Evolution of the Deep Sea Protobranch Bivalves

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By J. A. Allen

University Marine Biological Station, Millport, Isle of Cumbrae, KA28 0EG, U.K.

The number of protobranch species of the continental shelves of the world comprise between 10 and 15 % of the total number of bivalve species present. This is in contrast to the bivalve fauna of the deep sea which, distant from the lower continental slopes, is dominated by the protobranchs. The protobranchs may comprise more than 70 % of the bivalve species in a sample and more than 95 % of the total number of bivalve specimens present.

The Subclass Protobranchia has one of the longest recorded geological histories and its continuing success, particularly in the deep sea, is probably due to a suite of physiological characters that enable it to utilize a low and refractory food supply at considerable depths and pressures. Probably as a result of the lack of competition from bivalves of more recent origin as well as the long stability of their environment, the deep sea bivalves show a radiation of form and habit that is analogous to that shown by the more recently evolved lamellibranchs of the continental shelf. The study of the bivalve fauna of the deep sea helps in the understanding of the evolution and ecology of the Mollusca of late Cambrian and early Ordovician periods.

Pojeta (1971), in his review of Ordovician Bivalvia, is of the opinion that, while it is reasonable to infer that there must have been Cambrian representatives of the Class, all 17 genera described to that date are suspect for one reason or another. In this category Pojeta (1971) even includes the mid Cambrian genus *Lamellodonta* recently and authoritatively described by Vogel (1962). In marked contrast, bivalves are well represented in the early Ordovician, and Pojeta (1971) believes that by that time six major lineages had been established. Furthermore, most Ordovician bivalves were infaunal suspension or deposit feeders, and many of them were siphonate. Only later, in the middle Ordovician, were epifaunal species common.

The majority of deep sea bivalves (table 1) belong to groups whose ancestry dates back to the Ordovician and the dominant bivalve group of the deep sea, the Subclass Protobranchia are present in the earliest assemblages of the fossil record. They were well represented in the early Ordovician both in numbers and number of species (McAlester 1963, 1968; Pojeta 1971). Until recently most Ordovician protobranchs with chevron-shaped taxodont teeth have been placed in a single family the Ctenodontidae. In none is there clear evidence of a resilifer, the recess or process where the internal ligament joins the shell. In most of these early protobranchs the hinge teeth are a continuous series on the hinge plate without break below the umbo (figures 1 and 2); however, the teeth below the umbo are proportionately smaller than those lateral to them. Pojeta (1971) notes that the evolution of an internal ligament in protobranchs appears to have been a post-Ordovician development. This is not unreasonable for there are *a priori* grounds for believing that the primitive condition is an external ligament possibly, though not conclusively, amphidetic in form (Allen 1960; Yonge 1976).

Other notable points should be stressed. Ordovician protobranchs were a highly varied and successful group: both nuculoid and nuculanoid morphologies were present and existed at the same time. Both types are not only included within the family Ctenodontidae but are also

TABLE 1. THE DISTRIBUTION OF THE MAJOR GROUPS OF THE BIVALVIA IN SHALLOW AND DEEP SEAS OF THE WORLD

(The number of stars gives some indication of the species and numerical dominance of the group (s, g and f represent species, genus and family).)

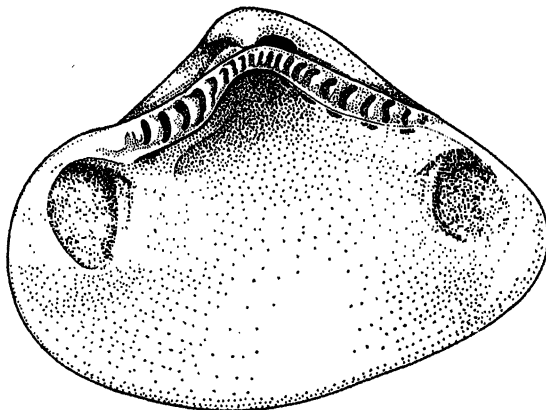|	shelf	slope	abyss
Protobranchia			
Solemyoida	*	*	*
Nuculoida	**	**	**
Nuculanoida	*	*	****
Lamellibranchia			
Arcacea	**	*	*
Limopsidacea	*	*	***
Mytilacea	****	*	* (1g)
Pinnacea	*	—	—
Pectinacea	**	*	**
Pteracea	**	—	—
Limacea	**	*	*
Ostreacea	*	*	—
Astartacea	**	*	—
Glossacea	*	*	* (2g)
Lucinacea	**	*** (1f)	* (1f)
Carditacea	*	—	—
Cardiacea	***	*	—
Galeommatacea	*	*	—
Solenacea	*	—	—
Veneracea	****	*	—
Tellinacea	****	*	* (1g)
Mactracea	***	* (1s)	—
Myacea	***	—	—
Pholadacea	***	*	* (1g)
Anomalodesmacea	***	*	—
Poromyacea	*	*	***

FIGURE 1.

