar to that already described; however, the oesophagus is strongly and longitudinally ridged, invariably with four ridges. Although the stomach is taller than it is long, dissection shows that there is no essential structural difference from other species. The gastric shield is large and the associated axial fold is very well developed; the kidney and pericardium are not unusually large, but, as in *L. minuta*, the degree of folding of the inner epithelium is less marked than in *L. aurita*.

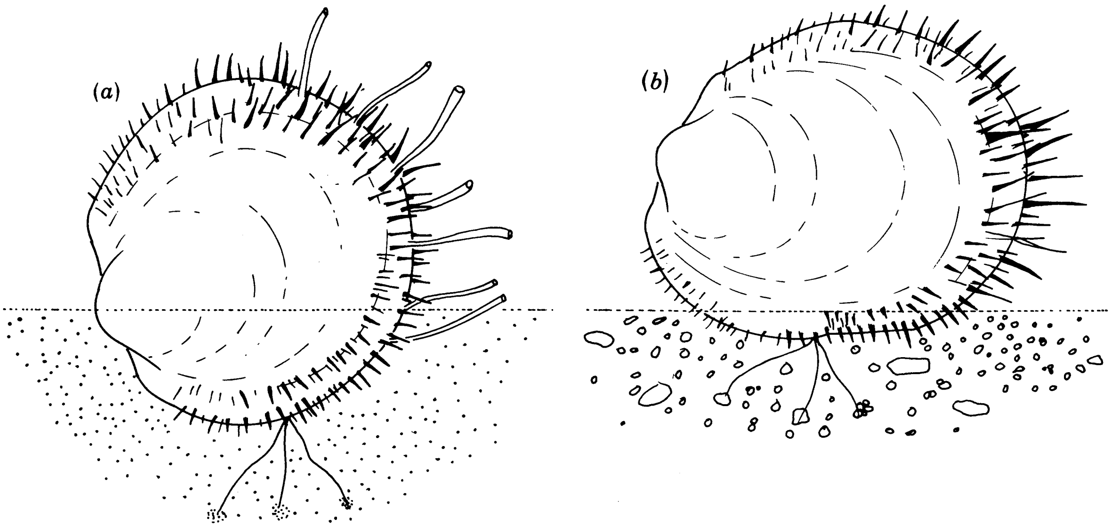

FIGURE 25. *Limopsis cristata*. Probable orientation of living specimens (*a*) *L.c. cristata*, (*b*) *L.c. affinis*.

The foot is very slender, and the toe and heel are more pronounced than in *L. aurita*. The byssus glands are functional and open via a slit in the toe, the byssus consisting of two or three long fine hairs.

In form and size the gonad is similar to that of *L. minuta*, but the number of eggs is fewer. The size of the eggs fixed in alcohol is approximately 95–105 μm.

Habitat and mode of life. The presence of a fine byssus suggests an endobyssate habit, as also does the position of the epifauna on the shells of *L.c. cristata* and *L.c. affinis*; however, differences between the shape of these shells and the distribution of epifauna on them suggest slightly different habits for each subspecies. The greater obliqueness and straight anterior margin of large specimens of *L.c. affinis* suggest a habit similar to that of modioliform bivalves. The epifauna is sparse and restricted to the posterior part of the shell; a semi-infaunal endobyssate habit is proposed (figure 25). *L.c. cristata* differs in that the shape is less oblique and the epifauna is even further restricted to the posterior and ventral margins, suggesting an even more infaunal habit (figure 25).

Limopsis spicata n.sp.

Type.	*Limopsis spicata*. Location: Museum of Comparative Zoology, Harvard.
Type locality.	Off Argentina, *Atlantis II*, station 262, 2440–2480 m.

Station data.

ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Atlantis II	60	27.03.71	262	36° 05.2′ S	52° 17.9′ W	2440–2480	10
Atlantis II		28.03.71	264	36° 12.7′ S	52° 42.7′ W	2041–2048	21

Distribution. This species is known only from the Argentine Basin. Depth range: 2041–2480 m.

This species is similar to *L. cristata* but is easily distinguished from the latter by the characteristic form of the periostracal bristles (see below). There are very few records of limopsids from the Argentine Basin and none is similar to *L. spicata*.

Description. Shell, small, equivalve, inequilateral, compressed, shape of shell and outline changes with increasing size from circular to obliquely subcircular; posterior margin slightly curved, anterior margin round, dorsal margins moderately long, distance apart rather small, junction of the lateral and dorsal margins marked by small projection visible only from interior; ligament small; sculpture cancellate, obscured; bristles sparse and arranged in well spaced radial rows, concentric arrangement obvious, sixteen concentric rings of bristles in the largest specimens; base of bristles broad, but bristles terminate in a sharp point as in blade of short dagger, usually erect, especially on the anterior and central parts of the shell; hinge not strongly developed, few, relatively large teeth in two sets of four, anterior set orientated vertically, posterior set somewhat oblique; adductor muscle scars distinct, anterior scar much smaller than posterior, ridge present from anterior adductor to umbo; interior margin of the shell moderately broad, flat with weak crenulations that extend in from margin (figures 26–28). Maximum shell length 7.5 mm.

The gross anatomy is very similar to that of *L. cristata* (figure 27) except that the foot is orientated with its ventral edge towards the ventral margin of the shell. The gill filaments are not fully reflected but it is possible that this represents an intermediate stage in development similar to that described for *L. cristata*. Because of the small number of specimens available a histological examination was not carried out.

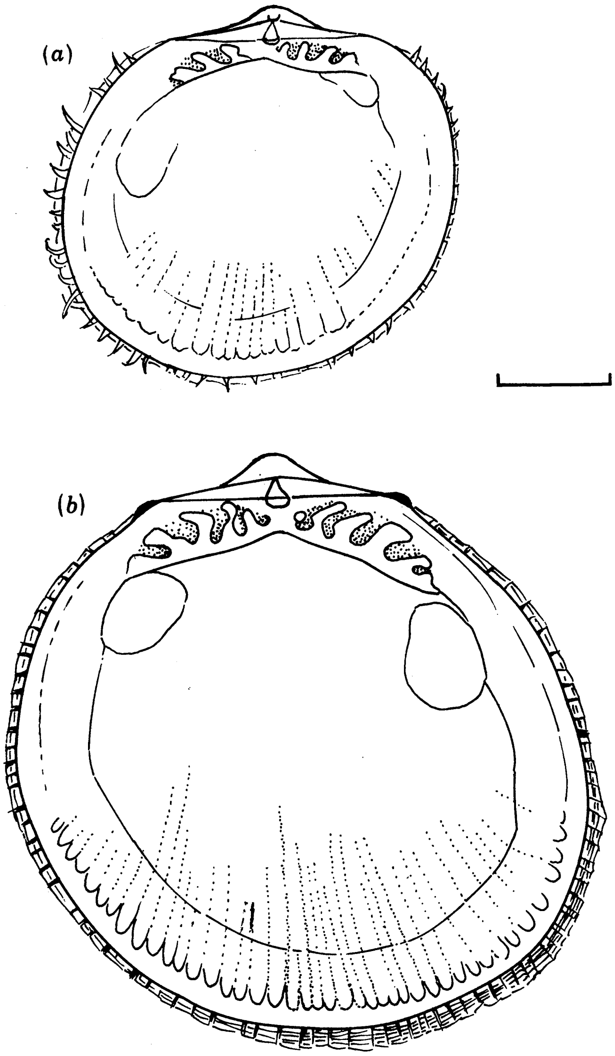

FIGURE 26. Internal view of left valve of (*a*) *Limopsis spicata* and (*b*) *L. galathea*. Scale bar, 1 mm.

Limopsis galathea Knudsen 1970

Type. *Limopsis galathea* Knudsen. Location: Zoological Museum, University of Copenhagen.

Type locality. Monrovia–Takoradi, *Galathea*, station 30, 5160 m.

Synonymy.

