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THE FUNCTIONAL AND ADAPTIVE MORPHOLOGY OF THE DEEP-SEA SPECIES OF THE ARCACEA (MOLLUSCA: BIVALVIA) FROM THE ATLANTIC

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CONTENTS

Species of two genera, *Bathyarca* Kobelt (1891) and *Bentharca* Verrill and Bush (1898), occur beyond the shelf–slope break of the continental margins of the Atlantic. Little is known of these species and descriptions of the morphology of *Bathyarca glacialis*, *B. pectunculoides*, *B. inaequisculpta*, *B. corpulenta*, *Bentharca nodulosa* and *B. asperula* are given.

The species of *Bathyarca* show a progression in form from an epibyssate nestling habit to an infaunal endobyssate habit. Correlated with this are various morphological changes. Thus the byssus, which is short and stout and controlled by strong retractor muscles in the epibyssate *B. glacialis*, is long and slender with weak associated musculature in endobyssate *B. inaequisculpta*. The mantle/shell form is increasingly heteromyarian in character in deeper-living species, with the increasing development of mantle flaps and muscles of the gill axis. In contrast, the species of *Bentharca* have largely retained their epibyssate habit. Their morphology is conservative and differs little from shallow-water arcids.

Features are found in both genera that are related to the small quantity of suspended food present in the deep sea. These include the lack of glands in mantle tissue, the reduced palps and lack of sorting areas in the stomach. In *Bathyarca corpulenta* alone the (body biomass) : (shell volume) ratio is reduced.

Introduction

The Arcacea is well represented in shallow, warm waters by a large variety of species. Two types predominate, epibyssate nestling species confined to hard substrates and shallow-burrowing cardioid species, either endobyssate or without a byssus in the adult (Yonge 1955). In the deep sea the Arcacea is very poorly represented. From the literature and the samples available it appears that only two genera, *Bathyarca* Kobelt (1891) and *Bentharca* Verrill and Bush (1898), occur below the continental margin zone. Within the genus *Bathyarca* there are probably no more than twenty valid species and in *Bentharca* only three.

A number of causes have been proposed to explain the limitation of this superfamily largely to shallow warm waters. From palaeontological data it would appear that the Arcacea underwent considerable adaptive radiation during the Triassic and this was confined to shallow warm waters (Newell 1969). It is possible that early-established conservatism limited further radiation into deeper and/or colder waters. It may be that suspension feeding is disadvantageous in the deep sea because of the lack of suspended matter in that environment (Jorgensen 1966); however, as pointed out by Knudsen (1970), there are numbers of suspension feeders present in the deep sea, not only in the Bivalvia but in many other taxa too. The form of the ligament in arcids probably limits the morphological pliability of the mantle/shell (Thomas 1976) and because of this they are restricted to nestling trapezoidal or unattached or endobyssate cardioid hapes. None of these shapes is very suitable for life in soft oozes. Thus, of the epibyssate species of the genus *Bentharca*, only one is abyssal, whereas there are five endobyssate species of the genus *Bathyarca*, which might indicate that the bathymetric restriction of the Arcacea is related more to substrate than to depth.

As with the Limosacea, the deep-sea arcaceans are derived from genera with predominantly cold-water distributions. *Bathyarca* and *Bentharca* are the only arcaceans found in boreal and arctic seas at shallow depths, and *Bathyarca* alone occurs in antarctic shallow water. No species has a bipolar distribution, but the phenomenon of equatorial submergence is shown by both genera.

The two genera have been considered to be closely related, so much so that some early authors (Smith 1885; Verrill & Bush 1898) used *Bathyarca* to include them both. Of more recent authors, Knudsen (1967, 1970) has doubted this, while Newell (1969) has maintained the earlier view. All species of *Bentharca* are trapezoidal with a byssal sinus and clearly belong close to *Acar* in the Arcinae; species of *Bathyarca* are more heterogeneous, but as the majority are oval and endobyssate they are assigned to the Anadarinae.

BATHYARCA KOBELT 1891

This genus was first recognized by Kobelt (1891), who designated *B. pectunculoides* Scacchi the type species. Most species resemble this in shape, but there are exceptions of rather different shape that are not immediately recognizable as belonging to *Bathyarca*, e.g. *B. corpulenta* (p. 62). While the shape of the shell is not always diagnostic, a feature common to this genus and, as far as is known, unique to it is a so-called pair of mantle flaps. These mantle flaps are situated postero-ventrally and consist of muscular extensions of the mantle. They were described first by Pelseneer (1911) and later by Heath (1941), and were thought to be extendable, acting as a primitive form of siphon.

Information on the morphology and biology of the genus is sparse and is confined to these two references and a few notes, by Ockelmann (1958), on the reproduction of arctic shelf species.

Species of Bathyarca from the Atlantic continental shelf edge and slope

Bathyarca glacialis (Gray 1824) (figures 1–5, 17)

Type. *Arca glacialis* Gray 1824. Location: British Museum (Natural History).

Type locality. ? (Prince Regents Inlet, Keewatin Territory, Canada) (Stevenson 1972).

Synonymy.

1824	*Arca glacialis*	Gray (p. 244)
1878	*Arca glacialis*	Sars (p. 43; figs 1A–C, pl. 4)
1879	*Arca glacialis*	Jeffreys (p. 572)
1927	*Bathyarca glacialis*	Dautzenberg (p. 283)

Station data.

ship	date	station no.	latitude	longitude	depth/m	number of specimens
Thalassa	21.10.73	Z392	47° 34.9′ N	07° 01.2′ W	390	19
	22.10.73	Z397	47° 33.8′ N	07° 12.6′ W	511	6

Distribution. This species ranges from the Arctic Ocean throughout the North Atlantic Ocean into the Mediterranean Sea and has a depth range of 6–4170 m (Clarke 1962). At the north of its range it is found in the sublittoral zone; it submerges equatorially and is limited to much deeper water at the south of its range. There are a few abyssal records (Clarke 1962), but the bulk of the data, especially that from the Bay of Biscay, suggests that *B. glacialis* does not normally occur below the continental margin zone.

Description. B. glacialis is listed in the literature of the late nineteenth century (Jeffreys 1879; Sars 1878; Verrill & Bush 1898) but since then it has been neither redescribed nor revised. There are no complete descriptions of the anatomy.

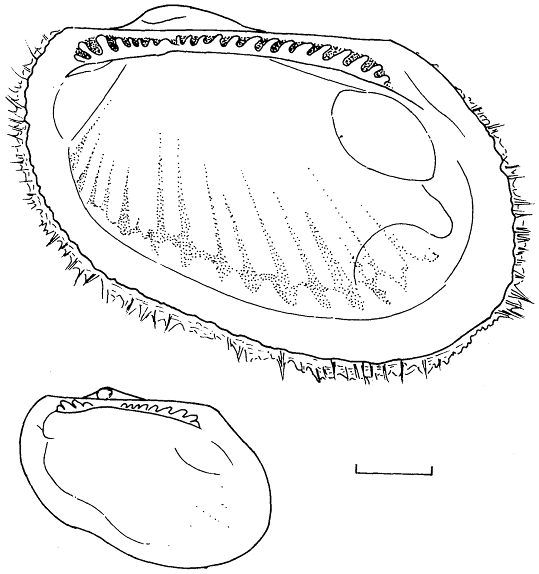

FIGURE 1. *Bathyarca glacialis*. Internal view of shell from Bay of Biscay. Scale bar, 1 mm.

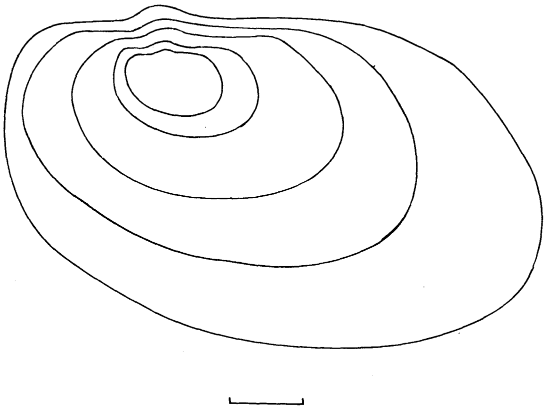

FIGURE 2. *Bathyarca glacialis*. Lateral outlines of a size series of shells. Scale bar, 2 mm.

The form of the shell of *B. glacialis* is not very variable and is easily recognizable throughout its size (figure 2) and geographical range. The northern specimens are larger than the southern ones (approximately 30 mm as compared to 15 mm). While normally equivalve, a few specimens were seen slightly inequivalve.

Shell longer than high, slightly compressed and roughly subtrapezoidal; outline rounded inequilateral, posterior region slightly expanded; umbos prominent, close together, dorsal area long and narrow; ligament posterior to the umbos, few chevrons, rather weak; northern specimens thin-shelled, weak decussate sculpture; southern specimens thicker-shelled, strong sculpture; periostracum with numerous fine, brown hairs (in southern specimens, only at shell margins); shell internally white, prominent subequal muscle scars; hinge long, narrow with two sets of moderately strong teeth, outer teeth oblique to dorsal margin, central teeth vertical; shell margin, smooth, may be slightly indented at exit of byssus.

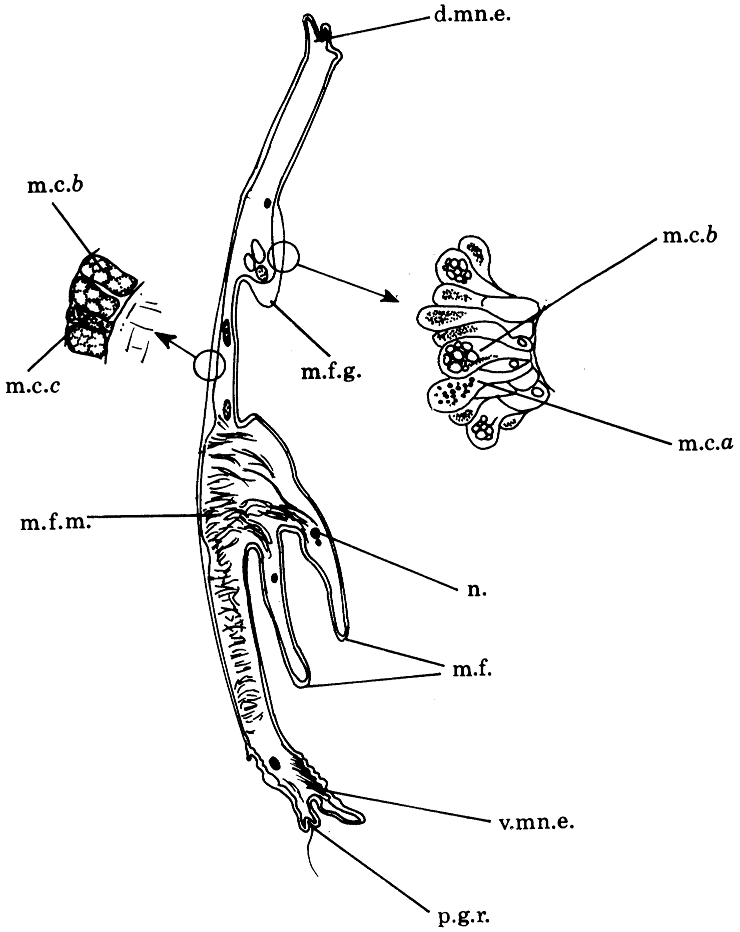

FIGURE 3. *Bathyarca glacialis*. Transverse section of the mantle in the region of the mantle flap. Enlarged detail of the glandular epithelia included as insets. For explanation of abbreviations used see list at the end of following paper.

The mantle edge (figure 3) typically has three folds, of which the inner muscular fold is the most prominent. The sensory fold is poorly developed and there are no eyespots. At the posterior margin the dorsal part of muscular fold is enlarged and forms a highly muscular flap of tissue (figures 3, 17). When contracted, the flaps are twisted on themselves and measure approximately one-sixth of the length of the shell. Associated with each flap and lying dorsal to it is a swelling, the mantle flap gland (m.f.g., figures 3, 4). Each swelling is elliptical in outline and derived from the inner mantle epithelium. In transverse sections stained with azan they consist of a layer of glandular cells lying on a mound of connective tissue. Three types of cell are present; the most numerous is narrow, rectangular and mucus-secreting, with amorphous contents that stain a pale mauve colour (figure 3, m.c.*a*). The second type, secreting mucoprotein, is much larger, roughly cuboidal in shape and contains large globules that stain a vivid orange-red colour (figure 3, m.c.*b*). Cells of the third type may be derivatives of those of the second, being similar in form and staining properties, but they differ in having much smaller globules and they have the appearance of being in the process of secreting their contents (figure 3, *m.c.c.*). These glands are placed to either side of the exhalant aperture and it is assumed that the mucus produced helps to bind and aids the removal of particulate wastes. The rest of the inner mantle epithelium is also glandular, with cells similar to those of the mantle flap gland. The most prominent gland cells are found below the floor of the kidney, between the foot and the gill axis. Again these must be presumed to be associated with the removal of unwanted material from the mantle cavity.

The outer mantle epithelium is also glandular, but with a larger proportion of cuboidal cells (figure 3). Unless they are concerned with laying down the scleroprotein layer of the shell, the function of mucoprotein-secreting cells next to the shell is obscure.

The glandular nature of the mantle of *B. glacialis* is not unusual and similar observations have been made for a number of species of Arcacea (Heath 1941). Heath (1941) suggested that this was a reflection of the primitive form of the Arcacea and that these species had not developed a differentiation of function of the mantle areas. Although this may in part be true, the large inhalant region allows much material to enter the mantle cavity, and thus gland cells are very necessary.

The gills (figure 4) are large, flat and homorhabdic. The filaments are fully reflected in both demibranchs and are joined by cilia at their tips and points of reflexion. The gill axis is muscular and is presumed capable of some extension. The palps are small and simple, with only six ridges.

The gut (figure 4) does not differ in gross form from those described by Heath (1941). The oesophagus is long, circular in cross section and not dilated. It joins the stomach high on the anterior face. The stomach is flask-shaped. The combined midgut and style sac leaves the stomach from the posterior ventral floor and curves slightly forward into the foot. The hindgut passes, in a series of weak sinuations, across the right posterior side of the stomach and through the pericardium, to end in a rather elongate anal region.