FIGURE 2.

FIGURE 1. Lateral view of the internal structure of the right valve of *Tancredopsis cuneata* (after McAlester 1963). Shell length 17 mm.
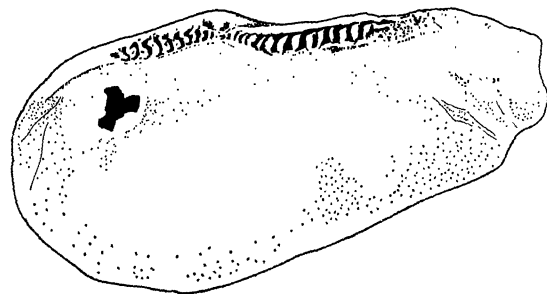
FIGURE 2. Lateral view of the internal structure of the shell of *Ctenodonta nasuta* (after Pojeta 1971). Shell length 70 mm.

included among the 180 recognized species of the genus *Ctenodonta* (Pojeta 1971). Both siphonate (figure 2), often with a well marked siphonal embayment, and non-siphonate species were extant in the Early Palaeozoic and the Ctenodontidae are almost certainly not a homogeneous group. This is reflected in the fact that the type genus of the family *Ctenodonta nasuta* (Hall) was originally described under the generic name *Tellinomya* and Pojeta (1971) must be correct when he states that the name *Ctenodonta* should be restricted to shells with the type of morphology hown by this species.

Most biologists with a moderately familiar knowledge of molluscs would recognize most protobranch bivalves immediately from a cursory glance at their external features, yet it is a paradox that the members of the most conservative of the major groups of molluscs have few characters in common. Possibly only two can be named with any certainty. Thus, all species have a foot with a longitudinally divided sole which is fringed with papillae and gill plates with abfrontal cilia. Shell characters such as hinge teeth and crystalline structure, and body structures such as the form of the palps and the digestive tract, all exhibit marked differences of form within the subclass. The reason for the paradox lies in the fact that the characters of the members of each of the major subdivisions are well defined and that most of the recent genera and subgenera are restricted to one of the subdivisions.

The Subclass Protobranchia can be divided primarily into two orders, the Solemyoidea (6 genera and subgenera), members of which have a minute triangular palp, large ctendia with elongate filaments, and an opisthodetic external ligament, and the Nuculoidea (60 genera and subgenera), with large palps with well defined palp proboscides capable of being extended out between the shell valves, and with small ctenidia with short plate-like filaments. The Nuculoidea are further divided into two major superfamilies, the Nuculacea (7 genera and subgenera) and the Nuculanacea (53 genera and subgenera).

The superfamilies can be distinguished by a suite of characters (Sanders & Allen 1973), but essentially the Nuculacea are without a posterior inhalent aperture, the respiratory current entering anteriorly, while the Nuculanacea possess a posterior inhalent siphon or aperture. In an entirely parallel manner to that in the Lamellibranchia, major radiation follows the advent of a posterior inhalent current.

The primitive nature of the protobranchs was first recognized by Pelseneer (1891) and later he recognized the distinctness of the three groups mentioned above (Pelseneer 1899, 1911). This was confirmed by the studies of Yonge (1939) and both he and McAlester (1964) stressed the primary binary branching of the Nuculoidea. It is clear that the protobranchs, if not the earliest, are among the earliest recorded bivalves and were already separated into the three major groups at that time. The geological history of the Solemyoidea is the least well known of the three and will be considered later (p. 399).

Although McAlester (1964) pointed out that the form of the nuculoid ligament, in terms of the balance between internal and external parts, has evolved independently in the Nuculacea and Nuculanacea and is unsatisfactory to use in the basic phylogenetic classification of the group (although it might be a useful phylogenetic indicator in the two major branches), it seems certain that the earliest protobranchs had external ligaments.

All Recent rostrate nuculanoids similar in outline to *Ctenodonta* (*sensu stricta*) have a resilifer, although this may be small and the greater portion of the ligament may be external; furthermore, some (e.g. *Ledella, Tindaria*) have a broad hinge plate that barely narrows below the umbo. In contrast, all known recent nuculoids, triangular–ovate in form, have an internal

ligament which interrupts the anterior and posterior tooth row. Despite this, a broad hinge plate may be present (e.g. *Brevinucula*), reminiscent of an Ordovician nuculoid genus *Similodonta* (Soot-Ryen 1964).