1885	*Limopsis cristata* var.	Smith (p. 325)
1927	*Limopsis minuta* parts	Dautzenberg (p. 285)
1970	*Limopsis galathea*	Knudsen (p. 81; text fig. 49B; figs 8, 9, pl. 9)

Station data.

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Gay Head–Bermuda transect	*Atlantis II*	12	23.08.64	70	36° 23.0′ N	67° 58.0′ W	4680	26

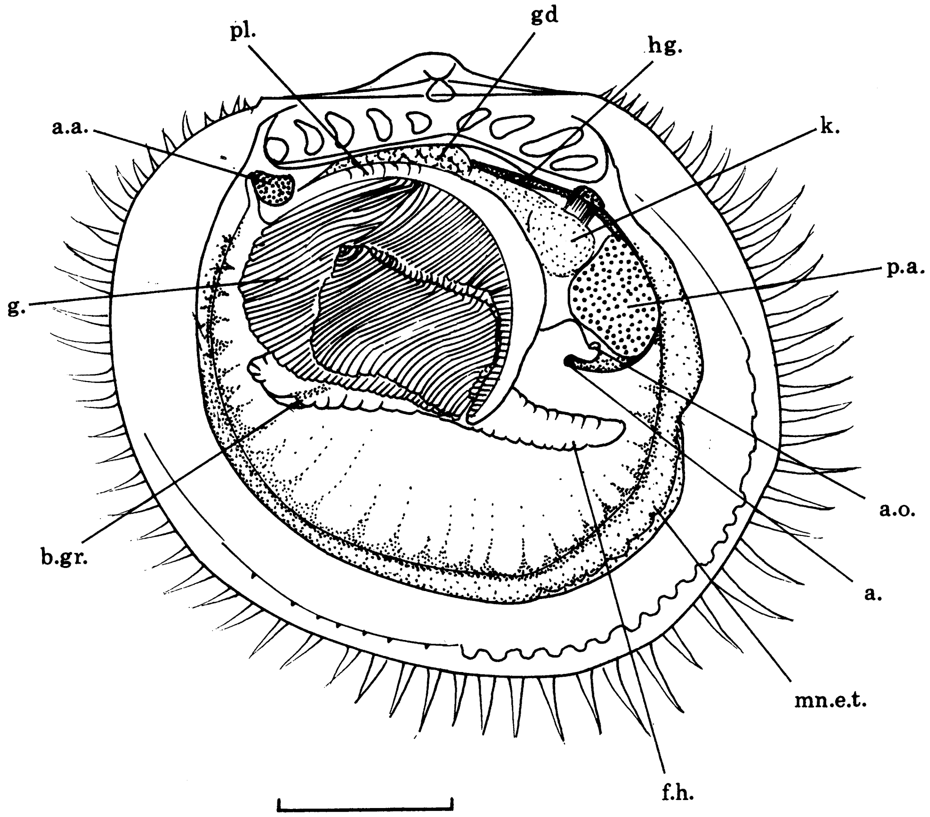

FIGURE 27. *Limopsis spicata*. Anatomy as seen from the left side. For explanation of abbreviations see key at end of paper. Scale bar, 1 mm.

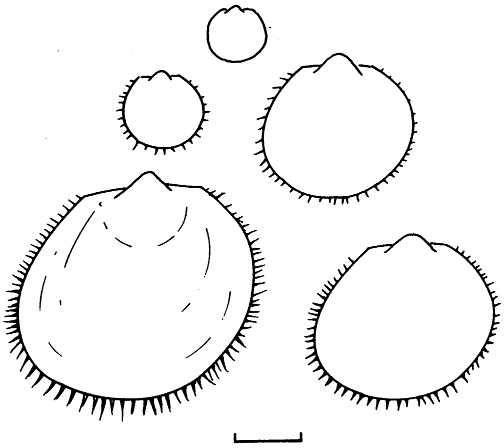

FIGURE 28. *Limopsis spicata*. Size series. Scale bar, 2 mm.

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Gay Head–Bermuda transect (*cont.*)	*Chain*	50	30.06.65	77	38° 00.7′ N	69° 16.0′ W	3806	11
			30.06.65	78	38° 08.0′ N	69° 18.0′ W	3828	1
			02.07.65	81	34° 41.0′ N	66° 28.0′ W	5042	32
			02.07.65	83	34° 46.5′ N	66° 30.0′ W	5000	20
			04.07.65	84	36° 24.4′ N	67° 56.0′ W	4749	173
			05.07.65	85	37° 59.2′ N	69° 26.2′ W	3834	16
	Chain	17	13.12.65	92	36° 20.0′ N	67° 56.0′ W	4694	11
	Atlantis II	24	23.08.66	125	37° 24.0′ N	65° 54.0′ W	4825	1
					37° 26.0′ N	65° 50.0′ W		
	Atlantis II	40	29.11.67	175	36° 36.0′ N	68° 29.0′ W	4667–4693	10
					36° 36.0′ N	68° 31.0′ W		
Dakar–Recife	*Atlantis II*	31	07.02.67	148	10° 37.0′ N	18° 14.0′ W	3814–3828	1
			13.02.67	155	00° 03.0′ S	27° 48.0′ W	3730–3783	27
southwest Africa	*Walda*		00.00.72	DS03	20° 03.8′ S	07° 59.9′ E	4829	2
			00.00.72	DS31	03° 17.5′ S	02° 01.7′ E	4279	2
	Atlantis II	42	21.05.68	196	10° 29.0′ S	09° 04.0′ E	4612–4630	22
				197			3865–4595	157
Puerto Rico–Surinam–Barbaros	*Knorr*	25	24.02.72	287	13° 16.0′ N	54° 52.2′ W	4980–4934	621
					13° 15.8′ N	54° 53.1′ W		
			25.02.72	288	11° 02.2′ N	55° 15.5′ W	4417–4429	111
					11° 03.8′ N	54° 04.8′ W		
			03.03.72	307	12° 34.4′ N	58° 59.3′ W	3862–3835	26
					12° 40.8′ N	59° 09.2′ W		

Distribution. *L. galathea* has been collected only from the Atlantic and apart from the present samples the only other records are the original *Galathea* specimens. It is recorded from the south-east, equatorial and northwest regions. Depth range: 3730–5042 m.

This is a true species and the systematics are clear. In shell form *L. galathea* is closest to *L. panamensis* Dall (1908) and *L. juarezi* Dall (1908) from the east Pacific. These latter consist of single specimens. It has not been possible to compare their anatomy.

Description. Shell small, equivalve, slightly inequilateral, somewhat inflated and thick, change in shell shape with growth not marked, small shells (2 mm) circular, intermediate size shells (5 mm) obliquely circular, largest shells (5–7 mm) obliquely oval; posterior margin slightly curved, anterior margin round, junction with dorsal margins projected as small ears, often darkly coloured brown or black, dorsal valve margins short, distance apart small; ligament very small; sculpture finely and evenly cancellate; periostracum forms dense mats of fine short erect bristles, barely projecting beyond margins; hinge plate short, deep with two sets of strong teeth, five in each set, posterior set more obliquely arranged than anterior set; adductor muscle scars distinct, heteromyarian condition moderately developed; ridge between anterior adductor scar and umbo weak; internal shell margin crenulate, in form a series of ridges distinct from the nodular type of crenulation found in *L. minuta* and *L. cristata* (figure 26). Maximum length 7 mm.

The mantle edge is thickened at the posterior ventral margin in the region of the inhalant and exhalant openings. The gills (figure 29) are unusual in that the filaments are not reflected† in either demibranch. The longer filaments of the right and left inner demibranchs interdigitate, but whether this is a true morphological feature or an artefact of preservation is not clear.

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† Other lamellibranchs with non-reflected filaments are *Heteranomia* and the Dimyidae (Yonge 1977, 1978).