The structure of the stomach was observed after an incision had been made along the dorsal surface. The major typhlosole passes forward and then left in a wide curve. To the right of it lies a deep embayment into which open four digestive ducts, two on the right and two below the oesophagus. A tongue of the major typhlosole enters a very small left pouch. The left pouch has no digestive ducts opening into it. To the left of the pouch is a low longitudinal fold corresponding to the axial fold. This fold separates the left pouch from the dorsal hood tract, which runs along the left side of the dorsal fold. The posterior part of the large dorsal fold is ridged. The gastric shield, which overlies part of the dorsal fold, is not large and has two teeth, one which is carried on the flange in the dorsal hood and another on the flange to the left pouch. Except for a

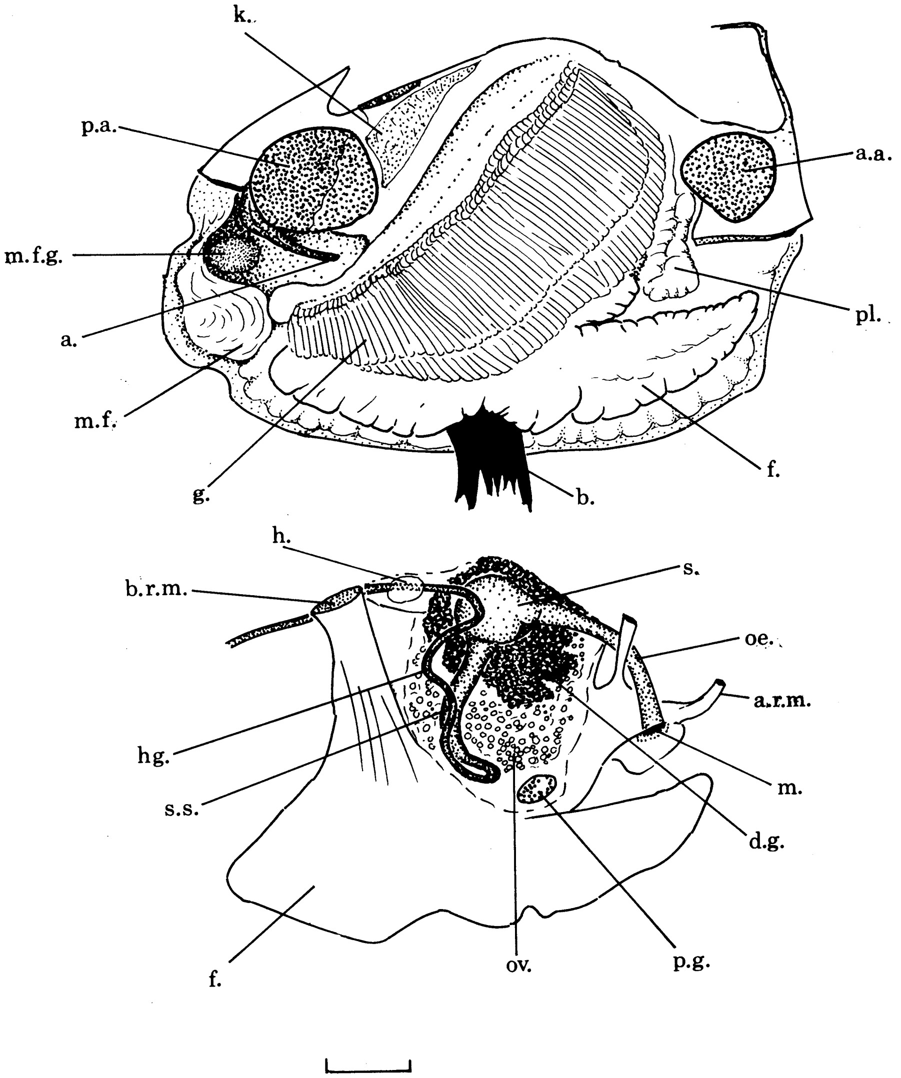

Figure 4. *Bathyarca glacialis*. Anatomy as seen from the right side. In the lower figure the gill and part of the body wall have been removed to show the course of the gut and the extent of the associated tissues. For explanation of abbreviations used see list at end of following paper. Scale bar, 1 mm.

narrow tract running along the anterior right side as far as the dorsal hood, the posterior wall and most of the wall on the right side of the stomach appear smooth. As live material was not available it was not possible to observe the functioning of the stomach, but, except for the dorsal fold, it is of similar construction to the stomach of arcids described by Purchon (1957) and by Dinamani (1967).

The remainder of the visceral mass is occupied by the digestive diverticula and gonad. The gonad is large, filling spaces in the foot as well as forming dorsal lateral pouches (figure 4). The sexes are separate. The eggs are 170 μm in diameter (Ockelmann 1958).

The kidneys are compact and highly ramified (figure 5).

The foot is moderately large, with a large toe and a small heel (figure 4). The musculature of the toe is poorly developed and appears to contain much connective tissue. The central and ventral portions of the foot are occupied by a large byssus groove and associated glands. The byssus groove opens midventrally and the byssus forms a wide thin sheet. The byssus is produced high in the byssal groove and the byssal rectractors are large relative to those of other species of this genus. A pair of statocysts is associated with the pedal ganglion.

B. glacialis has not been observed alive. From station data this species appears to inhabit a variety of substrates from rocks to muddy gravel but is most frequent in the latter. The overall shape, the form and the size of the byssus suggest that this species is epibyssate-living (figure 17), with its long axis close to and parallel to the substrate. It is probable that the inhalant current(s) carry sedimentary matter into the mantle cavity. This may account for the glandular nature of the mantle. The mantle flap may therefore be a modification to overcome the problems of suspension feeding in close proximity to the substrate.

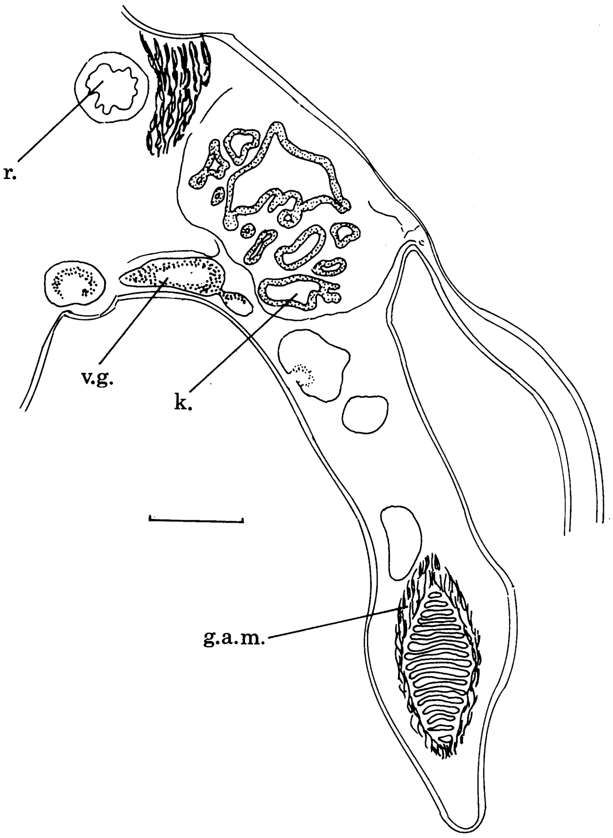

FIGURE 5. *Bathyarca glacialis*. Transverse section through the left kidney. For explanation of abbreviations used see list at end of following paper. Scale bar, 0.5 mm.

Bathyarca pectunculoides (Scacchi 1834) (figures 6, 17)

Type. *Arca pectunculoides* Scacchi 1834. Location?

Type locality. Pliocene fossil, Sicily.

Synonymy.

1834	*Arca pectunculoides*	Scacchi (p. 82)
1878	*Arca pectunculoides*	Sars (p. 43; fig. 2*a–c*, pl. 4)
1879	*Arca pectunculoides*	Jeffreys (p. 572)
1927	*Bathyarca pectunculoides*	Dautzenberg (p. 280)
1966	*Arca pectunculoides*	Tebble (p. 32; text fig. 16)

Station data.

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Gay Head–Bermuda transect	*Chain*	58	05.05.66	105	39° 56.6′ N	71° 03.6′ W	530	3
	Atlantis II	40	27.11.67	172	40° 12.3′ N	70° 44.7′ W	119	18
					40° 10.8′ N	70° 43.6′ W		
			27.11.67	173	40° 10.8′ N	70° 43.6′ W	122	3
					40° 10.6′ N	70° 44.0′ W		
	Chain	88	21.02.69	207	39° 51.3′ N	70° 54.3′ W	805–811	6
					39° 51.0′ N	70° 56.4′ W		
southwest Africa	*Atlantis II*	42	16.05.68	186	22° 57.0′ S	13° 05.0′ E	439–481	2
Canaries	*Discovery*		15.03.68	6696	28° 06.0′ N	13° 28.0′ W	1780	12
Bay of Biscay	*Sarsia*		12.07.67	29	47° 40.0′ N	05° 00.0′ W	119	2
			19.07.67	56	43° 43.0′ N	03° 47.8′ W	641	5
	Thalassa		21.10.73	Z392	47° 34.9′ N	07° 01.2′ W	390	1
			22.10.73	Z397	47° 34.9′ N	07° 12.6′ W	511	1
				Z399	47° 34.8′ N	07° 18.1′ W	825	4
			23.10.73	Z409	47° 43.1′ N	08° 04.0′ W	1035–1080	2
					47° 42.9′ N	08° 00.9′ W		
			24.10.73	Z413	48° 03.1′ N	08° 29.4′ W	805	3
			24.10.73	Z414	48° 05.0′ N	08° 29.8′ W	650	1
				Z417	48° 12.0′ N	09° 09.5′ W	865	4
			25.10.73	Z1431	48° 38.2′ N	09° 47.3′ W	800	2
			26.10.73	Z1437	48° 34.0′ N	10° 23.7′ W	610	4
	Challenger		21.06.75	2	48° 40.0′ N	09° 43.0′ W	300	1

Distribution. B. pectunculoides has a wider distribution than *B. glacialis*, occurring in the Caribbean and southwest Atlantic as well as the Arctic and North Atlantic oceans. This species also exhibits equatorial submergence, being recorded from the sublittoral in the Arctic and the lower slope in the Atlantic. There are also a number of abyssal records (Clarke 1962), but these may be doubtful and the animals confused with small *B. inaequisculpta*, an endemic abyssal species (p. 58). The deepest record of *B. pectunculoides* from the present samples is from 1780 m, off the Canary Isles. Depth range: 40–3310 m.

B. pectunculoides is a variable species with a number of recorded varieties from the arctic and boreal regions (e.g. *B.p. raridentata* Woods, *B.p. septentrionalis* Sars). None was found in the present collections; however, the Caribbean variety *B.p. orbiculata* Dall is discussed (pp. 56, 62) in connection with *B. inaequisculpta* and with *B. corpulenta*. The present samples all come from the Atlantic slope and consist of smaller individuals than those from arctic regions.

There are a number of previous shell descriptions (see for example, Jeffreys 1868; Sars 1878), but that by Verrill & Bush (1898) is the best. Heath (1941) describes the anatomy; therefore only details essential to this study are given here.

B. pectunculoides is less elongated than *B. glacialis* and is only slightly longer than it is high. The ventral margin is markedly curved. It is more inequilateral than *B. glacialis*, the anterior portion of the shell being reduced and the posterior expanded. Usually, in the anterior ventral margin of the shell there is a distinct byssal notch, through which passes the small stalk of the byssus. All but the very smallest specimens are inequivalve, the right valve fitting into the larger left valve. The inner margin of the left valve is crenulate and that of the right is smooth. The hinge line is reduced anteriorly and there is an edentulous space separating anterior and posterior sets of teeth. Up to eight teeth form the posterior set, but no more than five form the anterior set. The latter are usually confined to a slightly swollen area of the hinge plate and the teeth may be distorted.

Mantle flaps (figure 17) are present and are proportionately larger than those of *B. glacialis*, being about one-fifth to one-quarter of the length of the animal in the contracted state. Both they and the mantle flap glands are similar in structure to those of *B. glacialis*, but the mantle flap glands are smaller and the glands of the outer mantle epithelium much less numerous. The stomach of this small species was examined from serial transverse sections and proved similar to that of *B. glacialis* except that the dorsal fold is not so well developed. The contents of the stomach, clearly visible in section, consist almost entirely of diatom skeletons. The gills (figure 6) are contorted from fixation and appear to be large. The gill axis is muscular, if anything more so than in *B. glacialis* although the difference in size of the two species makes comparisons unreliable. The foot (figure 6) is more muscular, especially the toe, and this is probably correlated to the smaller byssus gland. The byssal groove is narrow and the byssus consists of a single cylindrical stalk.

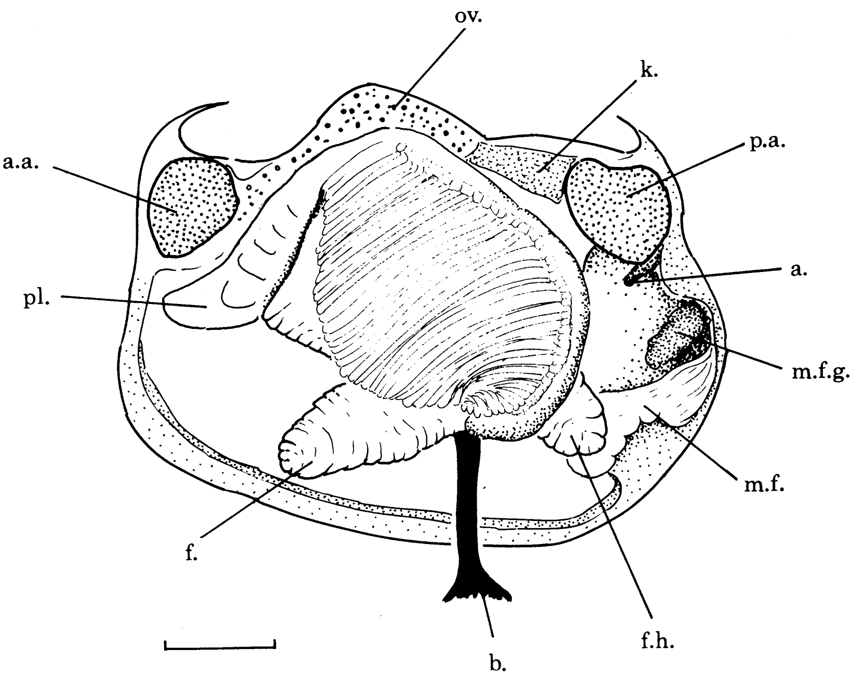

FIGURE 6. *Bathyarca pectunculoides pectunculoides*. Anatomy as seen from the left side. For explanation of abbreviations used see list at end of following paper. Scale bar, 1mm.