A third shell form exhibited by recent nuculoid protobranchs is an elongate–ovate outline, which might suitably be called 'tindaroid'. This also has an Ordovician counterpart in *Palaeoneilo*. Recent work on the family Tindariidae (Sanders & Allen 1977) has shown striking resemblances
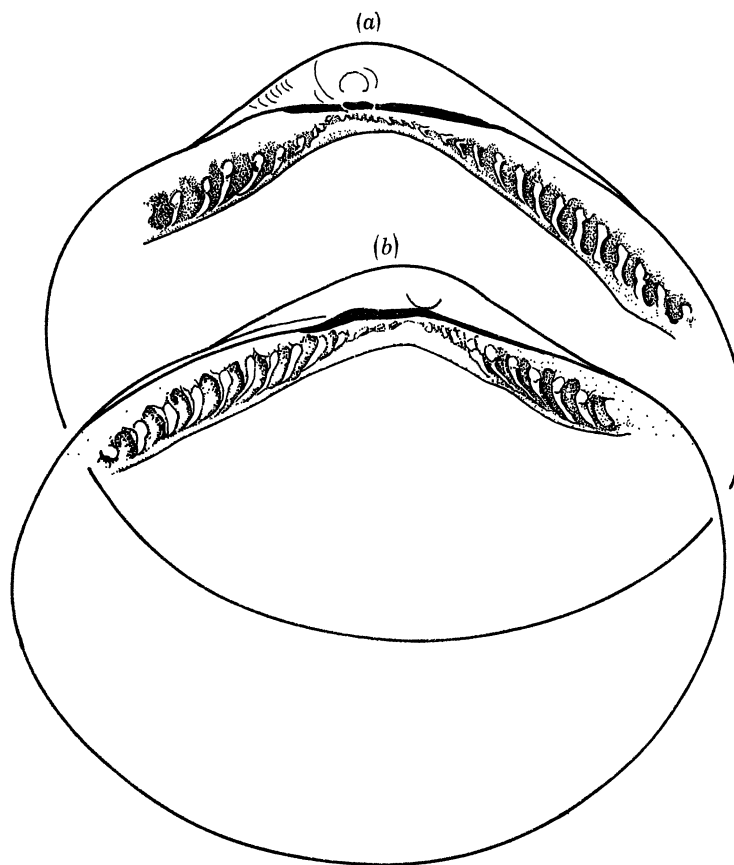

FIGURE 3. (*a*) Lateral view of the internal structure of the right valve of *Tindaria hessleri*. Shell length 5 mm. (*b*) Lateral view of the left valve of *Pseudotindaria erebus*. Shell length 5 mm.

in shell form between the genus *Tindaria* and *Palaeoneilo*, so much so that it would be difficult to separate them on shell characteristics. Thus *T. hessleri* (figure 3*a*) has an external ligament and a broad hinge plate bearing an uninterrupted series of teeth below the umbo. In some species of *Tindaria*, centrally, the inner layer of the ligament barely encroaches the hinge plate dorsal to the hinge teeth. On shell features alone there is no reason to place the genus *Palaeoneilo* in a family separate from that of *Tindaria*. Present evidence shows that, with the exception of nuculacean forms with an external ligament, species of the Ctenodontidae can be encompassed within Recent families. Nevertheless, taxonomic difficulties remain. Examination of the anatomy of Recent species with strikingly similar shell characteristics (figure 3) has shown that the valves may enclose bodies so different in form that there can be no hesitation in distinguishing them as genera belonging to different families. Thus *Tindaria* (*sensu stricta*) of the family Tindariidae and *Pseudotindaria*, probably a member of the family Neilonellidae, impossible to

separate on shell characters, have markedly different anatomies (figures 4 and 5). Thus it is impossible to be certain whether *Palaeoneilo* is related to *Tindaria* or *Pseudotindaria*, and furthermore it could well be that its anatomy was different from either.