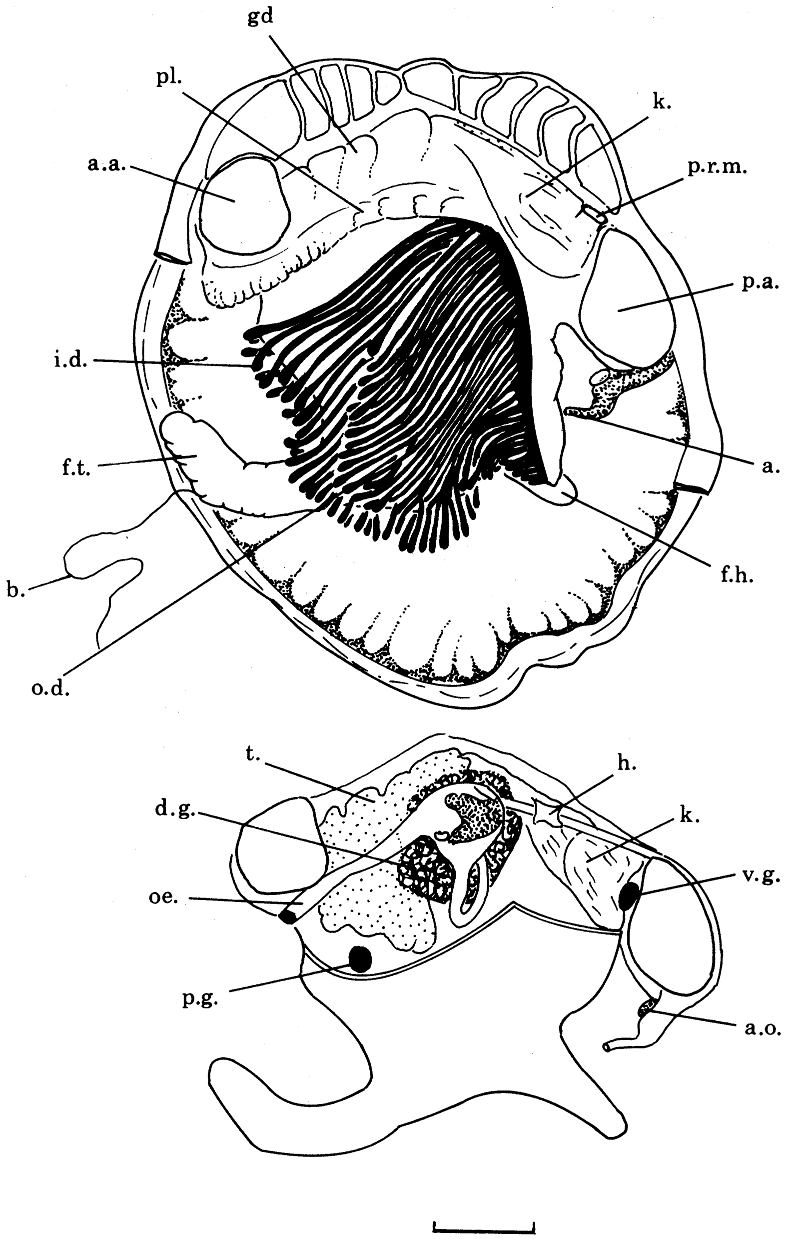


FIGURE 29. *Limopsis galathea.* Anatomy as seen from the left side. Lower figure shows the visceral organs, following removal of part of the body wall. For explanation of abbreviations see key at end of paper. Scale bar, 1 mm.

Interfilamentar junctions are weak, with the filaments frequently in disarray. The filaments are few in number, between 30 and 40 composing the inner demibranch. The tips of the filaments are larger and more swollen than those observed in other species. As in other species the gill covers a large area, but in contrast the gill axes are only slightly muscular. The palps are poorly developed with only four weak, ill-defined ridges and a long unridged surface anterior to them.

The gut shows but few differences from that of other species; the gastric shield is large with a large area of pigmented wall on the left and posterior sides. The number of digestive ducts is few, five, but this may be related to the small size of the species. Few specimens had contents in the stomach but those few contained large particles.

The kidneys are large, the inner epithelium being without folds. The pericardium is also large, although the heart is of normal proportions.

The gonads are small and contain no more than 60 eggs, these eggs having an average diameter of 135 μm (in alcohol). The foot has a large muscular elongate toe but a small heel. The byssus gland is small but functional and opens on the ventral surface of the toe. The byssus consists of up to three very fine, long threads (figure 30). The nervous system is of the same basic plan as in other *Limposis* species but in *L. galathea* the ganglia appear to be unusually large.

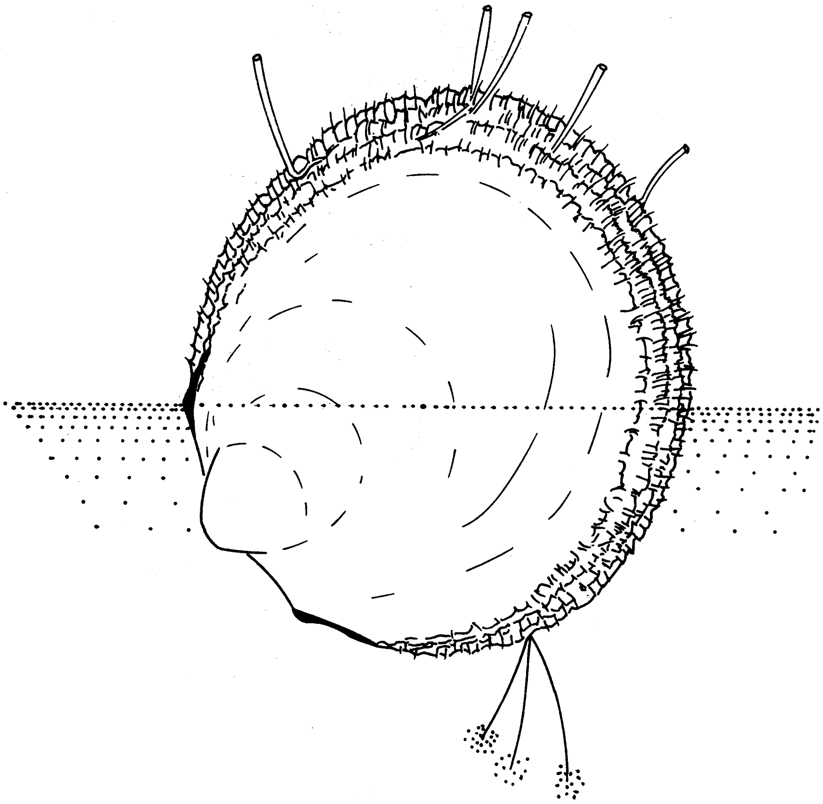


FIGURE 30. *Limopsis galathea*. Probable orientation of a living specimen.

Habitat and mode of life. The slightly tumid, near-circular shape, the elongate toe and the short periostracal bristles suggest that *L. galathea* is a more active burrower than any of the preceding species. The byssus although functional is very weak. The shells have an epifauna consisting of an unnamed encrusting sponge and a coelenterate similar in form to *Stephanoscyphus*, which would demonstrate that at least some portion of the shell protrudes above the surface of the sea bed. The coelenterate is confined to the ventral and posterior margins while the sponge was found over the posterior area of the shell. These observations suggest that the orientation of this animal may vary from only the anterior half being buried to a state in which the umbos and part of the posterior area is buried (figure 30).

Although stomach contents do not suggest that this is a deposit feeder, it seems likely that, with the inhalant aperture in close proximity to the surface of the sediment, some surface deposit might be ingested.

Comparison of populations of *L. tenella* from different depths

Only *L. tenella* was available in sufficient numbers for an intraspecific comparison of populations.

It was first assumed that a cosmopolitan species such as *L. tenella* would be constant in form over its range. Recent work by Allen & Sanders (personal communication) and by Rex (1979) has shown that local variation occurs in deep-sea bivalves and gastropods.