B.p. pellucida n. sub sp. (figures 7–9)

Type. *Bathyarca pectunculoides pellucida.* Location: Museum of Corporative Zoology, Harvard.

Type locality. '*Atlantis II*' cruise number 24, station 118, between Gay Head and Bermuda at a depth of between 1135 and 1153 m.

Station data.

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Gay Head-Bermuda transect	*Atlantis II*	24	18.08.66	118	32° 19.4′ N	64° 34.9′ W	1135–1153	24

This subspecies is characterized by very low and inconspicuous umbos which only just project above the dorsal margin of the shell. No byssal notch is apparent; otherwise the shape of the shell is similar to *B.p. pectunculoides*. Sculpture is absent and the shell surface is entirely smooth, although radial marks within the shell substance itself were observed. The shell is almost transparent and the adductor muscle and mantle edge are clearly seen through the shell. The shell is inequivalve but the internal margins of both valves are smooth. The hinge is greatly reduced, there being only three posterior teeth and three anterior teeth separated by a long edentulous space.

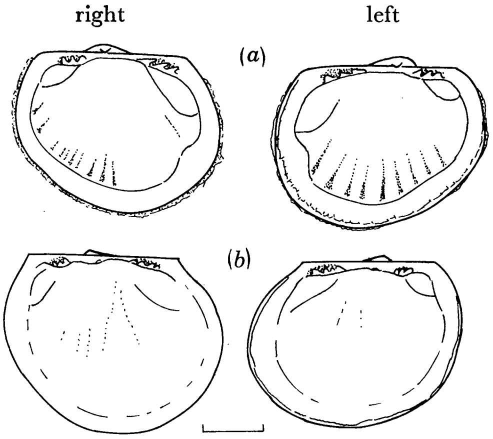

FIGURE 7 (*a*) *Bathyarca pectunculoides pectunculoides* and (*b*) *B.p. pellucida*. Internal views of left and right valves. Scale bar, 1 mm.

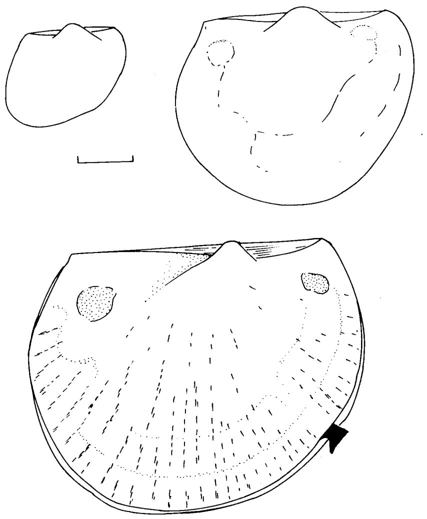

FIGURE 8. *Bathyarca pectunculoides pellucida*. External view of right valves; variation in shape in relation to size. Scale bar, 0.5 mm.

The internal anatomy (figure 8) is similar except that the mantle flap glands are circular and smaller than in *B.p. pectunculoides*. The adductor muscles are also smaller.

Observations on living B.p. pectunculoides (figures 9, 10)

A single specimen was collected alive, together with the 300 *Limopsis aurita*, from *Challenger* station 2 in the Bay of Biscay, from muddy shell gravel. This animal was observed, over a number of months, in the laboratory and confirmed inferences made from morphological studies both past and present.

The animal was kept in a small tank with a gravel bottom but was occasionally removed for closer study under a binocular microscope. In the tank it attached itself to a pebble and remained at a single site for a number of days. After disturbance, as well as on its own initiative, it would detach itself from its byssus stalk and crawl to a new site and reattach.

At rest the animal is orientated with its long axis parallel to the bottom. On commencement of feeding it contracts the byssus retractor muscles and then pulls the anterior end of the shell towards the substratum. With the posterior end raised into the water, the valves open and the mantle flaps extend. These flaps then consist of flat sheets of tissue, with a straight dorsal edge and curved ventral margin and are bent towards each other, often touching distally. When fully expanded they are about one-third of the length of the shell. Once the flaps are extended the

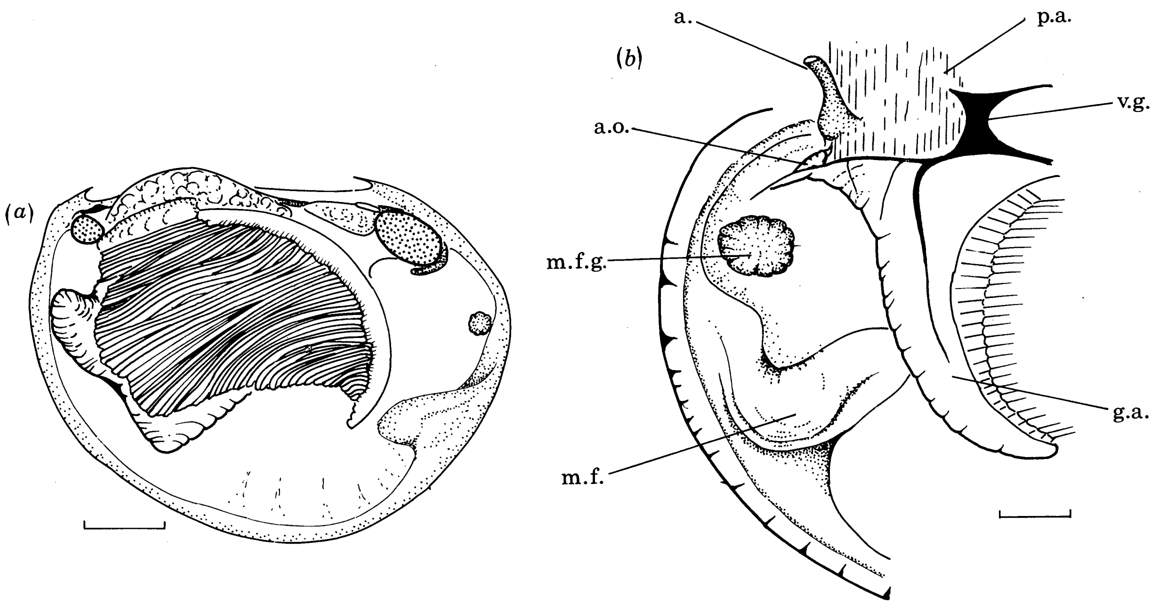

FIGURE 9. *Bathyarca pectunculoides pellucida.* (*a*) Anatomy as seen from the left side and (*b*) detail of the postero-dorsal region of the mantle and body from the right side. For explanation of abbreviations used see list at end of following paper. Scale bars: in (*a*), 500 μm; in (*b*), 150 μm.

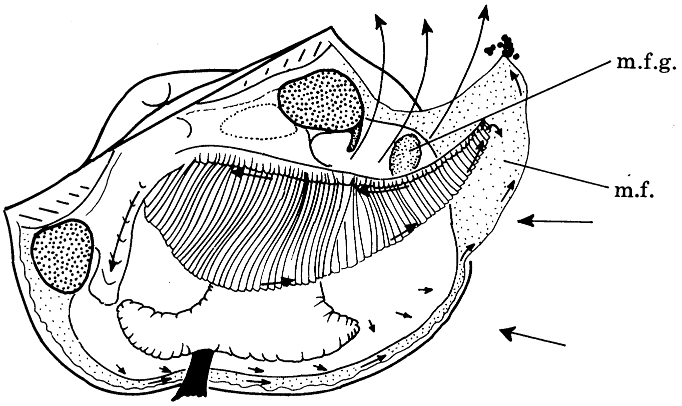

FIGURE 10. *Bathyarca pectunculoides pellucida.* Major currents on mantle and body as seen from the left side. For explanation of abbreviations used see list at end of following paper.

gills also extend beyond the shell margin, to about one-half of the length of the flaps. With use of carmine and graphite some of the ciliary currents were observed. As in *Arca senilis*, which lives just below the surface of soft sediments (Yonge 1935), the inhalant current of *B.p. pectunculoides* is confined to the posterior ventral margin. The strong exhalant current is confined to the posterior dorsal margin and directed upwards away from the mantle flaps. The ventral edge of the flap is continuous with the rejection tract at the mantle edge, and pseudofaeces were observed passing to the tips of the flaps, where they fell away from the shell. On occasions this seemed disadvantageous as these were carried back into the mantle by the ventral inhalant current, to be quickly expelled via the exhalant current. When this solitary living specimen was finally dissected, it was observed that the ciliary currents on the gills and mantle were similar to those described for *Limopsis aurita* (Oliver & Allen 1980) and typical of those of the arcids as a whole (Atkins 1936).

There are two consequences that follow the raising of the posterior end of the shell. In common with all phylogenetically superior bivalves, the anterior inhalant current is lost and the point of entry of the posterior inhalant current is distant from the sediment surface. If for efficient suspension feeding the intake of surface sediment is disadvantageous, e.g. because of high inorganic load or the clogging of ciliary mechanisms, then the change is highly adaptive.

The mantle flaps enhance the effects of anisomyarianism and allow for a larger gill and thus increase feeding efficiency. They also facilitate the removal of pseudofaeces and enable the animal to feed when heavily sedimented, maintaining a clear passage beyond the end of the shell.

Atlantic abyssal species of Bathyarca

Specimens from the abyss show a high degree of variability in form, which is related to growth and to geographical distribution. There is, however, little doubt that specimens from the present samples represent a single Atlantic species. Existing literature would contradict this view and a number of species are described based on relatively few specimens collected from widely separated localities. Some of these species must be regarded as having unusual bathymetric ranges. The determination of synonymy is therefore somewhat complicated and ideally it should be based on comparisons of specimens of the same size. Unfortunately this has not always been possible and some doubtful species remain.

To simplify comparison, the major diagnostic characters are tabulated (table 1) for all described species of *Bathyarca* from the Arctic, Atlantic and Antarctic oceans. Of these, specimens of *B. polycyma* Dall 1881, *B. glomerula* Dall 1881, *B. abyssorum* Verrill & Bush 1898, and *B. dakarensis* Locard 1898 for various reasons have been unobtainable.

Of those examined, *B. pectunculoides* and *B. glacialis* have been considered above and need no discussion. *B. frielei* Jeffreys 1849 is distinct, with a long, coarsely hairy periostracum, and is restricted to bathyal and abyssal depths in arctic and subarctic waters. *B. polycyma* also has a characteristic nodulose sculpture and is a shallow-water species from the Caribbean. *B. strebeli* Melville & Standen 1907 has an equivalve shell that is slightly longer than it is high. It resembles small specimens (2 mm) of the present samples but is itself 4–5 mm long. While it is possible that larger specimens would be inequivalve, its isolated distribution in the abyssal Weddell Basin of the Antarctic Ocean suggests that it is a separate species.

B. abyssorum matches the present samples from the N.W. Atlantic, as does *B. dakarensis* those from the east equatorial Atlantic, and thus both are positively synonymized with the present specimens.

B. orbiculata Dall 1881 (figure 11) is known from valves only and is restricted to abyssal depths in the Gulf of Mexico. It has a very thin shell and a weak hinge. As in *B. pectunculoides*, the anterior teeth are confined to a slightly swollen hinge plate. The sculpture of an intact specimen cannot be assessed as no pair of valves exists. Other specimens labelled *B. orbiculata* taken by the *Blake* from 1800 m are more elongated and, as suggested by Dall (1908), appear to be intermediate between *B. pectunculoides* and the type of *B. orbiculata*. There is sufficient uncertainty not to synonymize *B. orbiculata* for the present, but it may be that this species represents an extreme variety.

B. inaequisculpta (Smith 1885) was synonymized with *B. glomerula* by Dall (1908) on the basis of the inequisculptured valves. This character is not unique to this species or to *Bathyarca* but

Table 1. Diagnostic characters of the Atlantic species of *Bathyarca*

species	length/mm	bathymetric range/m	geographical range	equivalve	equisculptured	inner margin indented	edentulous space	height/length	notes
B. glacialis Gray 1824	8	2–1000	Arctic, N. Atlantic	+	+	–	–	–	see anatomy
B. pectunculoides Sch. 1834	6	2–2000	Arctic, Atlantic	–	+	+	+	–	see anatomy
B. frielei Jeff. 1879	6	?–4000	Arctic, subarctic	+	+	–	+	–	long bristles
B. orbiculata Dall 1882	4	2900	Gulf of Mexico	–	?	+	+	+	
B. glomerula Dall 1882	8	200–800	Caribbean	?	–		±	±	beaded inner margin
B. polycyma Dall 1882	4	200	Caribbean	+	+	–	?	–	nodulose sculpture
B. inaequisculpta Smith 1885	8	700	Caribbean	–	–	+	–	+	
B. abyssorum V. & B. 1898	6	3400	N.W. Atlantic	–	?	+	+	+	
B. dakarensis Locard 1898	6	3200	E. eq. Atlantic	–	?	+	–	+	
B. strebeli M. & S. 1912	4	3700	Antarctic	+	+	?	?	–	
present samples	4	2000–5000	eq. Atlantic	–	–	+	+	±	
	6			–	–	+	±	+	
	8			–	–	+	–	+	
	4		N.W., N.E. Atlantic	–	±	+	+	–	
	6			–	–	+	+	+	

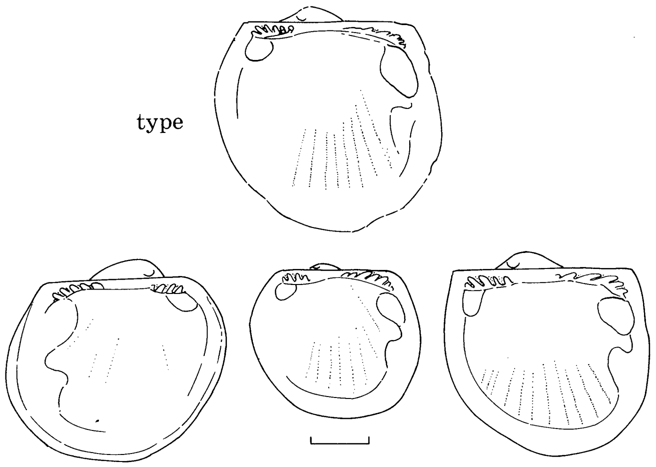

Figure 11. *Bathyarca orbiculata*. Internal views of valves of shells obtained by the Blake Expedition. Scale bar 1 mm.

occurs in many inequivalve anadarids and especially in *Scapharca*. There are a number of differences between the two species; thus the form of the crenulation that Dall describes as 'raised nodules continuous with internal radial lines' is not that found in *B. inaequisculpta;* the teeth of *B. glomerula* are regular with a small edentulous space and contrast with the complete but irregular dentition of *B. inaequisculpta* of equivalent size (8 mm); *B. glomerula* is marginally longer than it is high, whereas *B. inaequisculpta* is higher than it is long. The two species therefore appear to be distinct.