Present studies have highlighted a further confusion. Shells of tindariids have been distinguished from those of neilonellids on the belief that all tindariids have a broad hinge plate that remains broad below the umbo while in the neilonellids the hinge plate is broad laterally but narrow below the umbo. This is no longer true: both forms of hinge are found in both families and as an example *T. miniscula* possesses a narrow edentulous region of the hinge plate below the umbo, a condition also seen in *Pseudotindaria championi* (figure 6).
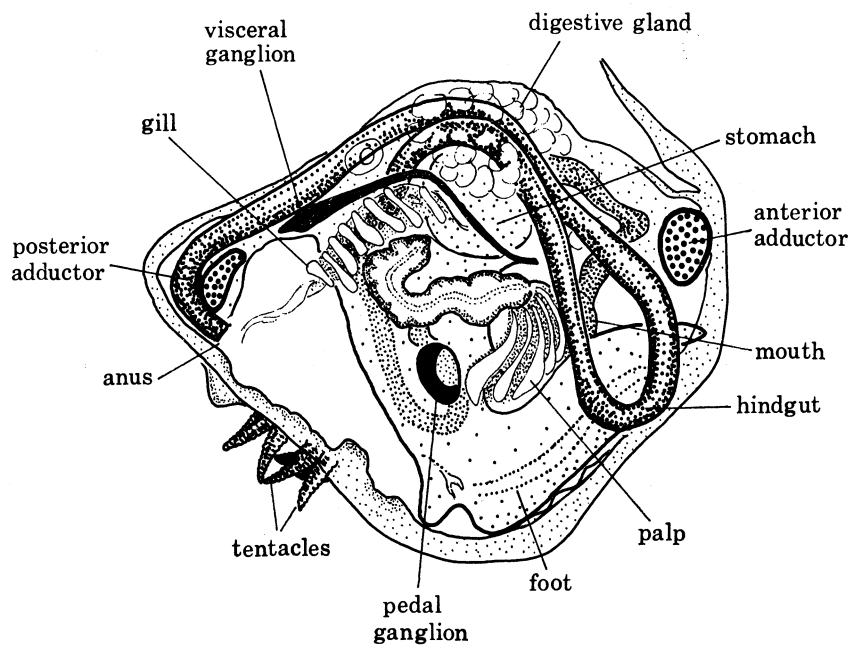

FIGURE 4. Lateral view of the right side of *Tindaria callistiformis* with the shell removed. Shell length 4 mm.
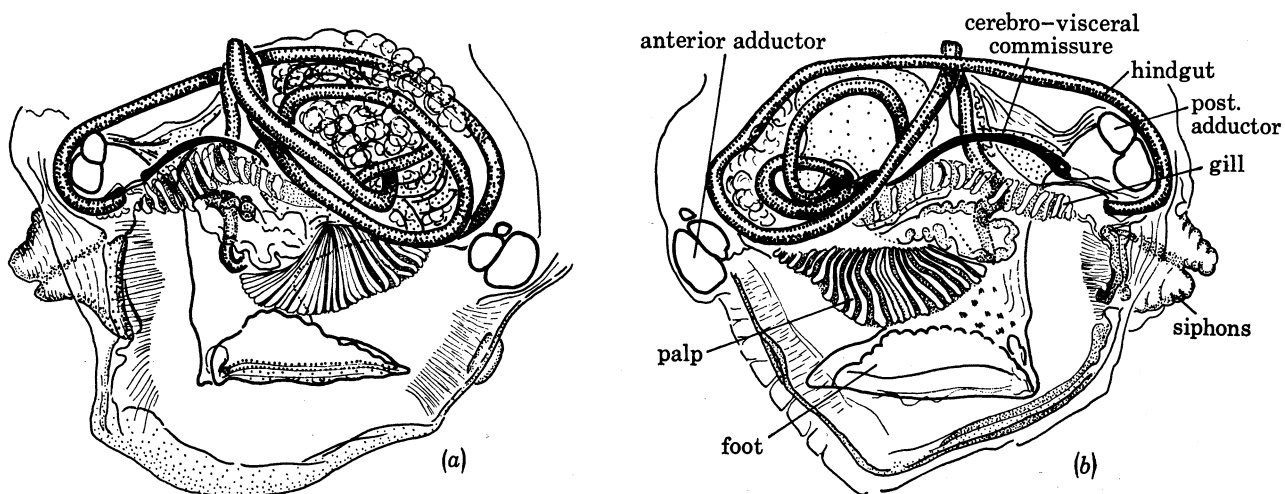

FIGURE 5. Lateral view of the left and right sides of *Pseudotindaria championi* with the shell removed. Shell length 4 mm.