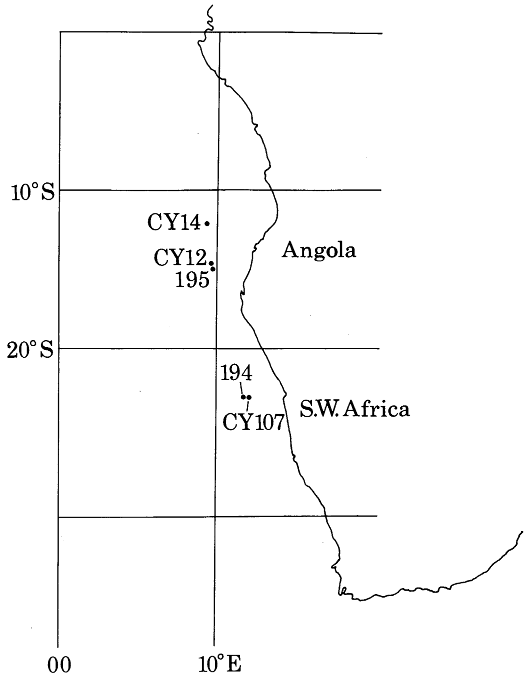


Figure 31. *Limopsis tenella.* Geographical positions of stations used for intraspecific comparisons.

The present study was confined to populations from the southeast Atlantic (figure 31). The bathymetric range of the samples is from 2800 to 3800 m. Over this range and within the geographical area the temperature is constant at 2.5 °C and the sediments are broadly similar. While it is known that upwelling currents do exist in the southeast Atlantic, nothing in the literature suggests that there are any major variations in currents at abyssal depths. Thus, morphological differences could be due to pressure or metabolic effects.

The study concentrated mainly on two samples from the *Walda* expedition CY07 (1840 m) and *Walda* CY12 (3875 m). A third sample CY14 (3431 m), more recently received, was also examined, as were samples taken by *Atlantic II* three years before the *Walda* samples, which, despite their smaller size, show remarkable similarity to the *Walda* samples from corresponding depths.

Superficial observations on the gross appearance of samples CY12 and CY07, collected with the same gear, showed that specimens from the shallower station CY07 appeared to be larger and paler in colour. This colour difference proved unreal and was due to the fact that sediment had been retained on the periostracal bristles to give a darker and dirtier appearance. The CY07 specimens had a very sparse epifauna whereas CY12 specimens were heavily fouled by the brachiopod *Atlantodiscus atlanticus* and the bivalve *Bentharca asperula*. Specimens from CY14, similar in periostracum to those from CY12, are equivalent in size to specimens from CY07. Specimens from CY14 also had attached *Atlantodiscus*, but instead of *Bentharca* another brachiopod, of the genus *Waldheimia*, was present.

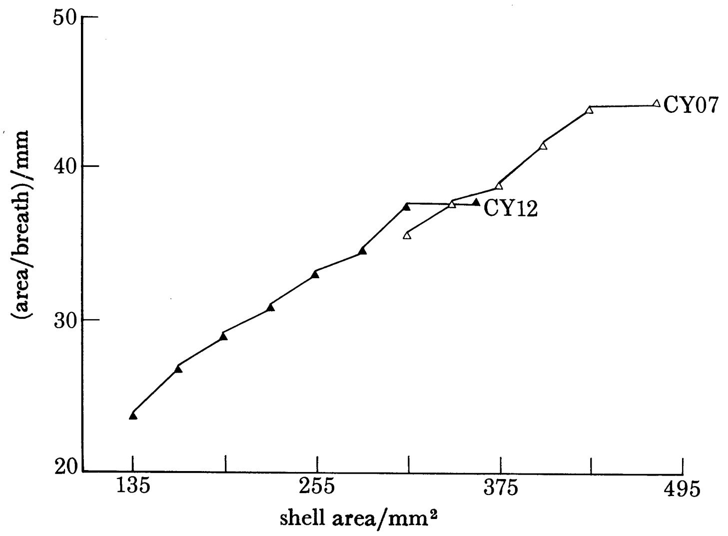


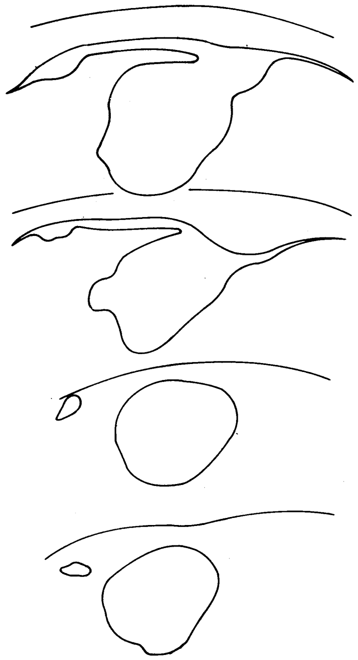
Figure 32. *Limopsis tenella*. Comparison of (area/breadth): shell area indices of two populations, showing the points of onset of disproportionate interumbonal growth.

Morphological observations

That *Limopsis* species are variable in form was recorded by Dell (1964) for *L. marionensis*. *L. tenella* is similarly variable, especially in the degree of the obliqueness of its outline. The range in form varies from a shell that is very oblique to one that is almost circular (figure 13). The hinge, ligament and width of the dorsal area are also variable (figure 14). While all the populations examined showed a similar range of variation, specimens from station CY12 appeared to have the greatest variety of form.

Although all the samples show variation in the form of the ligament, the onset of disproportionate ligament growth (figure 32), accompanied by changes in interumbonal growth, takes place at different lengths in different samples. In sample CY12 the onset of this change appeared at 17–19 mm, in CY14 at 21–22 mm and in CY07 it was only seen in the largest shells, of the size range 24–27 mm.

A frequent, though not constant, difference between specimens from CY12 and CY07 was the shape of the posterior adductor scars (figure 33). In the latter specimens the scar is impressed, is confluent with the pedal retractor scar and is roughly square in shape, while in CY12 specimens the scar is raised, somewhat rounded and separate from the pedal retractor scar. A few



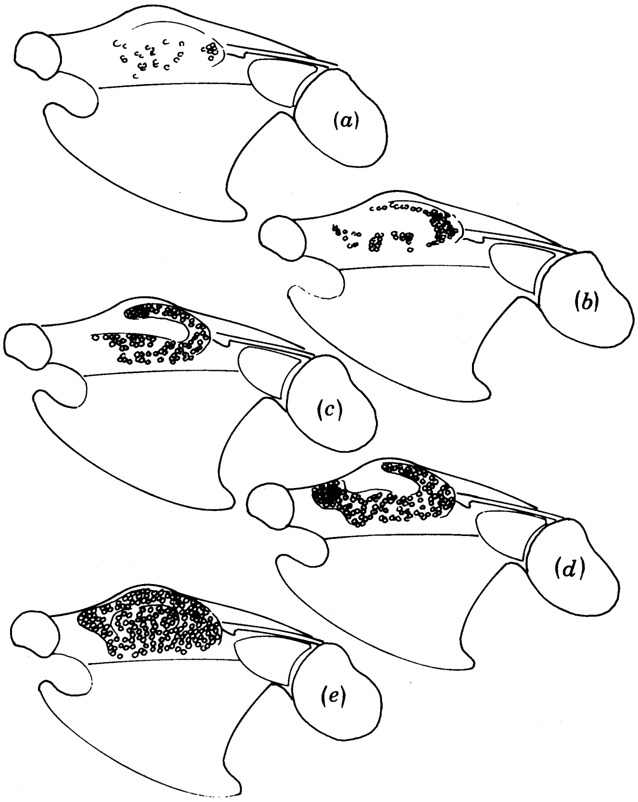


Figure 33. *Limopsis tenella*. Variation in the form of the scar of the posterior adductor muscle.

Figure 34. *Limopsis tenella*. Five stages (*a*)–(*e*) in the development of the ovary.