B. inaequisculpta is identical in shell form to large specimens from the Surinam Basin in the present samples. The original specimens taken by *Challenger* were from 690 m, which is very shallow in comparison to the truly abyssal range of the present specimens; however, the log of the *Challenger* (1895, pt 1, pp. 170–171) for station 24 states that initial sounding was 350 fm (640 m), but that during the lowering of the dredge a sounding of 800 fm (1465 m) was taken. The actual depth of the sample is therefore uncertain but may have been a lot deeper than thought. This is confirmed in the station list, which contains mainly bathyal and abyssal species.

The present specimens are considered to be examples of *B. inaequisculpta.*

Bathyarca inaequisculpta (Smith 1885) (figures 12, 13, 17)

Type. *Arca* (*Scapharca*) *inaequisculpta* Smith 1885. Location: British Museum Natural History).

Type locality. Off Culebra Island, West Indies. *Challenger* station 24, 690 m.

Synonymy.

1885	*Arca* (*Scapharca*) *inaequisculpta*	Smith (p. 267; fig. 8a–d, pl. 17)
1898	*Bathyarca abyssorum*	Verrill & Bush (p. 843; fig. 9, pl. 76)
1898	*Bathyarca dakarensis*	Locard (p. 321; figs 25–28, pl. 8)
1916	*Batharca abyssorum*	Sheldon (p. 66)
1962	*Bathyarca abyssorum*	Clarke (p. 55)
1962	‘*Arca*’ *dakarensis*	Clarke (p. 55)
1962	*Bathyarca inaequisculpta*	Clarke (p. 56)
1970	*Arca orbiculata*	Knudsen (p. 76, parts)

Station data.

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Gay Head–Bermuda transect	*Chain*	50	30.06.65	77	38° 0.70′ N	69° 16.0′ W	3806	1
	Chain	50	05.07.65	85	37° 59.2′ N	69° 26.2′ W	3834	5
	Atlantis II	24	24.08.66	126	39° 37.0′ N	66° 47.0′ W	3806	10
Dakar Recife	*Atlantis II*	31	04.02.67	138	10° 36.0′ N	17° 52.0′ W	1944–76	2
			04.02.67	139	10° 33.0′ N	17° 53.0′ W	2099–2187	2
			05.02.67	143	10° 35.0′ N	17° 44.0′ W	2095	9
			05.02.67	144	10° 36.0′ N	17° 49.0′ W	2051–2357	12
			06.02.67	145	10° 36.0′ N	17° 49.0′ W	2185	9
			06.02.67	146	10° 39.5′ N	17° 44.5′ W	2842–2891	1
			06.02.67	147	10° 38.0′ N	17° 52.0′ W	2934	5
			07.02.67	148	10° 37.0′ N	18° 14.0′ W	3814–3828	1
			13.02.67	155	00° 03.0′ S	27° 45.0′ W	3697	2
S.W. Africa	*Atlantis II*	42	19.05.68	195	14° 40.0′ S	09° 54.0′ E		
					10° 29.0′ S	09° 54.0′ E	3797	40
					10° 29.0′ S	09° 04.0′ E		
			21.05.68	196	—	—	4612–4630	5
			21.05.68	197	10° 29.0′ S	09° 04.0′ E	3865–4595	24
S.W. Africa	*Atlantis II*	42	21.05.68	198	10° 24.0′ S	09° 09.9′ E	4559–4566	20
			22.05.68	200	09° 29.0′ S	11° 34.0′ E	2644–2754	15
				201	09° 05.0′ S	12° 17.0′ E	1964–2031	39
S.W. Africa	*Walda*		06.06.71	CY02	18° 52.1′ S	07° 23.1′ E	5175	2
				CY12	14° 31.8′ S	09° 46.0′ E	3975	2
				DS30	04° 04.1′ N	03° 42.0′ E	3109	1
				DS31	03° 17.5′ N	02° 01.0′ E	4279	3

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
Puerto Rico–Surinam–Barbados	*Knorr*	25	24.02.72	287	13° 16.0′ N	54° 52.2′ W		
					13° 15.8′ N	54° 53.1′ W	4980–4934	108
					11° 02.0′ N	55° 05.5′ W		
			25.02.72	288	11° 03.8′ N	55° 04.8′ W	4417–4429	44
			29.02.72	301	08° 12.4′ N	55° 50.2′ W	2424–2542	20
			1.03.72	303	08° 28.8′ N	56° 04.5′ W	2842–2853	58
			02.03.72	306	09° 31.3′ N	56° 20.6′ W	3392–3429	39
			03.03.72	307	12° 34.4′ N	58° 59.3′ W		
					12° 40.8′ N	59° 09.2′ W	3862–3835	48
Bay of Biscay	*Jean Charcot* *Biogas III*		27.08.73	DS44	47° 33.2′ N	09° 42.0′ W	3992	41
	Jean Charcot *Biogas IV*		19.02.74	DS53	44° 30.4′ N	04° 56.3′ W	4425	6
	Cyros *Biogas V*		19.06.74	DS68	46° 26.7′ N	10° 23.9′ W	4550	2
	Jean Charcot *Biogas VI*		25.10.74	CP15	46° 32.2′ N	10° 20.5′ W	4715	61
	Jean Charcot		26.10.74	DS79	46° 30.4′ N	10° 27.1′ W	4715	7
	Jean Charcot		27.10.74	DS82	44° 25.4′ N	04° 52.8′ W	4462	5
	Chain	106	21.09.72	323	50° 08.3′ N	13° 53.7′ W	3356–3388	2
					50° 08.3′ N	13° 50.9′ W		

Distribution. Recorded from all parts of the Atlantic Ocean except the Argentine Basin. Except for the type locality, which lies between 700 and 1600 m (see above), *B. inaequisculpta* has only been taken from abyssal depths (1964–5175 m).

Description. The following description is based on samples from the Surinam transect, which represent the largest size range.

Small shells to 2 mm, inequilateral, beaks in front of the midline, marginally inequivalve, longer than high, not inflated; sculpture more or less equal on both valves, finely decussate, covered by fine, short-haired periostracum; umbos low, dorsal area very narrow; hinge weak, teeth few (2–4) on each side, separated by a broad edentulous space; internal margin of larger left valve very lightly marked by the line of right valve, often not visible; no internal radial striations.

Medium shells, 2–5 mm, as above except obviously inequivalve; at 5 mm, length equal to height, tumid; sculpture unequal that of right valve more strongly developed; dorsal area broader; hinge strong, teeth numerous, regular, obliquely set, with very small edentulous space; internal margin of left valve strongly marked with indented and crenulated line; muscle scars visible, posterior much larger than anterior; faint, wide radial lines on inner shell surface.

Large shell, 5–8.5 mm, as above except: very inequivalve, height greater than length, very tumid, thick shelled; hinge very strong, teeth numerous but irregular in centre, no edentulous space; internal radial lines less faint.

S.E. Atlantic specimens. Reaching 8.5 mm in length but not higher than long. Large shells are very thick, very tumid with a strong irregularly toothed hinge. Internal striations very marked. (Figure 12.)

W. equatorial Atlantic specimens. Reaching 6 mm, but subcircular and tumid at this size. Teeth regular, with a small edentulous space at all sizes. Internal striations faint. (Figure 12.)

N.E. Atlantic specimens. Not exceeding 6 mm, shell thinner and less tumid, edentulous space at all sizes. Internal striations marked. (Figure 12.)

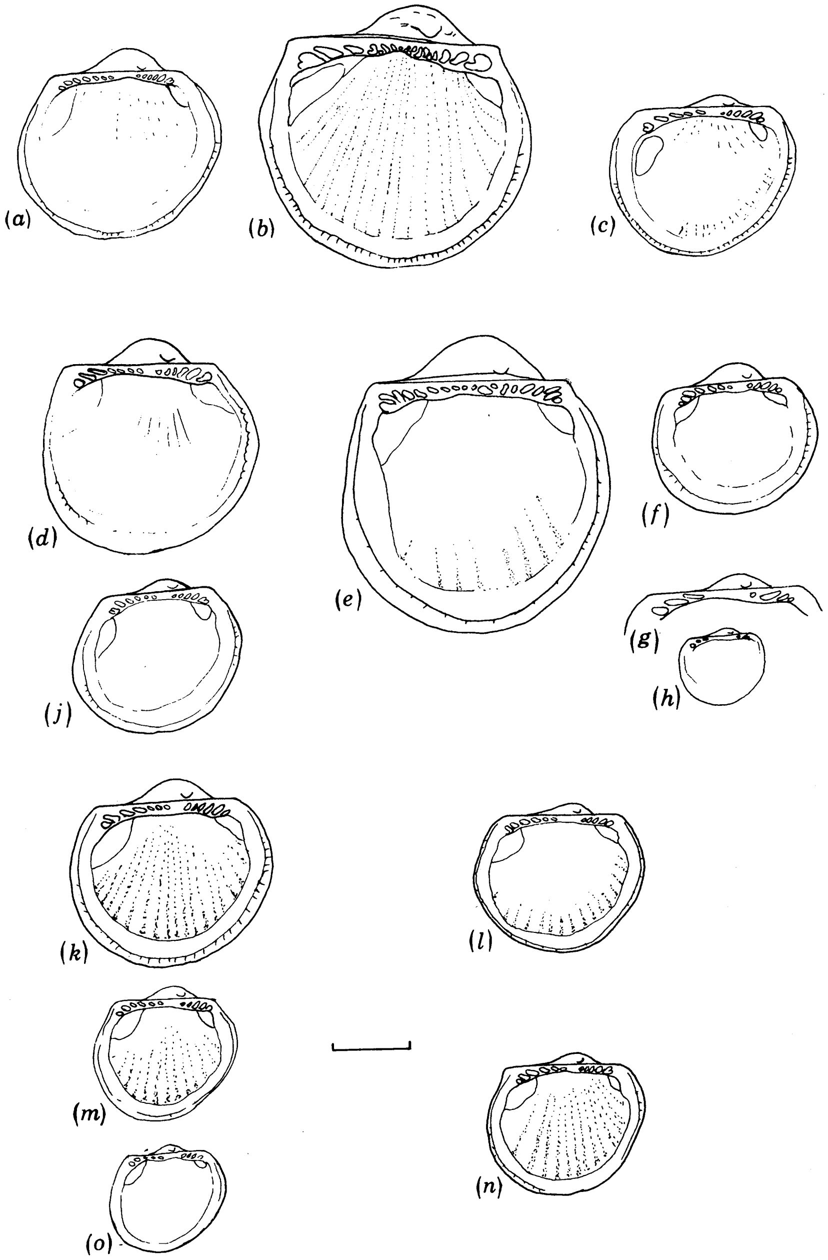

Figure 12. *Bathyarca inaequisculpta*. Internal views of the valves of shells taken from various localities in the Atlantic; (*a*) *Vema*, sta. 14, 30° S 13° E; (*b*), (*c*) *Atlantis II*, sta. 197, 10° S 10° E; (*d*), (*j*) *Atlantis*, sta. 144, 10° N 17° W; (*e*), (*f*), (*g*) (*h*) *Knorr*, sta. 12° N 58° W; (*k*), (*m*), (*o*) *Chain*, sta. 85, 38° N 70° W; (*l*), *Chain*, sta. 323, 15° N, 15° W, (*n*) *Charcot*, sta. DS 79, 46° N 5° W. Scale bar, 2 mm.

N.W. Atlantic specimens. Not exceeding 5 mm, less tumid, thin-shelled, not becoming higher than long, hinge and teeth weak, edentulous space at all sizes. Internal striations faint. (Figure 12.)

The mantle possesses few gland cells, in particular the large red-staining cells are sparse. In whole mounts the mantle flap gland is hardly visible but in section it shows as a small round area with increased numbers of gland cells that are not raised by underlying connective tissues. The mantle flaps are very large when contracted, approximately one-half of the length of the animal.

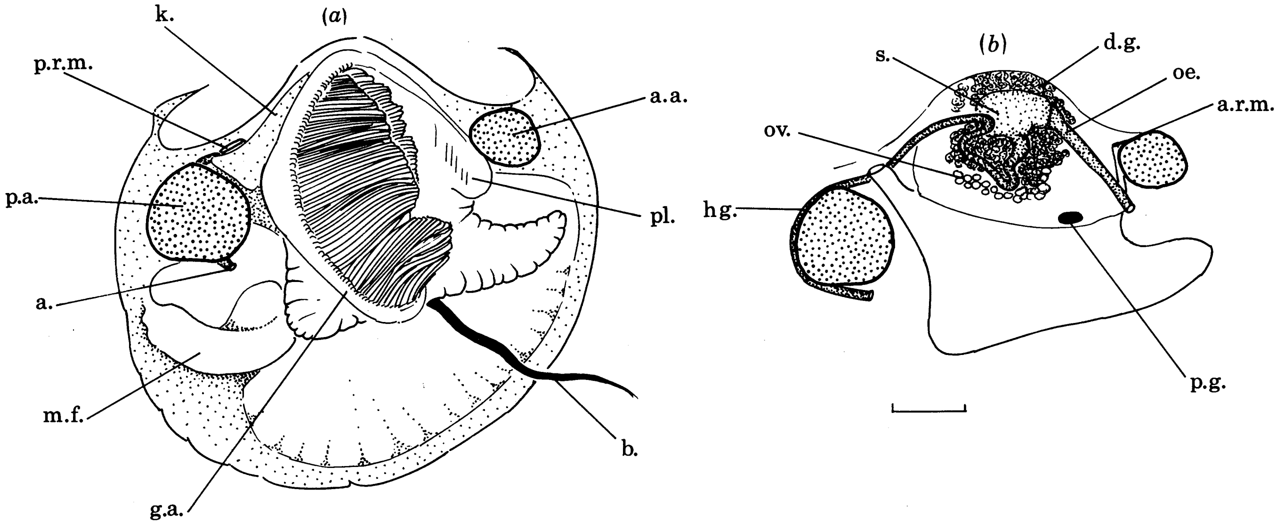

Figure 13. *Bathyarca inaequisculpta*. Anatomy as seen from the right side. In (*b*) the gill and part of the body wall have been removed to show the course of the gut and the extent of the associated tissues. For explanation of abbreviations used see list at end of following paper. Scale bar, 1 mm.