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These observations reflect the overall difficulties of identification of the Protobranchia. The present studies highlight the essential conservativeness of the shell form of the subclass, particularly when it is compared, not with the Subclass Bivalvia as a whole, but with the non-byssate infaunal Eulamellibranchia of soft sediments.
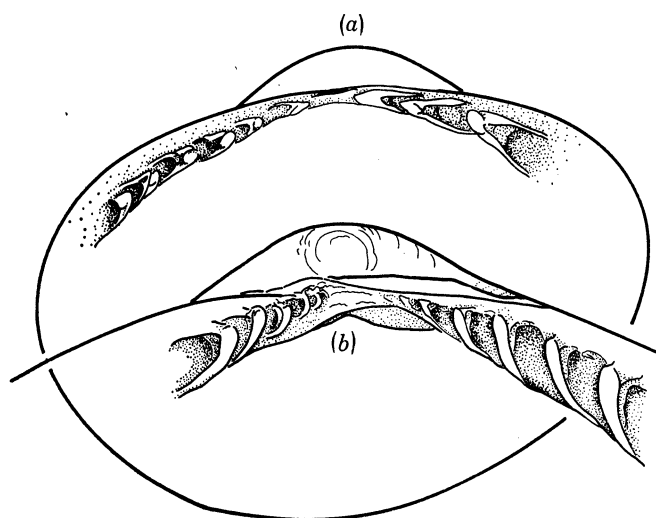

FIGURE 6. (a) Lateral view of the internal structure of the left valve of *Tindaria miniscula*. Shell length 2 mm. (b) Umbonal region of the hinge of the right valve of *Pseudotindaria championi*. Total shell length 4 mm.

TABLE 2. THE DISTRIBUTION OF THE FAMILIES OF THE PROTOBRANCHIA IN SHALLOW AND DEEP SEAS OF THE WORLD

(The number of stars gives some indication of the dominance of the group.)

	shelf	slope	abyss
Solemyoida			
Solemyidae	*	*	*
Nucinellidae	—	*	—
Nuculoida			
Nuculidae	**	**	**
Pristiglomidae	—	*	**
Nuculanoida			
Nuculanidae	*	*	****
Malletiidae	—	—	*
Tindariidae	—	*	*
Ledellidae	—	*	**
Yoldiellidae	—	*	****
Neilonellidae	—	*	***
Siliculidae	—	—	*
Lametilidae	—	—	*

To the casual observer of bivalves of the soft sediments of the continental shelf, the triangular or ovate or ovate–rostrate, solid, non-gaping protobranch shells, covered with a thick olivaceous periostracum and, at most, with simple regular concentric ornamentation, contrasts greatly with the variety of shape, colour and ornamentation of the eulamellibranchs. This marked contrast of form in shallow water species is in part due to the fact that relatively few species of the Protobranchia occur on the continental shelf (table 2) and that these few are restricted