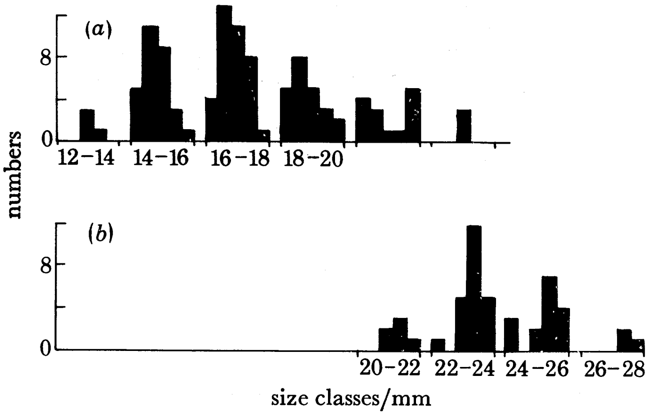


Figure 35. *Limopsis tenella*. Numerical frequencies of stages in ovary development in two populations: (*a*) CY12, 3975m; (*b*) CY07, 2840m.

specimens from CY12 were found to be similar to those from CY07 but these were in a minority.

Differences in the morphology of the internal structures could not be found at any level, but it was noted that the development of the ovary varied greatly within each population. To investigate this, stages of ovary development were categorized into five groups (figure 34). The numerical occurrence of each category was then summated and the results for the whole

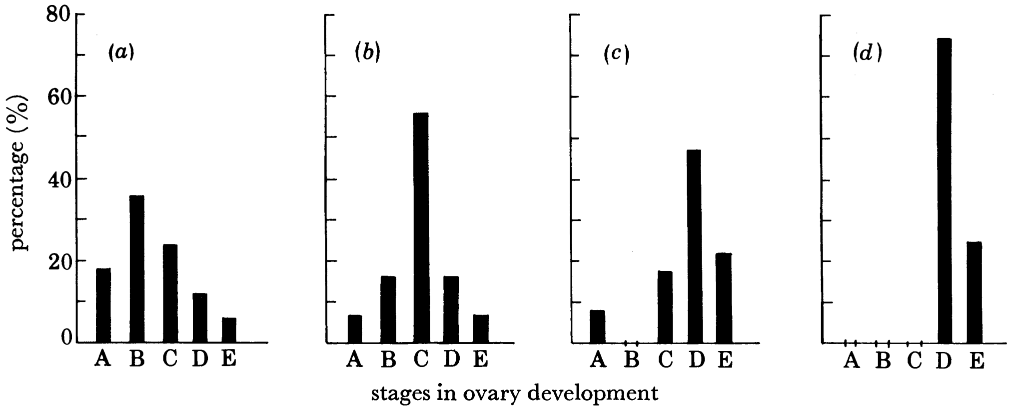


FIGURE 36. *Limopsis tenella.* Percentage frequencies of stages in ovary development in four samples from different stations: (*a*) CY12, (*b*) 195, (*c*) CY07, (*d*) 194.

population are shown in figure 36 and for a series of size classes in each population in figure 35. The difference in degree of development is clearly shown and also to be noted is the greater degree of synchrony shown in sample CY07.

In figure 37, size frequency histograms are given for three stations; these graphs clearly demonstrate that the modal size of the populations decreased with increasing depth.

A good measure of the point when disproportionate amount of interumbonal growth occurs is the ratio of breadth of the shell to overall size. As the length of the shell is related to the amount of oblique growth, the best measure of size is the area of the shell. Therefore the ratio area: breath was plotted against the area (figure 34) and the point of change of slope indicates the point where the disproportionate interumbonal growth commences. These results confirm the initial observations that disproportionate interumbonal growth takes place in smaller individuals in the deeper sample.

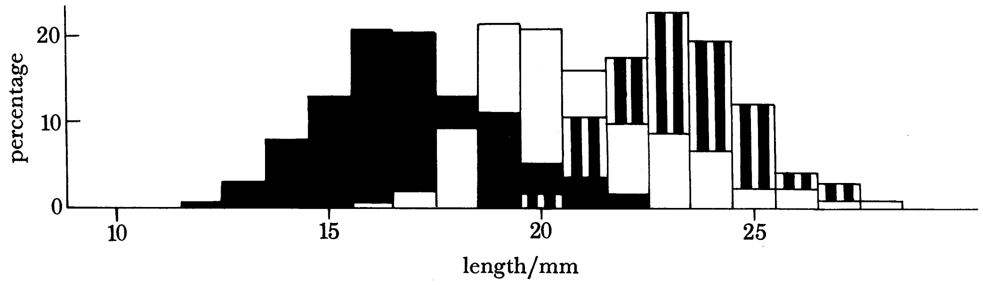


FIGURE 37. *Limopsis tenella.* Percentage size frequencies of three samples (CY07 solid; CY14 open; CY12 hatched).

A measure of the obliqueness of growth was made by means of the ratio of posterior area: total area, the dividing line being a vertical line drawn through the umbo. As the degree of obliqueness increases with size, direct comparisons between the populations could not be made. To overcome this, each population was divided into size classes and the variation of each was measured as the coefficient of variation of the ratio posterior: total area. These coefficients are not related to size and can be compared directly. The coefficients were then plotted against

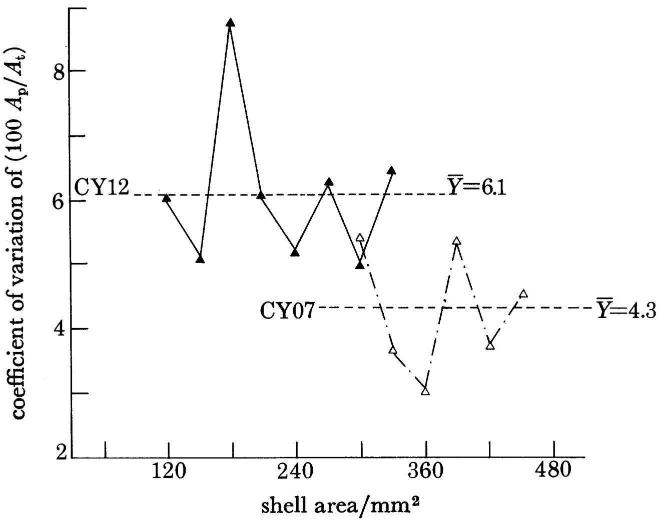


FIGURE 38. *Limopsis tenella.* Comparison of the coefficients of variation of the ratio posterior area (A_p): total area (A_t) (%) of two samples.

total area (figure 38) and subjected to an *F*-test for significance. The results show that the deeper sample CY12 is more variable than the shallower CY07.

In cross section shells are not normally of even thickness and because of this no direct measurements were made. Instead the thickness has been expressed as the mass of the shell and to take into account changes in form only the largest shells were used. Mass was plotted against the area of the shell (figure 39) and, as expected, specimens from CY07 have much thicker shells than those from CY12 and CY14. The bathymetrically intermediate sample CY14 is not intermediate in shell thickness but is similar to the deeper sample CY12.