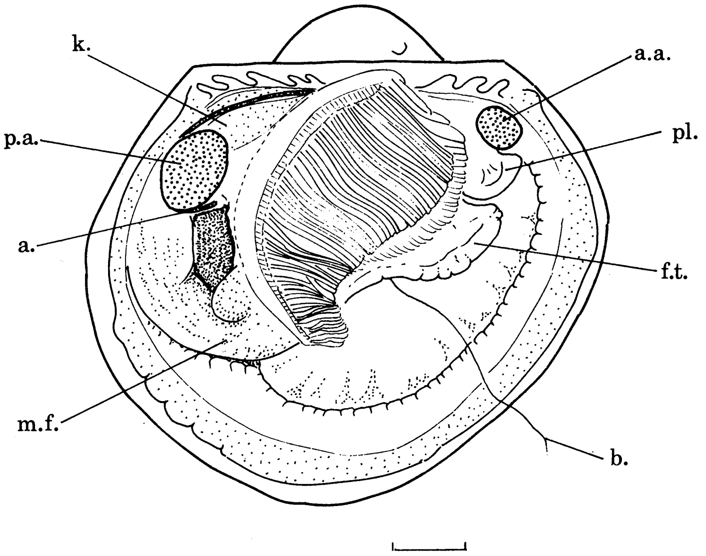

Figure 14. *Bathyarca inaequisculpta*. Anatomy of a specimen from *Vema* sta. 14 as seen from the right side. For explanation of abbreviations used see list at end of following paper. Scale bar, 1 mm.

The gill axis is more muscular than in *B. pectunculoides* and the gills are larger. The filaments in preserved specimens are highly contorted and folded over each other (figure 13). The palps have 2–4 ridges, which are hardly visible.

The gross structure of the gut is similar to that of the other species. The gonads are small and more or less restricted to the lateral pouches. The eggs are large (of 130 μm diameter in alcohol), and only a few are seen in any one individual. The sexes are separate.

The kidneys, typical of abyssal species, are large and without convolutions of the inner epithelium.

The byssus glands are small, with corresponding increase in the musculature of the toe. The byssus retractor muscles are also reduced in size. The byssus consists of 2–4 long fine threads with split ends.

B. inaequisculpta is confined to abyssal oozes and is probably endobyssate (figure 17). Fine byssus threads are typical of such a habit, as too is the rotund shape. The muscular toe will function both in digging and extending the byssus far into the ooze; however, this species does not bury itself completely as there is usually some epifauna on the posterior portion of the shell.

(*b*) *Bathyarca corpulenta* Smith 1885 (figures 15–17)

Type. *Arca* (*Barbatia*) *corpulenta* Smith. Location: British Museum (Natural History).

Type locality. Various (Pacific Ocean) (see Stevenson 1972).

Synonymy.

1885	*Arca* (*Barbatia*) *corpulenta*	Smith (p. 263; fig. 5a–b, pl. 17)
1908	*Bathyarca nucleator*	Dall (p. 397; fig. 9, pl. 18)
1908	*Bathyarca corpulenta* var. pompholyx	Dall (p. 398)
1970	*Bathyarca orbiculata*	Knudsen (p. 76, parts)

No specimens of this species are present in Atlantic samples and those described here were kindly donated by Dr J. Knudsen from the University Museum of Copenhagen.

ship	date	station no.	latitude	longitude	depth/m	number of specimens
Galathea	24.02.52	663	36° 31.0′ S	178° 38.0′ W	4410	2

Distribution. This species has been recorded from a few widely scattered localities through the Pacific Ocean from abyssal depths.

Knudsen (1970) synonymized the majority of Pacific and Atlantic abyssal species of *Bathyarca* under *B. orbiculata* Dall 1881 (see p. 56). Among the material donated by Dr Knudsen was a single specimen labelled *B. orbiculata* from the South Atlantic (Vema st. 14) and this is conspecific with *B. inaequisculpta* (figure 14). The large Pacific specimens differ from the Atlantic specimens of *B. inaequisculpta* in a number of significant features: the shell is equivalve with equal sculpture on the valves; the internal margin is smooth; the valves are thin and the hinge weak with few teeth; the periostraceal bristles are much longer and coarser; the mantle flaps are relatively much smaller; the gill axis is broader; the kidneys are relatively much larger with a conspicuous pericardial gland; the attachment of the posterior pedal retractors is very small.

B. corpulenta is of considerable interest in that it reaches a large size (25 mm).

Shell extremely inflated, equivalve, much higher than long, obliquely oval, inequilateral, curving anterior and ventral margins and somewhat straighter posterior margin; dorsal margin straight with slightly projecting ends; dorsal area narrow, ligament very weak; umbos very prominent; sculpture finely decussate and equal on both valves; periostracum, straw-coloured and drawn into long coarse hairs retained only at margins; hinge plate, very narrow with few weak teeth; teeth set obliquely at end of hinge, with long edentulous space; inner shell margins entirely smooth.

The most noticeable feature of the anatomy (figure 16) is the small size of the visceral mass compared to the volume of the shell. The major part of the mantle cavity is not filled, the viscera being confined to the space between the umbos. A similar situation was recorded for

Limopsis tenella (Oliver & Allen 1980) and *Dacrydium* spp. (J. A. Allen, personal observation) but *B. corpulenta* is even more extreme.

The mantle flaps are relatively small, about one-eighth of the length of the animal, but remain muscular. The mantle flap glands are visible only in one specimen and are very small. They were seen only in section, reflecting the paucity of glandular cells in the mantle as a whole.

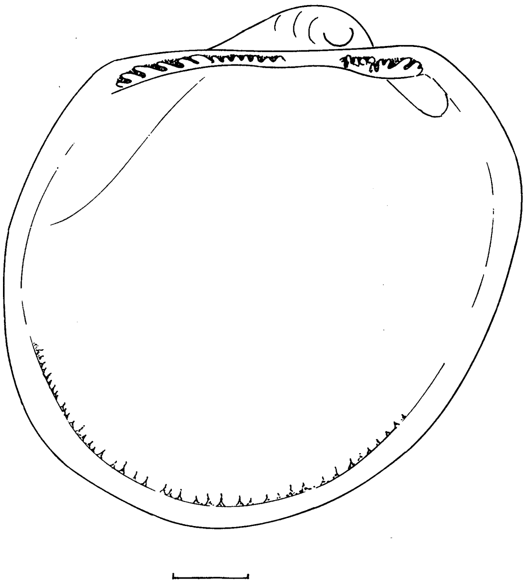

Figure 15. *Bathyarca corpulenta*. Internal view of the left valve. Scale bar, 2 mm.

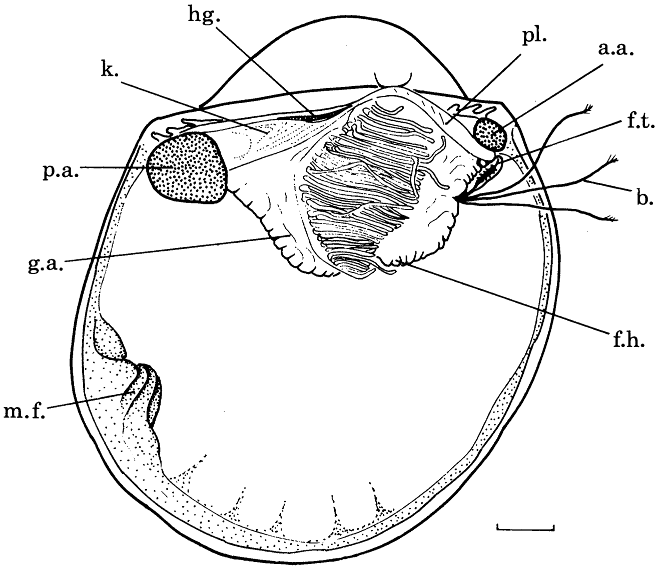

Figure 16. *Bathyarca corpulenta*. Anatomy as seen from the right side. For explanation of abbreviations used see list at end of following paper. Scale bar, 2 mm.

The gills are very ragged and the filaments tangled with each other. It is difficult to assess their size, but as the gill axis is large and muscular it is assumed that the gills would be extensive when expanded. The palps are poorly developed and traces of only four outer palp ridges were seen.

The structure of the gut is similar to that of the other species. The kidneys are very big, consisting of two large flat sacs extending from the posterior adductor muscle to the digestive gland. The extensive pericardium is brown, suggesting that a pericardial gland is present (White 1942).

The foot is small and blade-like, without a projecting heel but with a well developed toe. The byssus gland is functional, with a long fine four- or five-stranded byssus. The ventral edge of the foot lies parallel to the anterior shell margin and this is where the byssus emerges.

The gonads are small and poorly developed. Knudsen (1970) records an egg size of 190 μm.

B. corpulenta has only been collected from abyssal oozes. The inflated rounded shell and the type of byssus suggest that this species is endobyssate. The observations by Knudsen (1970) on the presence of epifauna on the posterior portion of the shell suggest that it lies half buried in the sediment and is anchored by the byssus (figure 17).

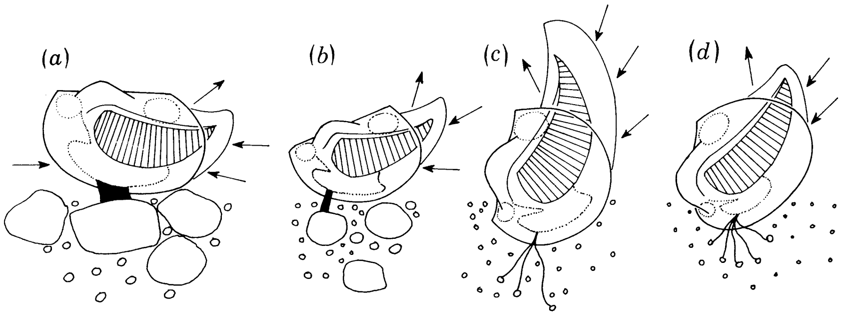

FIGURE 17. Attitude in life of (*b*) *Bathyarca pectunculoides* and suggested attitudes of three other species of *Bathyarca*, (*a*) *B. glacialis*, (*c*) *B. inaequisculpta*, (*d*) *B. corpulenta*, viewed with sediments to bottom of figures.

BENTHARCA THIELE 1931

The genus *Bentharca* was originally created to separate the abyssal species *Bathyarca asperula* Dall from other species of the genus. The reasons for doing so were entirely correct, *B. asperula* having a trapezoidal shell unlike the rounded shells of *Bathyarca*. *Bentharca* has arcinid affinities; Knudsen (1967), realizing the affinity, synonymized *Bentharca* with *Acar*. While the similarities are considerable, from re-examination of species of both genera it is concluded, on the grounds of differences in shell morphology, internal organs and geographical distribution, that *Bentharca* is a distinct genus. Thus, species of *Acar*, e.g. *A. gradata*, have a very narrow dorsal area and a strong decussate sculpture; the oesophagus has lateral pouches (Heath 1941). *Acar* is distributed in shallow tropical and subtropical seas. In contrast, *Bentharca* has a wide dorsal area and a sculpture predominantly of concentric lamellae cut by radial lines. The oesophagus has no lateral pouches.

Bentharca is a cold-water genus†. Although systematic descriptions are adequate for all the species and Knudsen (1967, 1970) gives some additional details about the morphology of *B. asperula*, as with *Bathyarca* very little is known about the morphology of the genus.

Bentharca nodulosa (Müller 1776) (figures 18–21)

Type. *Arca nodulosa* Müller 1776. Location?

Type locality. ?

Synonymy.

1776	*Arca nodulosa*	Müller (p. 247)
1878	*Arca nodulosa*	Sars (p. 42; fig. 3*a–c*, pl. 4)
1879	*Arca nodulosa*	Jeffreys (p. 570)

Station data.

region	ship	date	station no.	latitude	longitude	depth/m	number of specimens
	Discovery	18.06.68	6709	27° 29.8′ N	15° 20.1′ W	2351	1
		19.03.68	6710	27° 23.6′ N	15° 39.6′ W	2670	1
			6711	27° 14.9′ N	15° 36.3′ W	2938	8

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† An examination of the literature and the collections of the British Museum (Natural History) and Royal Scottish Museum has yielded two other species that should be placed in *Bentharca*, namely *Arca* (*Acar*) *nodulosa* Müller and *Bentharca xenophoricola* Kuroda. Both are temperate boreal species.

region	ship	date	station no.	latitude	longitude	depth/m	number of specimens
Bay of Biscay	*Sarsia*	24.07.67	61	46° 20.5′ N	04° 36.0′ W	952	25
	Thalassa	22.10.73	Z397	47° 33.8′ N	07° 12.6′ W	511	15
			Z399	47° 34.8′ N	07° 18.1′ W	825	2
			Z402	47° 39.5′ N	07° 28.5′ W	450	2
	Thalassa	24.10.73	Z413	48° 03.0′ N	08° 29.4′ W	805	123
			Z414	48° 05.0′ N	08° 29.8′ W	650	18
			Z417	48° 12.0′ N	09° 09.5′ W	865	5
			Z421	48° 22.5′ N	09° 33.5′ W	950	6
		25.10.73	Z431	48° 38.2′ N	09° 47.3′ W	800	23
			Z435	48° 39.7′ N	09° 53.2′ W	1050	73

Distribution. This species is recorded from the northeast Atlantic from Norway to Portugal and south to the Canaries and the Azores. It has a wide depth range, from the sublittoral to the abyss (20 m–4134 m) (Clarke 1962).