almost entirely to the families Nuculidae and Nuculanidae. The present paucity of species of shallow water protobranchs is without doubt due to the success of more recent infaunal suspension and deposit feeding lamellibranchs. Of those protobranchs that do occur in shallow water, the mobile deposit feeding species of *Nucula* have no counterparts among the Lamellibranchia, and although the dominant and highly successful Tellinacea must compete with the Nuculanidae, their habits and methods by which they select their food are so different that, at least, niche separation can be postulated to account for the coexistence of, say, *Nuculana* and *Abra*.
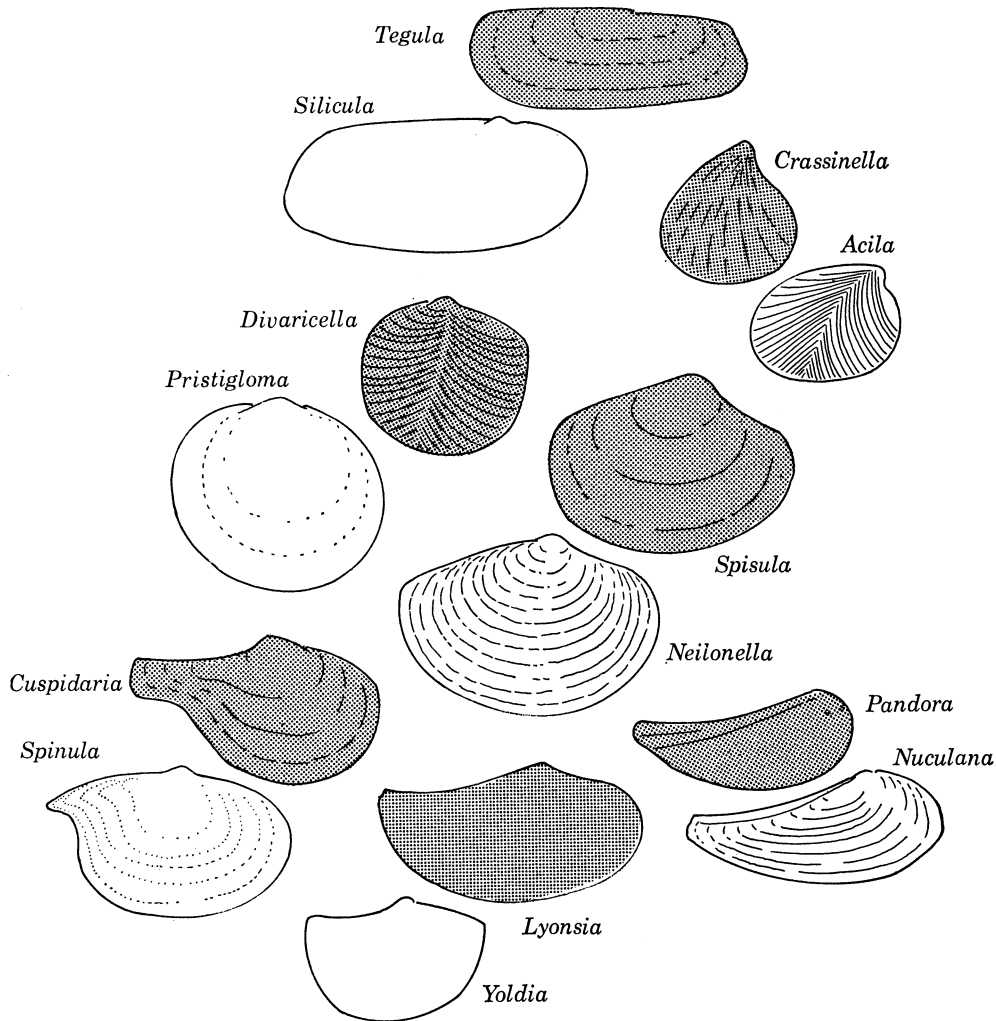
FIGURE 7. Comparison of the shell shapes of various deep-sea protobranchs with shallow water eulamellibranchs (stippled).

With the advent of modern sampling techniques and the change from relatively haphazard sampling to well ordered traverse work in the abyssal basins of the Atlantic and Pacific (Sanders, Hessler & Hampson 1965; Hessler & Jumars 1974) it is now evident from the wealth of specimens that the contrast between protobranchiate and eulamellibranchiate mantle/shell form is no longer so marked. While some of the conservativeness of protobranch shell remains (e.g. olive-yellow colour, lack of extravagant ornamentation) a wide range of protobranch types are evident.

Thus, in addition to *Nucula* and *Nuculana*, there are flattened and inflated, rounded and elongate shells, many rostrate to a varying degree (figure 7), which are the deep sea counterparts of the extremes of form exemplified by the shallow water burrowing eulamellibranch genera *Astarte*, *Gari*, *Cultellus*, *Cardium*, *Lyonsia*, etc. The two groups are in contrast in that suspension feeders dominate the shallow water eulamellibranch fauna while deep sea protobranchs are deposit feeders. Nonetheless, suspension feeding in protobranchs is known to occur and particles filtered by the gill plates are transferred to the palps (Stasek 1961, 1965; personal observations). The siphons of some protobranch species may extend considerably above the level of the benthic boundary, and rostrate shells, reminiscent of *Cuspidaria*, are particularly common and although the siphons do not function in the same manner as the latter genus, the very existence of the rostrum indicates an incurrent at or above the level of the seabed with an inflow of particles additional to any that may be taken in by the palp proboscides.
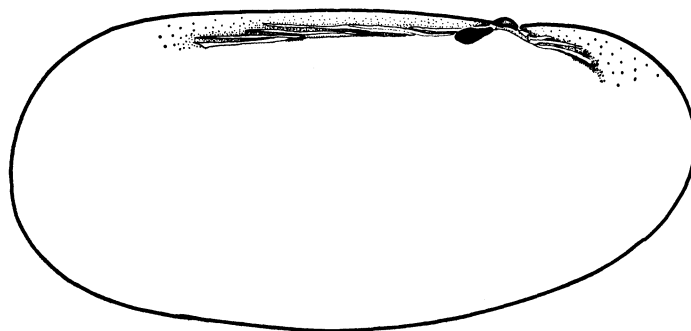

FIGURE 8. Lateral view of the internal structure of the left valve of *Silicula ronchi*. Shell length 16 mm.