The above results can be separated into two groups. Those concerned with size, interumbonal growth and variability of outline can be associated with the age and the rate of growth of the specimens. Size frequency data suggest that the modal size of the populations decreases with depth but without information on age this cannot be certain. The onset of disproportionate

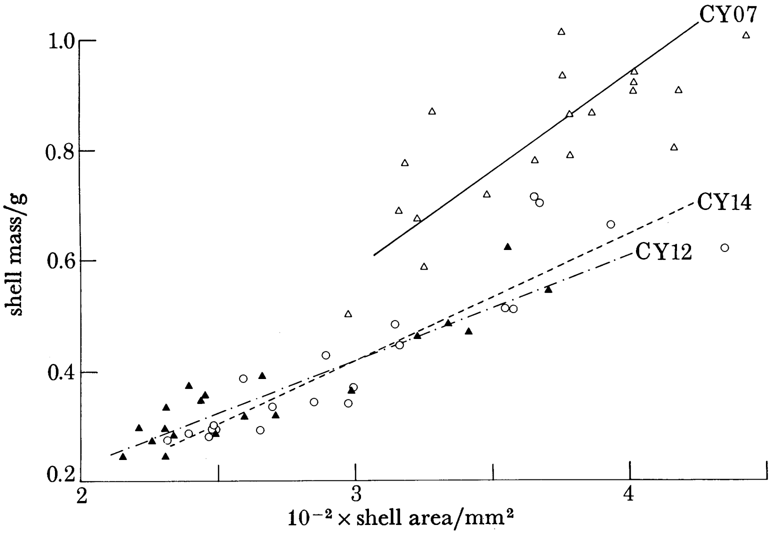


FIGURE 39. *Limopsis tenella.* Comparison of the ratio shell mass: area for three samples.

ligament and interumbonal growth is not related to size. This change is associated with worn and eroded shells and it is believed that these shells represent the oldest and possibly senile portion of the population. If this is so and this is an age indicator, it implies that the deeper the population the smaller is the model size and that the deeper populations have slower growth rates. The greater variability of the shell form of the deeper population may also reflect this slower growth rate. It is known that populations of bivalves living in unfavourable conditions have stunted and irregular shells (Rendall 1956). In the less favourable conditions of the lower abyss a similar situation may exist; however, such reductions in size and growth rate are entirely in keeping with the expected adaptations of abyssal species.

The second set of results are those associated with shell thickness. The difference in form of the adductor scar can be attributed to differences in shell thickness. In specimens from station CY07 the form of the scar is typical, with the myostracum imbedded in the inner crossed lamellar layer (Taylor, Kennedy & Hall 1969). In specimens from CY12, however, the crossed lamellar layers are very thin and the myostracum consequently appears raised and is separate from the myostracum of the posterior pedal retractor. These observations show the unreliability of the form of the adductor scar as a taxonomic character. Shell thickness is not linearly related with depth, although members of the most shallow population do have the thickest shells. There is a widely accepted generalization that deep-sea species have thin shells. There are many exceptions and the thickness must be related to the metabolic adaptations of each species. If a population is living under stress, as perhaps is the case at station CY12, it is possible that the metabolic processes act to maximize the available energy. Thus specimens from CY12 have slow growth and thin shells. At CY14 growth is faster but still shells are thin and only at CY07 are the conditions favourable for fast growth and formation of thick shells.

COMPARATIVE OBSERVATIONS ON REPRODUCTION AND GROWTH WITHIN THE GENUS *LIMOPSIS*

Although the available samples are far from ideal because not part of a series taken at regular intervals from a single station, any information on reproductive strategy of deep sea benthos is of considerable value. The sizes of the eggs and larval shells are indicators of developmental types and reflect the strategies adopted (Ockelmann 1965). Reproductive potential was estimated as the ratio of gonad volume : body volume. Shell length cannot be used as a measure of total body volume (Scheltema 1972) for *Limopsis;* body volume was measured by displacement. Gonad volume was measured directly from serial cross sections, by calculating the area of the gonad in section and multiplying by the thickness of each section, a very time consuming process. For *L. tenella* and *L. aurita*, tissue dry mass : total egg volume was determined.

Measurements of eggs and larval shells of *Limposis* fall into two groups: species from slope depths have medium-sized eggs and prodissoconchs and species with an abyssal distribution have relatively large eggs and prodissoconchs. Both groups are characterized by lecithotrophic development with short-lived non-feeding larvae. Planktotrophic and direct developments are not common in the deep sea (Knudsen 1967, 1970) and thus these results are not atypical. There is no evidence in bivalves of a passage of larvae to and from the photic zone (Allen, personal observation).

The adaptive significance of lecithotrophic development are discussed by Thorson (1950), Ockelmann (1965) and Dunbar (1968). They conclude that the reduced length of the larval life ensures a higher rate of survival in that competition and predation are avoided and yet the dispersive function is maintained. The limit of this adaptive trend is direct development with brooding of the larvae, but this restricts the dispersal function. This type of reproduction is mainly confined to high latitudes or to species with a restricted habitat. That abyssal species have larger eggs and larvae than the slope species is of significance. The larger egg supplies more energy for development, metamorphosis and postmetamorphic growth and it implies that fewer eggs are needed to ensure replacement of the population, with a possible saving in energy, which is advantageous in the low-energy environment of the abyss. Information on egg number, gonad volume and total egg volume indicates a low reproductive potential and the results are similar to those obtained by Scheltema (1972). It can be argued that if abyssal species have a low reproductive potential then the survival rate of the larvae must be greater or replacement must be maintained by increased longevity and/or reproductive span.

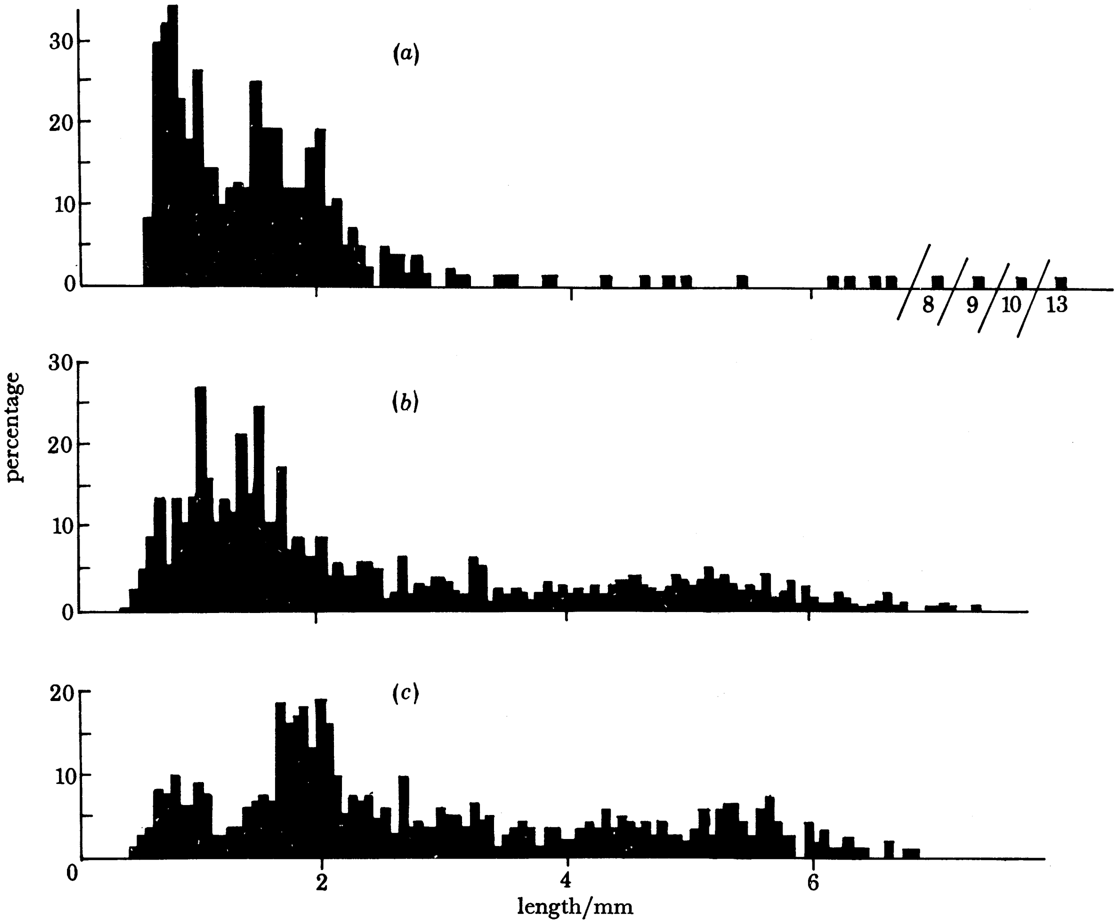


Figure 40. Size frequency histograms of three species of *Limopsis* from widely different depths: (*a*) *L. surinamensis*, 500 m; (*b*) *L. cristata*, 1500 m; (*c*) *L. galathea*, 3500 m.