B. nodulosa is a species variable in both shape (figure 18) and sculpture and this variability is probably related to the nestling habit. The majority of specimens are trapezoidal, inequilateral, equivalve and not inflated. However, large specimens tend to lose the neat angular outline and become rounded and distorted. The anterior part of the shell is reduced and the posterior is expanded. In well formed individuals there are two lateral carinae, one small and anterior, the other much larger and posterior. Between them there is a byssal notch in the form of a shallow groove; however, the ventral margin is more or less straight. The anterior margin is curved whereas the posterior and dorsal margins are elongate and more or less straight. The dorsal area is long, rhomboidal and flat, but expands with age. Sculpture is concentric and except in the smallest specimens forms low frilled ridges, which become more noticeable with age. Undulations in the ridges occur at regular intervals, giving an overall radial appearance to the sculpture. Very large specimens may become worn and lose their sculpture. The periostracum is thin, very pale and bears fine hairs. Internally the shell is white with prominent, unequal

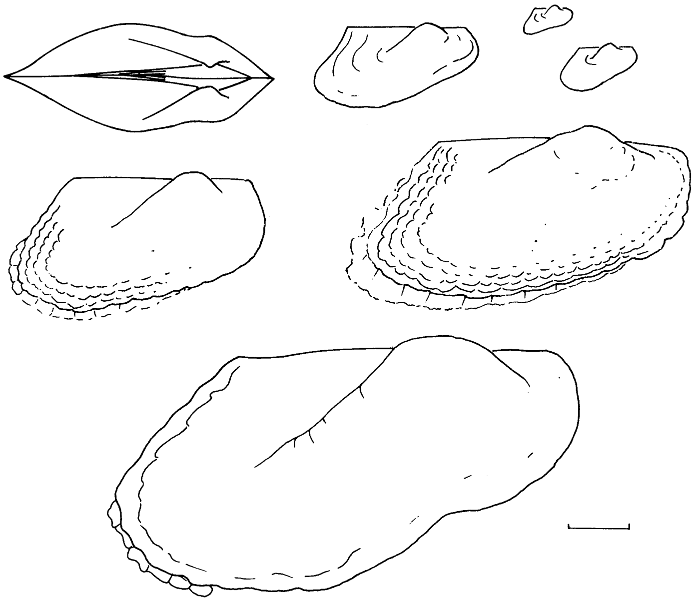

FIGURE 18. *Bentharca nodulosa*. Lateral view of the right valves of a size series of shells. Scale bar, 2 mm.

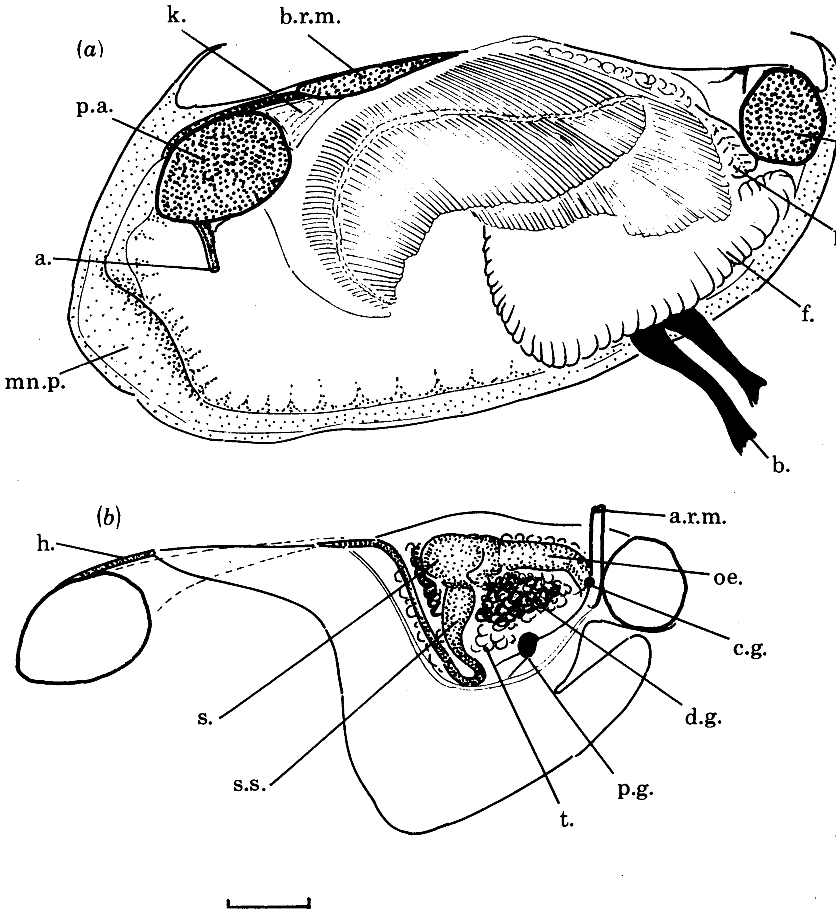

FIGURE 19

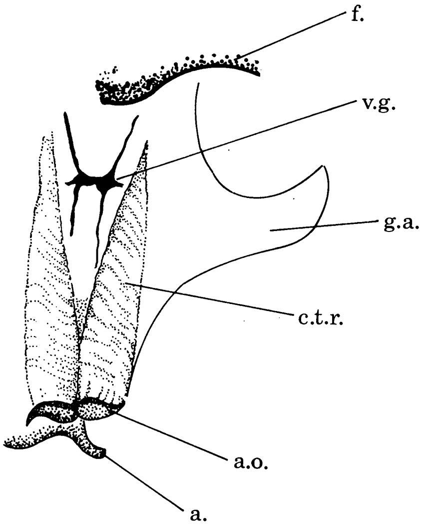

FIGURE 20

FIGURE 19. *Bentharca nodulosa.* Anatomy as seen from the right side. In the lower figure the gill and part of the body wall have been removed to show the course of the gut and the extent of the associated tissues. For explanation of abbreviations used see list at end of following paper. Scale bar, 1 mm.

FIGURE 20. *Bentharca nodulosa.* Detail of the postero-dorsal region of the body, looking down on the ventral wall of the kidney. For explanation of abbreviations used see list at end of following paper.

muscle scars. The hinge is long and narrow, with a continuous set of teeth, of which those central are small and set vertically while those lateral increase in size and are set obliquely.

Except at the posterior ventral margin, where the muscular fold is enlarged, the folds of the mantle edge are simple. At the edge of the middle fold there is a frill that is dotted with pigmented areas more or less confined to the anterior and posterior margins (figure 19). In section the pigment appears as accumulations of black granules within the normal epithelial cells. Although they may represent degenerate eye spots it is more probable that they are accumulations of waste products. The mantle epithelium is moderately thick, with few gland cells. There is a diffuse glandular area between gill axis and foot. Posteriorly this area is raised as a pair of ridges that form a funnel-shaped groove running from the foot to the anus (figure 20). The gland cells stain red in azan and are similar to those described for *Bathyarca glacialis.* The mucoproteins produced by these glands probably aid in the removal of pseudofaeces, the ridges funnelling particles into the exhalent stream.

The gills are flat and homorhabdic, ciliary junctions being restricted to the tips of the filaments and points of reflexion. There is no morphological evidence to suggest that the ciliary currents differ from those of *Arca tetragona* (Atkins 1936). The gill axis is muscular. The palps are small and bear six or seven well defined ridges.

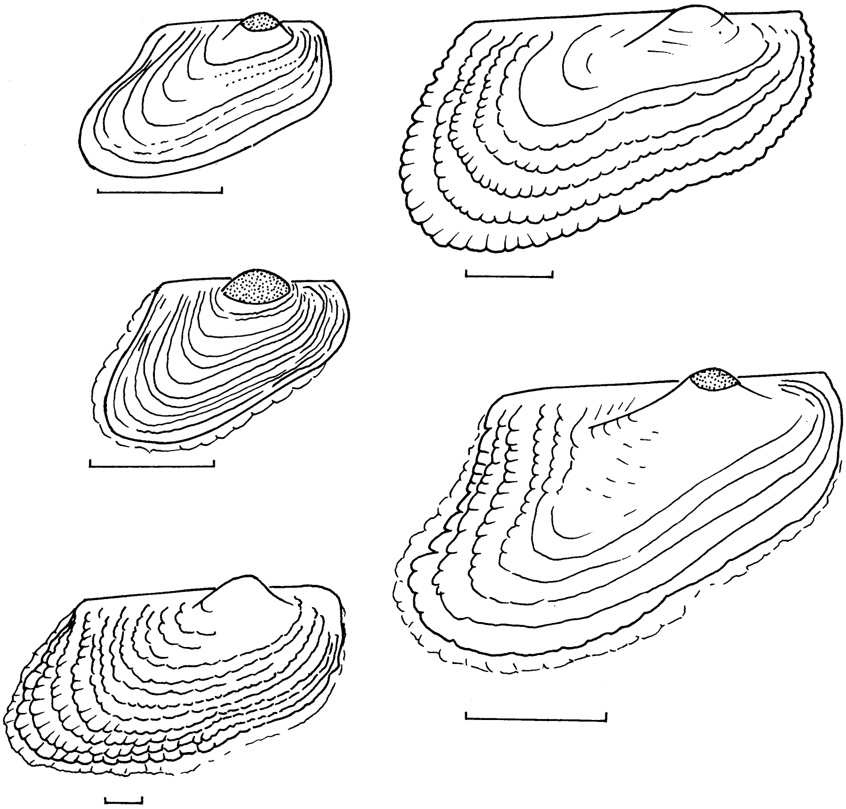

FIGURE 21. *Bentharca nodulosa.* Lateral view of the right valves to show variation in the prodissoconch. Each scale bar, 1 mm.

The gut, reproductive, renal and nervous systems are similar to those described previously for *Bathyarca* and require no further description (figure 19).

The foot, byssus and associated musculature are typical of a nestling species. There is a short toe with a byssus slit; the heel is almost non-existent. The posterior byssus retractor has a large attachment to the dorsal part of the shell. The byssus gland is large and fills a major proportion of the central part of the foot. The byssus is secreted around a number of finger-like processes of the byssus stalk and takes the form of a stout sheath. Relatively, the byssus is not as large as that of *Arca* and *Acar*.

The recorded habitats range from muddy gravel to deep-water coral. The majority of the Biscay samples were taken from coral debris.

The trapezoidal form and the strong byssus are indicative of an epibyssate habit.

No detailed study of reproduction was made but measurements of prodissoconch size are unusual. The Biscay samples give two widely separated measurements for larval shells (175 and 350 μm). Prodissoconch measurements relate to the first larval shell in each instance. Specimens from individual stations are consistent in their measurements but no bathymetric or geographical trend is apparent. The possibility of two species being present was considered but examination of the animals shows that this is not so (figure 21) and suggests either that there are populations of *B. nodulosa* that have lecithotrophic development and others that have direct development or that the planktonic stage varies in time. No similar observations have been made for other deep-sea arcids.

Bentharca asperula (Dall 1881) (figures 22–24)

Type. *Macrodon asperula* Dall 1881. Location: United States National Museum.

Type locality. Off S.E. United States, Blake station 33, 2857 m.

Synonymy.

1881	*Macrodon asperula*	Dall (p. 120)
1885	*Arca profundicola*	Verrill and Smith, Verrill (pp. 439 and 44; fig. 23)
1885	*Arca (Barbatia) pteroessa*	Smith (p. 262; fig. 4, pl. 17)
1898	*Bathyarca profundicola*	Verrill & Bush (p. 844; fig. 2, pl. 78)
1931	*Arca (Acar) profundicola*	Thiele & Jaeckel (p. 20)
1935	*Acar (Bentharca) asperula*	Thiele (p. 793)
1967	*Acar asperula*	Knudsen (p. 258; figs 9, 10, 11, 12)
1970	*Acar asperula*	Knudsen (p. 73; figs 4–6, pl. 7; figs 1–10, pl. 8)

Station data.

region	ship	cruise no.	date	station no.	latitude	longitude	depth/m	number of specimens
			28.06.60	5	32° 11.4′ N	64° 41.6′ W	2000	1
			04.09.61	7	32° 15.0′ N	64° 32.6′ W	2500	2
	Atlantis	1277	27.05.62	2	33° 57.0′ N	65° 02.2′ W	4667	1
	Atlantis II	12	23.08.64	70	36° 23.0′ N	67° 58.0′ W	4680	30
	Chain	50	02.07.65	80	34° 49.8′ N	66° 34.0′ W	4970	1
			04.07.65	84	36° 24.4′ N	67° 56.0′ W	4749	177
	Chain	17	13.12.65	92	36° 20.0′ N	67° 56.0′ W	4694	31
			14.12.65	93	34° 39.0′ N	66° 26.0′ W	5007	2
	Atlantis II	24	19.08.66	119	32° 15.8′ N	64° 31.6′ W	2095–2223	70
			24.08.66	126	39° 37.0′ N	66° 47.0′ W	3806	504
Dakar–Recife	*Atlantis II*	31	13.02.67	155	00° 03.0′ S	27° 48.0′ W	3730–3783	1
			14.02.67	156	00° 46.0′ S	29° 28.0′ W	3459	4
southwest Africa	*Atlantis II*	42	19.05.68	194	14° 40.0′ S 10° 29.0′ S	09° 54.0′ E 09° 03.0′ E	3797	22
			21.05.68	196	10° 29.0′ S	09° 04.0′ E	4612–4630	9
				197	10° 29.0′ S	09° 04.0′ E	3865–4595	5
				198	10° 24.0′ S 09° 47.0′ S	09° 09.0′ E 10° 29.0′ E	4559–4566	4
	Walda	71		CY12	14° 31.8′ S	09° 46.0′ E	3975	106
				DS17	09° 12.0′ S	10° 29.0′ E	4223	3
				DS18	06° 37.4′ S	08° 18.2′ E	4079	1
				DS23	00° 15.3′ S	05° 47.8′ E	3138	2

Distribution. *B. asperula* has been recorded from all oceans except the Arctic and Antarctic. Bathymetrically it has a wide range (430–5007 m) (Knudsen 1970).

Description. Good descriptions of the shell are given by Knudsen (1967, 1970). *B. asperula* differs from *B. nodulosa* in that it is slightly smaller, has reduced carination and is broader relative to its length (figure 23). In small specimens the sculpture of the two species is very similar, but *B. asperula* has decussate sculpture, of which the radial component is dominant, especially on the posterior part of the shell. The periostracum also differs and here, particularly in the larger specimens, takes the form of a thatch of stiff hairs. The variation in the shape and sculpture noted by Knudsen (1967, 1970) is confirmed.