To give additional detail of these shell variations: ligaments of protobranchs may be external or internal, elongate or short, amphidetic or opisthodetic; chevron-shaped hinge teeth may be a short or an elongated V and in some genera, such as *Silicula* (figure 8) or *Lametila*, one arm of the elongate V may be lost or almost so and give rise to a series of simple lateral teeth (Allen & Sanders 1973).

Although it is a matter of speculation, evolution of the lateral tooth as distinct from the cardinal may have come about by elongation in this manner, the chevron shape itself evolving from a simple short tooth set transversely to the hinge. Support would seem to come from examination of the condition in *Nucinella* (figure 9) confirmed as a protobranch (Allen & Sanders 1969) (see below and p. 399). Variation in the form of the mantle/shell is reflected in the path taken by the body axes. Primitively the axes lie at right angles to each other, one anterior–posterior the other dorsal–ventral. In elongate forms the dorsal–ventral axis is bent anteriorly in a manner comparable with that in many eulamellibranchs (*Siliqua*) (Yonge 1952; Owen 1959) with similar encroachment on anterior mantle space and reduction in the size of the anterior adductor. The anterior adductor is never lost in protobranchs although in *Nucinella*, a monomyarian, the posterior adductor muscle is lost.

Although suspension feeding occurs, the protobranchs are for the most part deposit feeders living in soft sediments collecting their food by means of the palp proboscides. As a result they have not radiated to quite the same extent as lamellibranchs: there are no wood or rock borers and because of the lack of a solid adhesive byssus thread they have never assumed an epifaunal habit. Analysis of the soft part anatomy of the nuculoid protobranchs shows that with increasing

depth there is a tendency for the number of gill plates to become reduced, for the palps to become enlarged, the stomach mechanisms to become simpler and the hind gut to become greatly lengthened (figure 10). It would appear that oxygen requirements and metabolic processes at high pressures (over Pa (200 atm)) generally are significantly different from those in shallow water. Small gills may be a reflexion of the small quantity of suspended material in deep water. Why the sorting surface of the palp should increase in size when food is scarce might
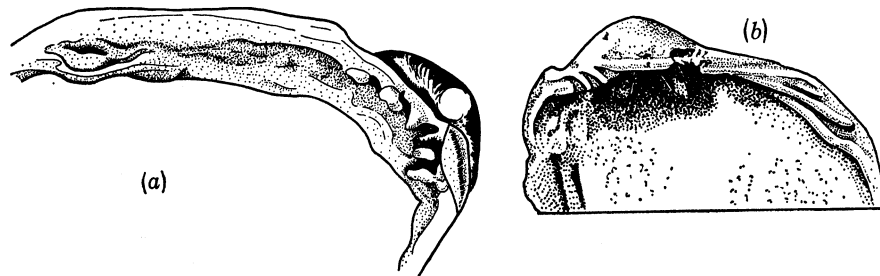

FIGURE 9. (a) Lateral view of the hinge of the right valve of *Nucinella serrei*. Shell length 5 mm. (b) Lateral view of the hinge of the *Cyrtodonta saffordi* (after Pojeta 1971). Shell length 48 mm.
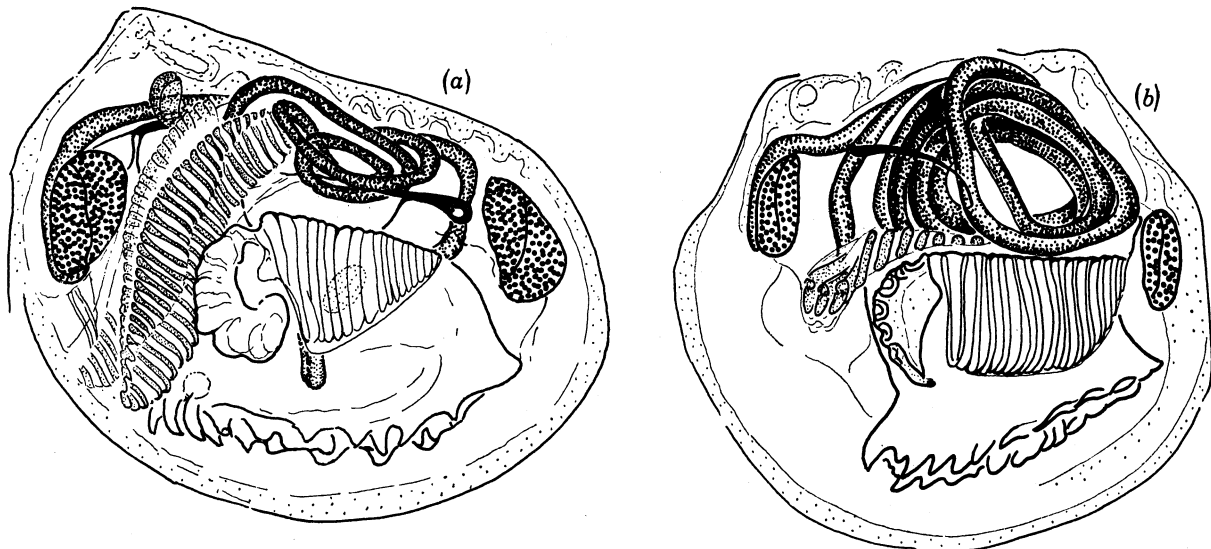