Many deep-sea species breed continuously (Rokop 1974), but while gamete release may be continuous few are released at any given time. Continuous breeding could possibly be confirmed from size frequency data. Histograms (figure 40) show that there are relatively few small animals in abyssal populations, which would indicate either that not many young are produced at once or that there is lack of settlement success. The number of bivalve larvae recorded from the deep sea is very small (Scheltema 1972).

Any conclusions on growth rates drawn from size frequency histograms must be somewhat speculative. Growth rings were seen only in very small specimens of *L. surinamensis* and *L. cristata*, both of which are slope species. None was present in the abyssal species *L. galathea*. Growth lines possibly indicate that *L. surinamensis* grows at a faster rate than *L. cristata*.

Modal size is greatest in species with deep distributions (figure 40) and a second larger size class peak is seen in the histograms of the two deeper species. The displacement of the modal class to the right is more marked in *L. galathea*, the deeper species, than it is in *L. cristata*. (Although the histogram of *L. cristata* taken from station 313 is shown (figure 40), similar distributions were also obtained from stations 74 and 78.) Such histograms suggest that the replacement of the population may be very slow, or that individuals may be long-lived, or both. Peaks in the larger size classes of *L. cristata* and *L. galathea* (figure 40) suggest that animals may reach a maximum size and continue to live or that growth slows considerably in later life. In *L. galathea*, gametes are not seen until specimens are one-third grown, similarly in *L. tenella* maturity was not observed in specimens smaller than 7 mm.

The size frequency histogram of *L. surinamensis* is more typical of a shallow-water species, with smaller individuals being the most numerous and the numbers of increasingly larger ones rapidly diminishing.

Circumstantial evidence therefore indicates that abyssal species have a lower reproductive rate, slower growth rate and greater longevity than slope species, and in like manner slope species differ from shelf species.

Discussion

Despite progressive environmental change, e.g. pressure increases, temperature decreases and sediments becoming finer as the deeper parts of the oceans are approached, there are a number of distinct habitats within the deep sea. Observed adaptations are the result of a number of interacting adaptive pressures. Here these pressures are divided into two groups: the direct factors, e.g. temperature, pressure, food and sediment type, to which animals adapt directly; and the indirect factors, e.g. age of the ecosystem, ecosystem stability, competition and niche availability, which control the extent of the adaptations to the direct factors.

The implications of the effect of direct factors are discussed in a number of papers on diversity (Hessler & Sanders 1966; Sanders 1968, 1969; Sanders & Grassle 1971; Dayton & Hessler 1972; Grassle & Sanders 1973; Hessler & Jumars 1974; Jannasch *et al.* 1971; Jumars 1975), but many of the indirect factors, acting in the deep sea, are poorly understood, and, to date, only the age and stability of the deep sea are generally accepted as being significant.

Both pressure and temperature have a direct effect on chemical reaction rates and are thought to have a similar effect on the metabolic rate. With the linear increase in pressure with depth and the lowering of the temperature to 2.5 °C at abyssal depths, it would be expected that deep-sea animals would be affected.

Metabolic rates of deep-sea organisms measured *in situ* (Thiel 1975) or under 'natural' conditions in the laboratory (Macdonald, Gilcrest & Teal 1972; Teal 1971) are lower than those of similar shallow-water organisms. This may be the result of combined pressure and temperature but it may also represent an adaptation to some other parameter. Deep-sea animals could have adapted their metabolic chemistry to maintain a high metabolic rate but have not done so because it was not to their advantage.

Low population density of animals and lack of *in situ* photic production indicate that food supply in the deep sea is small. Studies on particulate organic carbon confirm this. Not only are the amounts small but also much of the organic carbon is refractory (Menzel 1967; Rowe, Polloni & Horner 1974). Much of the food is in the form of sinking debris, primarily from the photic zone and secondarily from terrigenous outflow. The bulk passes through a number of planktonic levels. Other sources of organic matter include the sinking of higher plants such as *Thalassa* (Menzies, Zanveld & Pratt 1967) and *Sargassum* (Schoener & Rowe 1970), so-called 'green bodies' (Fournier 1972) and *Halosphaera* (Wiebe, Remsen & Vaccaro 1974) as well as large dead animals.

Suspension feeders by definition derive their food from the water column and the density of suspended matter is probably low over most of the deep sea. Photographic and photometric studies indicate that the water is clear, although nepheloid (cloudy) layers are known (Ewing & Thorndike 1965).

Rates of sedimentation are low, especially under the pelagic zone, and are of the order of 2–3 cm/1000 years (Griggs, Carey & Kulm 1969). On the continental slope and abyssal rise, sedimentation rates may be higher due to slumping and the higher frequency of turbidity currents. Such sedimentation is likely to be too fast to be of use to suspension feeders and may well cause local extinction due to burial. Resuspension of sediments is related to bottom current speeds and these are generally low (Menzies, George & Rowe 1973). There are no data to date relating the distribution of suspension feeders to areas of fast currents, nepheloid layers or turbidity currents.

It would appear that suspension feeders are under the same, if not greater, stress than the deposit feeders.

The consequences of a low food input are complex. Dunbar (1968) discussed this problem with relevance to the arctic ecosystem but the theory can be applied here. If the energy supply to an organism is limited it must partition the use of that energy to its vital functions, i.e. somatic growth, reproductive growth and activity, with a further loss to the low temperature environment. Any increase to one must be balanced by a decrease in one or all of the others. Figure 41 shows ways in which energy may be apportioned and the likely sequence of changes when the energy supply is decreased. The necessity to adapt is caused by food supply but the alternatives employed are usually controlled by the indirect factors. As activity in most invertebrates is associated with feeding it is unlikely that much reduction would occur. Reduced growth rate may be compensated by a long life span, while reduced reproductive growth may be compensated by a higher juvenile survival rate through direct life cycles.

Data from the deep sea are limited and the interpretation of them is speculative. Somatic growth is difficult to evaluate due to the difficulty of taking regular frequent samples from a single population. Some idea of growth rate has been gained from work by Turekian *et al.* (1975), using radium (^{228}Ra) dating, who estimated that *Tindaria callistiformis* grew to its maximum size of 8.5 mm in 100 ± 38 years. Circumstantial evidence is given by maturity, which in many bivalves is not reached until the animal has grown to half its maximum size (Grassle & Sanders 1973). Although size alone gives no indication of the growth rate, it is worth noting that most deep-sea bivalves are small ($<$ 5 mm).

Typically the eggs are few in number and relatively large. The gonad volume relative to size has been shown to decrease in abyssal species (Scheltema 1972). The number of ripe gametes at any one time is small (Rokop 1974) but this may be a reflection of the aseasonality of the deep sea and of continuous release of gametes. The size–frequency histograms of bivalves (Allen, personal observation) show that small size groups make up a very small percentage of the total population. This indicates a low recruitment rate.

It would appear that the situation illustrated in figure 41*c* is approached, i.e. deep-sea animals are generally small and slow-growing, maturing late and producing few gametes at a slow rate.

Morphological adaptations related to the energetics are few. Allen (1978, 1979) noted the increased length of the gut in deep-sea deposit feeders and interpreted this as being a way in which to offset the low food intake. The same author also noted that the gills of these deposit feeders were reduced and this was interpreted as being a consequence of the low metabolic rate.

Bivalve morphology is closely linked with the type of substrate in or on which the animal lives. The deep-sea sediments are mostly very fine and those away from the slope are also stable.