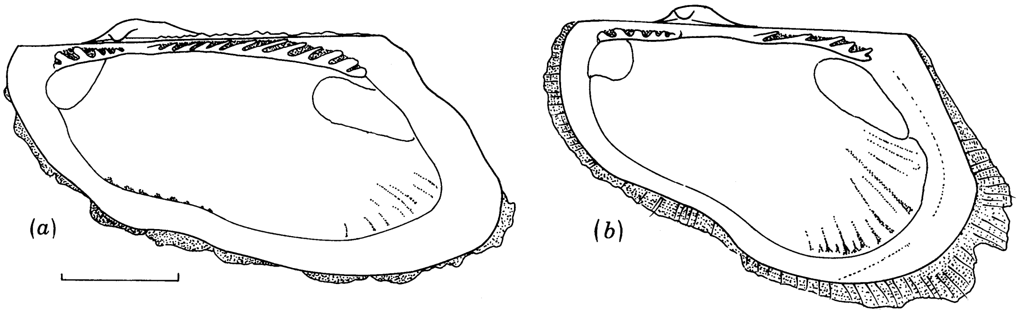

FIGURE 22. Internal view of the right valves of (*a*) *Bentharca nodulosa* and (*b*) *B. asperula*. Scale bar, 2 mm.

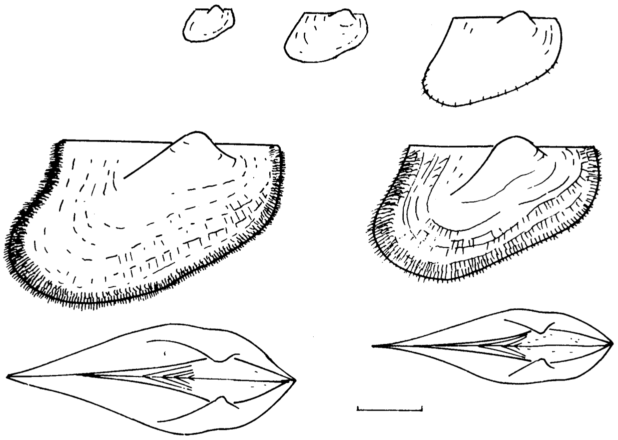

FIGURE 23. *Bentharca asperula*. Lateral view of the right valves of a size series of shells. Scale bar, 2 mm.

The two species of *Bentharca* are also very similar in their anatomy. The mantle edge of *B. asperula* is without pigment spots but it is thickened posteriorly (figure 24). The glandular area described for *B. nodulosa* are absent, as are the associated ridges. The kidneys show the typical abyssal adaptation of being simpler and larger than those in *B. nodulosa* from shallower depths. The gonads are relatively small, never being observed to cover the dorsal area of the body. The eggs are large (150 μm), but unlike with the previous species no variation in egg or prodissoconch size (225 μm) was noted. The byssus is smaller in *B. asperula* and this is reflected in the size of the glands and in the smaller size of the byssus retractor muscles (figure 28).

In some samples small specimens are attached to very small particles, such as pteropod shells or inorganic particles.

The two species are very similar and have similar habits. Perhaps the most remarkable feature is the presence of an epibyssate arcid on the abyssal plain. It is probable that the tranquil conditions of the deep sea are essential for the survival of *B. asperula*.

Of the differences that occur between the two species, those relating to the reduction of gland cells, the stomach, the simplification of kidney structure and the reduction in the size of the gonad have already been discussed under *Bathyarca*.

Measurement of interumbonal distance relative to total shell length shows a great difference between *B. asperula* and *B. nodulosa* (figure 25). The shells of *B. asperula* increase in width exponentially whereas those of *B. nodulosa* increase linearly. The much greater width of *B. asperula* can

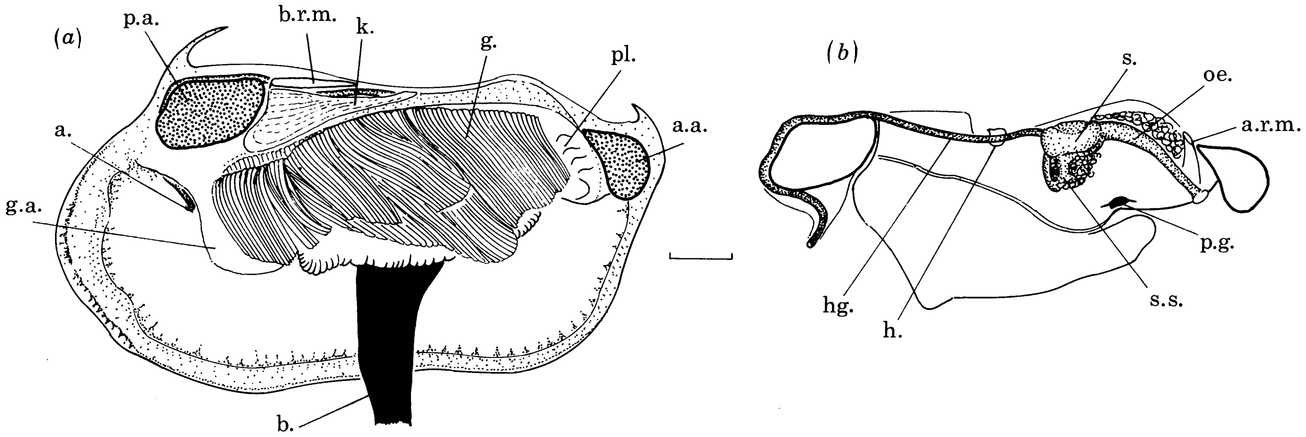

FIGURE 24. *Bentharca asperula*. Anatomy as seen from the right side. In (*b*) the gill and part of the body wall have been removed to show the course of the gut and the extent of the associated tissues. For explanation of abbreviations used see list at end of following paper. Scale bar, 1 mm.

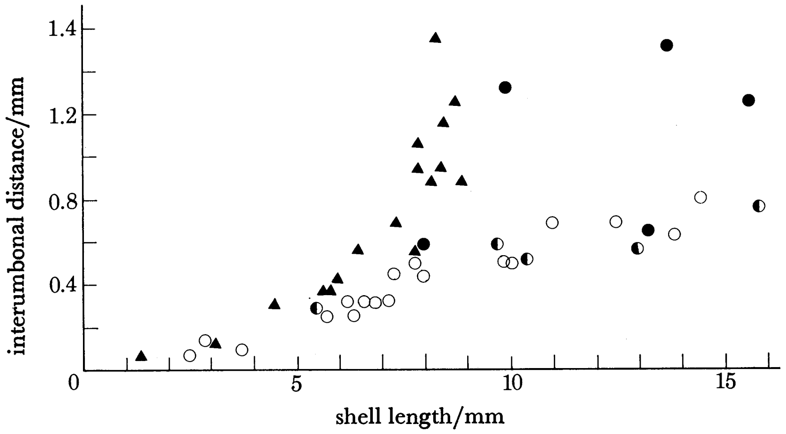

FIGURE 25. Comparison of the interumbonal distance: shell length ratios of a population of *Bentharca asperula* and three populations of *B. nodulosa*; ▲ *B. asperula*, sta. 126, 3806 m; ○ *B. nodulosa*, sta. Z435, 1050 m; ◐ *B. nodulosa*, sta. 156, 952 m; ● *B. nodulosa*, 6711, 2938 m.

be associated with the need to prevent sinking into the soft oozes. Of interest are the measurements of *B. nodulosa* from abyssal depths (*Discovery*, sta. 6711). The four specimens lie intermediate between *B. asperula* and *B. nodulosa* from typical depths. This implies that substrate may have a direct effect on growth form. A similar situation was reported for *Limopsis pelagica* (Oliver & Allen 1980), where it was proposed that disproportionate increases in width reflect great age and slow growth.

DISCUSSION

There are a number of differences in morphology between the species of *Bathyarca*. Four are interrelated in varying degree, namely, shell shape, byssus, mantle flap and the glandular nature of the mantle.

species	shape, *H*/*L*†	byssus	flap	mantle gland
B. glacialis	1/1.5	sheet	small	xxx
B. pectunculoides	1/1.35	stalk	medium	xx
B. inaequisculpta	1/1.11	threads	large	x
B. corpulenta	1/0.89	threads	small	x

† Height/length.

The shape of the shell is related to the mode of life i.e. either an endo- or epibyssate existence (figure 17). Observations by Stanley (1970) on H/L ratios for the Arcacea as a whole (figure 26) demonstrated that if the ratio was less than 1/1.35 then the species was endobyssate and, if more, epibyssate. The values for *Bathyarca* species shown above, together with assumptions made from morphologies and observations on living *B. pectunculoides*, agree with Stanley (1970). It also appears that the changing shape is related to increasing depth; however, if species other than those listed above are considered, it is found that there are exceptions. Thus *B. glomerula* is endobyssate but it is not abyssal; however, it is recorded from fine mud and ooze. As might be expected, shape is related to sediment type.

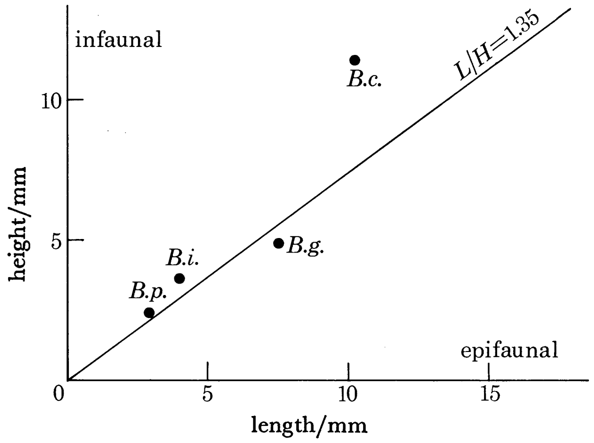

FIGURE 26. Length: height ratios of four species of *Bathyarca* (after Stanley (1970)). *B.c.*, *B. corpulenta*; *B.g.*, *B glacialis*; *B.i.*, *B. inaequisculpta*; *B.p.*, *B. pectunculoides*.

The form of the byssus in this genus is also indicative of the mode of life.

Observations on living *B. pectunculoides* show the mantle flaps to have at least two functions. They carry pseudofaeces away from the mantle cavity and the protect the gills. The size of the flaps is related to the size of the gill and the trend of increasing flap size from *B. glacialis* to *B. pectunculoides* to *B. inaequisculpta* is probably related to the decreasing food availability with depth. *B. corpulenta*, an abyssal species with a relatively very small flap, would appear to contradict this. This species has a low biomass to volume ratio; however, the gill is not reduced relative to a small body and the result in the food-catching capacity is functionally similar to an increase in gill size in other species (*Limopsis* spp. Oliver & Allen).

The number of mantle flap glands is related to the removal of unwanted matter. There is a general decrease in glandular tissue with depth and it must be concluded that bathyal and abyssal species have a lower intake of unwanted particles, which is presumably related to the decreasing amount of suspended matter with increasing depth. With the increasing development of the endobyssate habit the inhalent aperture becomes restricted to the posterior area, with the result that less surface sediment is taken into the mantle cavity. Abyssal species may do less sorting of particles and this is reflected not only in the lack of glandular tissue but also in the reduced number of palp ridges and the simplification of the stomach with depth. Few stomach contents have been observed in abyssal species. The only structure that remains prominent is the gastric shield, which may be necessary for the breakdown of large particles.

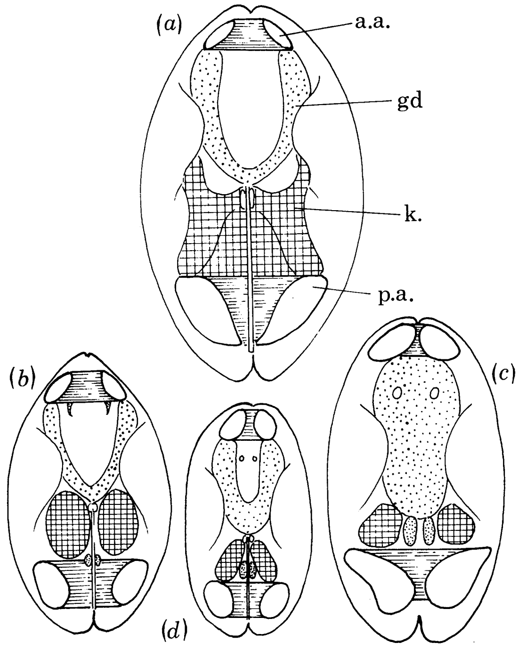

FIGURE 27. Diagrammatic comparison of the anatomy of *Bathyarca* as seen dorsally. (*a*) *B. corpulenta*; (*b*) *B. inaequiesculpta*; (*c*) *B. glacialis*; (*d*) *B. pectunculoides*. For explanation of abbreviations used see list at end of following paper.

There is a trend for increasing kidney size (figure 27) with depth, and a decrease in the convolutions of the inner epithelium. This is most noticeable in the largest species *B. corpulenta*.

There is no correlation between shell thickness and depth between species. The thinnest-shelled species is bathyal (*B.p. pellucida*) and the thickest abyssal (*B. inaequisculpta*), but within the latter species there is great variation of shell thickness from different areas but there is no evidence of depth-related variations.

It appears that *Bentharca* species show little gross adaptive change, possibly because of their unchanging habits. Such small differences that do occur are indicative of the low energy availability of the deep sea.

The deep-sea arcoids are relatively few in number and the reasons for this are probably related less to their suspension feeding habit as suggested by Knudsen (1970) than to their evolutionary history and the adaptive constraints on the group. The Arcoidea primarily evolved as a shallow warm-water epibyssate or semi-infaunal group and their spread to the deep sea involved major morphological and physiological changes. It is significant that all the deep-sea species are related to the few cold-water genera of arcoids, species display equatorial submergence and points to the likely origin of the deep-sea arcoids. The presence of but a single epibyssate species in the deep sea is a reflection of the inability of the group as a whole to invade this environment. Thomas (1976) argues (and probably over emphasizes) that the inability of the arcoids to radiate into a broader set of habits is due primarily to the restrictive qualities of the duplivincular ligament. Other suspension-feeding groups without such restrictions (e.g. Pectinacea) are more numerous in the deep sea.

In general the form of the deep-sea species is related to the sediment and habit and not to the

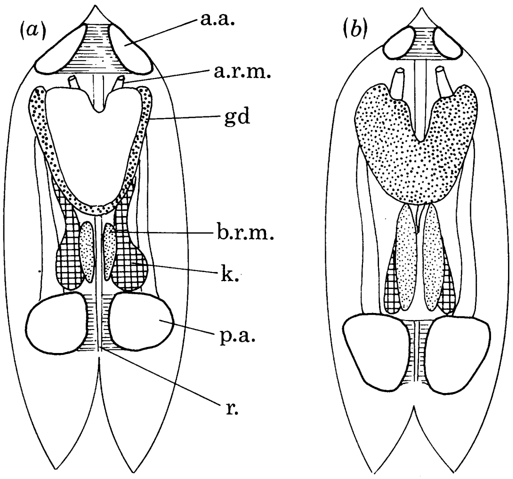

FIGURE 28. Diagrammatic comparison of the anatomy as seen dorsally of (*a*) *B. asperula* and (*b*) *Bentharca nodulosa* For explanation of abbreviations used, see list at end of following paper.

depth. The lack of similar forms in shelf sediments is probably associated with their inability to compete with more recently evolved infaunal species.

In general, deep-sea bivalves are small and thin-shelled (Allen 1979), but this is not entirely true of the Arcoidea. While the deep-sea species are smaller than their shallow-water relatives they are much bigger than deep-sea bivalves in general. Although thick-shelled arcoids, notably *Limopsis galathea* and *B. inaequisculpta*, occur in the abyss, other non-burrowing groups do not retain a thick shell. It seems probable that the thick shell is an evolutionary legacy.

General conclusions on other morphological adaptations can best be made with reference to figure 29. It is assumed that with increasing depth there is a marked decrease in energy supply and there is evidence to confirm this (Allen & Sanders 1966, 1973; Allen & Turner 1974; Sanders & Allen 1973).

Growth and reproduction as shown by the arcids and limopsids (Oliver & Allen 1980) are similar to those found by Turekian *et al.* (1975) and by Scheltema (1972) for other groups. Reduced levels are probably of general occurrence in non-opportunistic species (Turner 1973) of deep-sea bivalves.

Adaptations to low energy availability are somewhat different to those shown by protobranchs (Allen & Sanders 1973; Sanders & Allen 1973) or *Abra profundorum* (Allen & Sanders 1966). This is consistent with the different feeding habits of the species concerned. Thus the protobranchs are deposit feeders and as a consequence exhibit reduction of the gill and extension of the hindgut, the former possibly in part due to the non-active role of the gill in food collecting and sorting, the latter to the need to increase time in order to process large volumes of sediment and digest the small quantities of refractory organic matter present in it. Suspension-feeding arcoids ingest a smaller volume of food but one that is less refractory. The gills are the main food-collecting organs in lamellibranch suspension feeders; here they are not reduced but are even enlarged. An extended hindgut is unnecessary. Reduction in glandular tissue of the abyssal arcaceans, simplification of the gill of *L. galathea*, reduction in the number of palp ridges, and the sorting areas of the stomach all point to loss of selectivity and ingestion of all filtered particles. The lack of mantle glandular tissue reflects the general lack of suspended

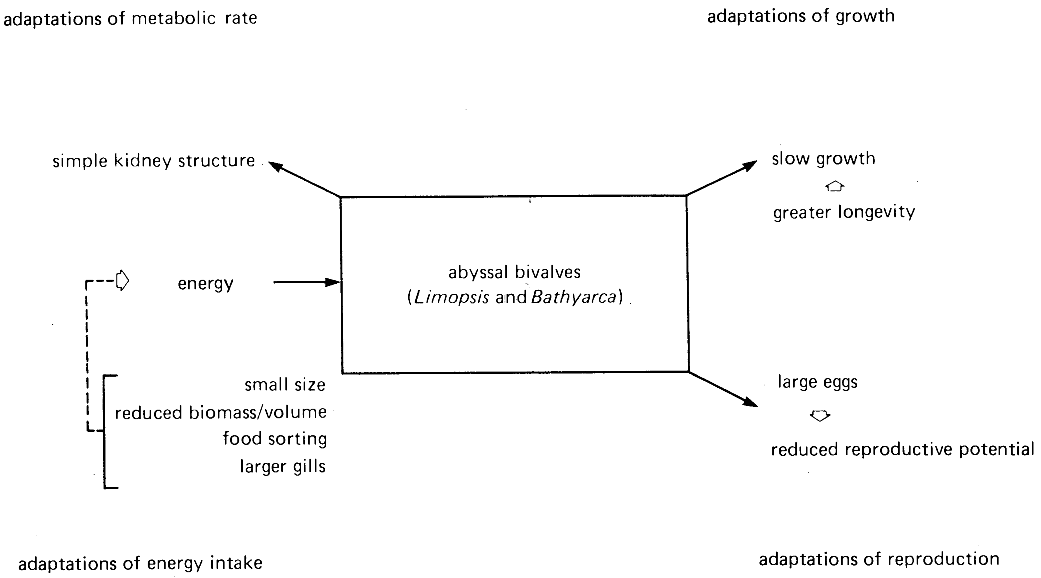

Figure 29. Adaptations in relation to reduced available energy as exhibited by *Limopsis* and *Bathyarca*.

particles in the abyss. The reduction in the biomass: volume ratio is but another sign of the low quantity of available food.

Reduction in metabolic rate cannot be conclusively proven but evidence of slow growth, reduced reproductive potential and modification of the kidney makes it a reasonable assumption.

The adaptations shown by deep-sea arcoids therefore fall into two groups: (*a*) those related to sediment and habit; and (*b*) those related to the energy budget of the species. Major adaptations to counter the possible refractive nature of organic material are few in comparison with those shown by deposit-feeding bivalves. While this may be in part due to the severe limitations posed by suspension feeding in the deep sea it is also in part due to the conservative nature of the arcoid form.

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

References

Allen, J. A. 1979 The adaptations and radiation of deep sea bivalves. *Sarsia* **64**, 19–27.

Allen, J. A. & Sanders, H. L. 1966 Adaptations to abyssal life as shown by the bivalve *Abra profundorum* (Smith). *Deep Sea Res.* **13**, 1175–1184.

Allen, J. A. & Sanders, H. L. 1973 Studies on deep sea Protobranchia. The families Siliculidae and Lametilidae. *Bull. Mus. comp. Zool. Harv.* **145**, 263–310.

Allen, J. A. & Turner, J. F. 1974 On the functional morphology of the family Verticordiidae (Bivalvia) with descriptions of new species from the abyssal Atlantic. *Phil. Trans. R. Soc. Lond.* B **268**, 401–536.

Atkins, D. 1936 On the ciliary mechanisms and interrelationships of Lamellibranchs. Part I. New observations on sorting mechanisms. *Q. Jl microsc. Sci.* **79**, 181–308.

Clarke, A. H. 1962 Annotated list and bibliography of the abyssal marine molluscs of the world. *Bull. natn. Mus. Can.* **181**, 1–114.

Dall, W. H. 1881 Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea, 1877–79, by the U.S. Coast Survey Steamer, '*Blake*'. XV. Preliminary report on the Mollusca. *Bull. Mus. comp. Zool. Harv.* **9**, 33–144.

Dall, W. H. 1908 The Mollusca and the Brachiopoda. Reports on the dredging operations off the west coast of central America by the U.S. Fish Commission Steamer '*Albatross*'. *Bull. Mus. comp. Zool. Harv.* **43**, 205–487.

Dautzenberg, Ph. 1927 Mollusques provenant des campagnes scientifiques du Prince Albert ler de Monaco dans l'Océan Atlantique et dans le Golfe de Gascogne. *Résult. Camp. scient. Prince Albert I* **72**, 1–400.

Dinamani, P. 1967 Variation in the stomach structure of the Bivalvia. *Malacologia* **5** (2), 225–268.

Gray, J. E. 1824 In *Journal of a voyage for the discovery of a north west passage, 1819–20 in H.M.S. 'Hecla' and 'Griper'* (ed. W. E. Parry). A supplement to the appendix, ccvi–ccxiv. London.

Heath, H. 1941 The anatomy of the pelecypod family Arcidae. *Trans. Am. phil. Soc.* (N.S.) **31**, 287–319.

Jeffreys, J. C. 1863–69 *British conchology*. London: Van Vorst.

Jeffreys, J. G. 1868 Reports on dredging. *Ann. Mag. nat. Hist.* (4), **2**, 448–449.

Jeffreys, J. G. 1879 On the Mollusca procured during the 'Lightning' and 'Porcupine' expeditions 1869–1870. Part II. *Proc. zool. Soc. Lond.*, pp. 553–588.

Jorgensen, C. B. 1966 *Biology of suspension feeding*. London: Pergamon.

Knudsen, J. 1967 The deep sea Bivalvia. *Scient. Rep. John Murray Exped.* **11**, 235–343.

Knudsen, J. 1970 The systematics and biology of abyssal and hadal bivalvia. '*Galathea*' *Rep.* **11**, 7–241.

Kobelt, L. 1891 In *Systematisches conchylien–Cabinet*, vol. 8 (ed. F. H. W. Martini & J. H. Chemnitz), pt 2, pp. 137–238. Nürnberg.

Locard, A. 1898 Mollusques testacés. *Expéditions scientifiques du Travailleur et du Talisman*, vol. 2. Paris: Masson.

Melvill, J. C. & Standen, R. 1907 The marine Mollusca of the Scottish national Antarctic expedition. I. *Trans. R. Soc. Edinb.* **46**, 119–157.

Muller, O. F. 1776 *Zoologiae Danicae Prodromus, seu animalium Daniae et Norvegiae indigenarium characteres, nomina et synonyma*. Hafniae.

Newell, N. D. 1969 In *Treatise on invertebrate paleontology* (ed. R. C. Moore), pt N (Mollusca 6: Bivalvia), vol. 1, pp. N205–N224. Kansas: Geological Society of America and University of Kansas.

Ockelmann, K. W. 1958 Marine Lamellibranchiata. In Zoology of east Greenland. *Meddr Grønland* **122**, 1–256.

Oliver, G. & Allen, J. A. 1980 The functional and adaptive morphology of the deep sea species of the family Limopsidae (Bivalvia: Arcoida) from the Atlantic. *Phil. Trans. R. Soc. Lond.* B **291**, 77–125.

Pelseneer, P. 1911 Les lamellibranches de l'expedition du Siboga. Partie anatomique. *Siboga Exped.* **71**, 1–125.

Purchon, R. D. 1957 The stomach in the Filibranchia and Pseudolamellibranchia. *Proc. zool. Soc. Lond.* **129**, 27–60.

Sanders, H. L. & Allen, J. A. 1973 Studies on the deep sea Protobranchia (Bivalvia). Prologue and the Pristiglomidae. *Bull. Mus. comp. Zool. Harv.* **145**, 237–262.

Sars, G. O. 1878 Bidrag til kundskaben om Norges arktiske fauna. *Mollusca regionis arcticae Norvegiae*, vol. 1. Christiana: A. W. Brogger.

Scacchi, A. 1834 Notizie intorno alle conchiglie ed a zoofiti fossili. Annali Civili (Sicilie) (Nov.–Dec. 1834), no. 6, 75–84.

Sheldon, P. G. 1916 Atlantic slope Arcas. *Palaeontogr. am.* **1**, 1–104.

Scheltema, R. S. 1972 Reproduction and dispersal of bottom dwelling deep sea invertebrates. A speculative summary. In *Barobiology and the experimental biology of the deep sea* (ed. R. W. Brauer), pp. 58–66. Chapel Hill: University of N. Carolina.

Smith, E. A. 1885 Report on the Lamellibranchiata collected by *H.M.S. Challenger* during the years 1873–76. *Rep. scient. Res.* '*Challenger*' **13**, 1–341.

Stanley, S. M. 1970 The relation of shell form to life habits of the Bivalvia. *Mem. Geol. Soc. Am.*, no. 125.

Stevenson, S. E. 1972 Arcacea (Mollusca: Bivalvia). Types in the British Museum (Natural History). *Bull. Br. Mus. nat. Hist.* D **24**, 195–204.

Tebble, N. 1966 *British bivalve seashells*. Edinburgh: H.M.S.O.

Thiele, J. 1935 Classis Bivalvia. *Handbuch der systematischen weichtierkunde*, vol. 2. Jena: von Gustav Fischer.

Thiele, J. & Jaeckel, S. 1931 Muscheln der Deutschen Tiefsee-Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped.* '*Valdivia*' **21**, 1–110.

Thomas, R. D. K. 1975 Functional morphology, ecology, and evolutionary conservatism in the Glycymerididae (Bivalvia). *Palaeontology* **18**, 217–254.

Thomas, R. D. K. 1976 Constraints of ligament growth form and function on evolution in the Arcoida (Mollusca: Bivalvia). *Paleobiology* **2**, 64–83.

Turekian, K. K., Cochran, J. K., Kharkar, D. P., Cerrato, R. M., Vaisnys, J. R., Sanders, H. L., Grassle, J. F. & Allen, J. A. 1975 The slow growth rate of a deep sea clam determined by ^{228}Ra chronology. *Proc. natn. Acad. Sci. U.S.A.* **72**, 2829–2832.

Turner, R. D. 1973 Wood-boring bivalves, opportunistic species in the deep sea. *Science, N.Y.* **180**, 1377–1379.

Verrill, A. D. 1885 Third catalogue of Mollusca recently added to the fauna of the New England coast. Consisting mostly of deep sea species with notes on other species previously recorded. *Trans. Conn. Acad. Arts Sci.* **6**, 395–452.

Verrill, A. D. & Bush, K. J. 1898 Revision of deep water Mollusca of the Atlantic coast of North America with descriptions of new genera and species. Part 1. Bivalvia. *Proc. U.S. natn. Mus.* **20**, 777–901.

White, K. M. 1942 The pericardial cavity and the pericardial gland of the Lamellibranchia. *Proc. malac. Soc. Lond.* **25**, 37–88.

Yonge, C. M. 1955 A note on *Arca* (*Senilia*) *senilis* Lamark. *Proc. malac. Soc. Lond.* **31**, 202.