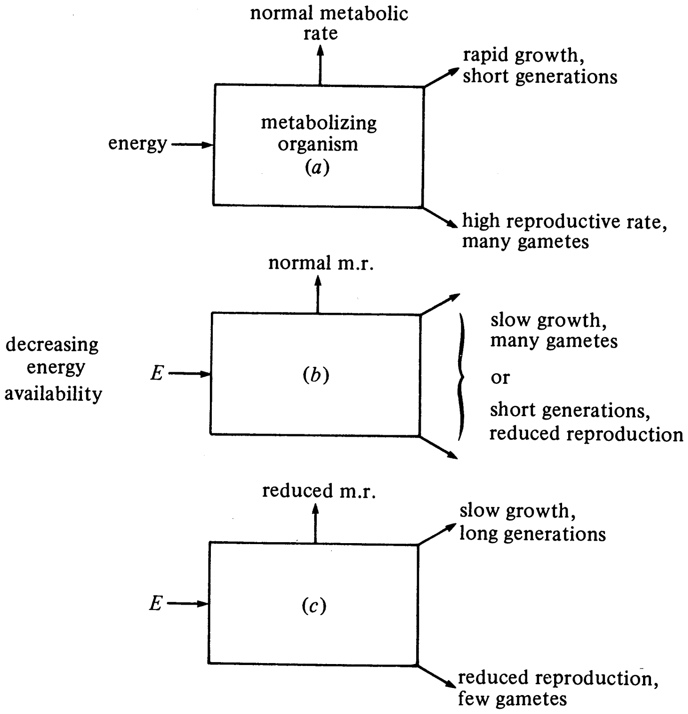


FIGURE 41. Hypothetical effects following a reduction in available energy on the metabolic processes of an animal.

Consequently the majority of deep-sea bivalves are infaunal. The form of the shell is related to the habits of the species, which in turn are modified by the type of sediment and the position of the animal within or on that sediment. While some limopsids are primarily semi-infaunal or infaunal in soft sediments, others are adapted to a more epifaunal existence on coarser substrates. Thus, the group is widely distributed.

Factors other than substrate affect the depth range of limopsids. Their exclusion from the Atlantic shelf is probably due to the genus not having made radical adaptations in form, cf. *Glycymeris* (Thomas 1976). They have not become rapid burrowers, nor have they evolved an extreme heteromyarian condition. What might be termed their 'generalist' form is probably a disadvantage competitively in the diverse shelf fauna. Only glycymeriform limopsids of the subgenus *Pectunculina* d'Orbigny have been successful in inhabiting shallow shelf waters and these are restricted to the tropical Indo–Pacific.

Consideration of endemism in the deep sea is restricted by the lack of historical data on the genus, but the abyssal species *L. galathea* is so restricted in range and so distinct in form that it might be considered to be endemic.

The abyssal species of *Limopsis* conform to the hypothesis shown in figure 41*c* with respect to growth, reproduction and, possibly, metabolic demand. An indication of a low metabolic rate may be reflected in the enlarged but simplified kidney of the abyssal species. This enlargement may be related to an increase in body fluid volume. Simplification reflects a reduction in the surface area of the endothelium, which could be interpreted as a reduction in function, with fewer waste metabolites derived from a lower metabolic rate.

Morphological adaptations to lack of food are few in *Limopsis*. The morphology of the feeding and digestive organs is similar in all species examined, except for the slight reductions in the numbers of the folds of the palps, the non-reflected gills of *L. galathea* and the possible reductions in grooves of the oesophagus and stomach. These reflect a reduction in the selective actions of the organs concerned, thereby broadening the diet. This would be in keeping with the variety and the occasional large size of particles observed in the stomach of the abyssal species.

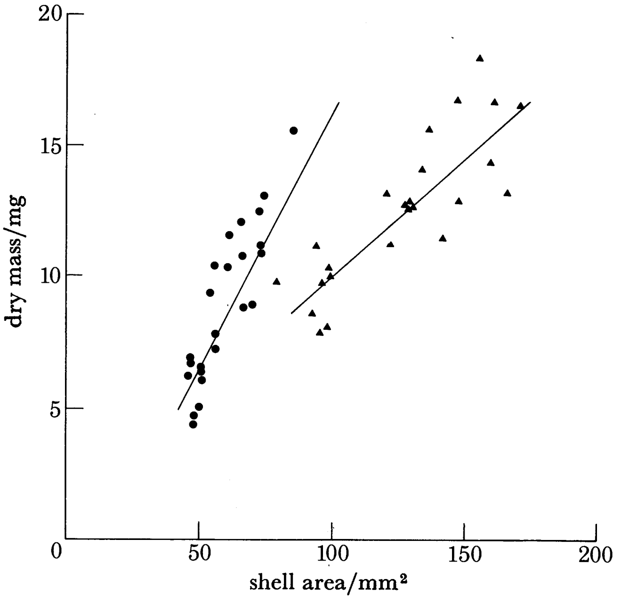


Figure 42. Comparison of the ratio dry mass: relative volume of *Limopsis aurita* (●) and *L. tenella* (▲).

The gills and viscera of *L. tenella* are highly contracted and fill only a small portion of the mantle cavity and, unlike those of *L. aurita*, the tissues in this species are very fragile. Fixation of the two species under identical conditions confirmed the difference. Comparison of the dry biomass of each species relative to the volume of the shell for the largest animals shows that the relative dry mass of *L. tenella* is much less than that of *L. aurita* (figure 42). Although a large mantle cavity space may be functionally significant the energy available may not be enough to sustain a large body size. This may or may not be consistent with the production of a large shell. There is no evidence that the gills are relatively large in this species. It may be that, although energy lack leads to reduction of biomass, lost volume is replaced by body fluid. While the gills will collect an amount of food proportionate to their area, such an adaptation will reduce metabolic demand, i.e. the effective feeding efficiency is enhanced. A similar condition exists in the large abyssal arcid *Bathyarca corpulenta* (Oliver & Allen 1980).

This paper forms part of a continuing series, based on bivalves collected by deep-sea benthic sampling programmes. Originating and continuing as part of a joint research programme with Dr H. L. Sanders and other staff of the Woods Hole Oceanographic Institution into the ecology and biology of the benthic infauna of the deep sea, latterly it has become extended by material obtained by the authors working from research ships of the Natural Environment Research Council and by other deep-sea investigators, notably by Dr L. Laubier and his staff at C.N.E.X.O., Brest, Dr J. Gage of S.M.B.A. Dunstaffnage and Dr A. Southward of M.B.A. Plymouth, to whom we are indebted and to whom we extend our most sincere appreciation for all their kindnesses.

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KEY TO ABBREVIATIONS USED IN THE FIGURES

a.	anus
a.a.	anterior adductor muscle
a.o.	abdominal organ
a.r.m.	anterior retractor muscle
ax.f.	axial fold
b.	byssus
b.d.	byssus duct
b.gr.	byssus groove
b.r.m.	byssus retractor muscle
c.g.	cerebral ganglion
c.t.r.	connective tissue ridge
d.d.	digestive duct
d.g.	digestive gland
d.h.	dorsal hood
d.mn.e.	dosral mantle edge
f.	foot
f.h.	heel
f.t.	toe
g.	gill
g.a.	gill axis
g.a.m.	gill axis muscle
gd	gonad
g.s.	gastric shield
h.	heart
hg	hindgut
h.t.	hood tract
i.d.	inner demibranch
k.	kidney
l.p.	left pouch
lt	left
m.	mouth
m.c.	mucous cell
m.f.	mantle flap
m.f.g.	mantle flap gland
m.f.m.	mantle flap muscle
mi.t.	minor typhlosole
mn.e.t.	thickened mantle edge
mn.n.	mantle nerve
mn.p.	mantle pigment spots
m.t.	major typhlosole
n.	nerve
o.d.	outer demibranch
oe.	oesophagus
ov.	ovary
p.a.	posterior adductor muscle
p.c.	pigmented cells
p.g.	pedal ganglion
p.gr.	periostracal groove
pl.	palp
p.r.m.	posterior retractor muscle
p.s.a.	posterior sorting area
r.	rectum
r.c.a.	right ciliated area
r.d.t.	right duct tract
rj.t.	rejection tract
r.p.m.	pallial retractor muscle
s.	stomach
s.s.	style sac
t.	testis
t.a.	anterior dorsal tract
t.s.a.	sorting area
v.g.	visceral ganglion
v.mn.e.	ventral mantle edge