FIGURE 10. Lateral view of the morphology of (a) *Nucula proxima* (Buzzards Bay 10 m) and (b) *Nucula cancellata* (Woods Hole Bermuda traverse 3834 m) drawn from the right side to show differences in the extent of gills, palps and hind-gut.

appear to be a disadvantage and one that is emphasized by the coincident simplification of the ciliary sorting mechanisms of the stomach. Gut contents indicate that particle sizes vary widely and that large and small skeletal remains may be present. For the most part, gut contents differ little from one genus or species to another or from the surface sediments in which the animals live. Only in the case of *Silicula* was any evidence found of selectivity with large loculate foraminiferan tests present in the stomach. The explanation of palp enlargement must lie elsewhere and it would seem to be consequent on gill reduction and that it is of importance that the amount of ciliation within the mantle cavity be maintained.

Major radiation of form of the Nuculanacea has taken place in deep water. Not only is there a great array of mantle/shell variations but also much evolutionary endeavour has been directed

to the disposition of a greatly lengthened hind gut within the confines of a body that is not enlarged in comparison with that of shallow water species. In fact the volume of body to total internal shell volume is much reduced in deep sea bivalves. Three main types of gut configuration can be identified, namely (1) an enlarged single loop to the right hand side (e.g. *Tindaria* figure 4), (2) a loop or loops to the right and left of the body passing from one side to the other behind the stomach (e.g. *Pristigloma*; Sanders & Allen 1973), (3) a multiple coil on the right side (e.g. *Nucula*, figure 10). In addition there are various miscellaneous configurations (e.g. *Lametila*; Allen & Sanders 1973). The three main types are to be found both in the Nuculoidea as well as the Nuculanoidea although usually not all in the same family. For example, all species of the Nuculidae have a loosely coiled hind gut on the right side of the body while the Pristiglomidae have a hind gut that is looped to the right and left of the body.
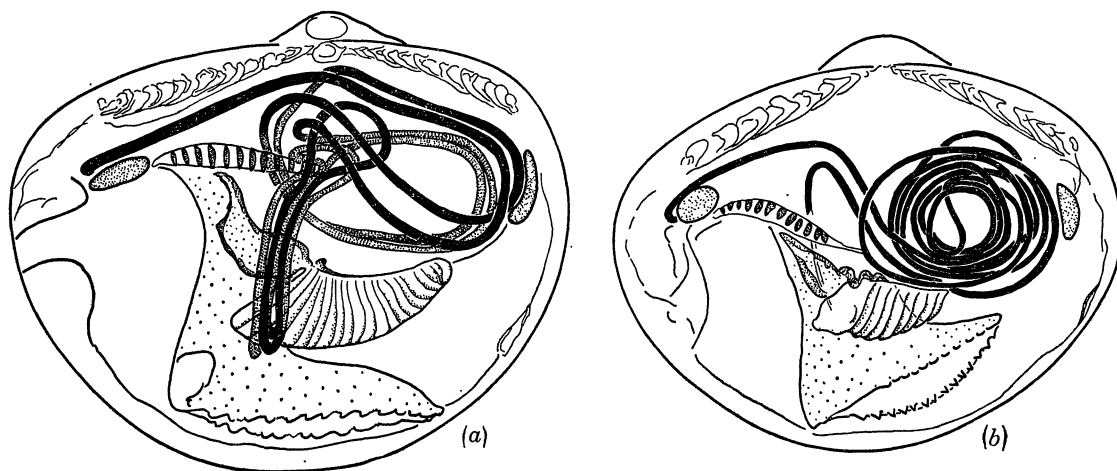

FIGURE 11. Comparison of the hind gut configuration of *Yoldiella* species K and *Yoldiella* species L.

The Nuculanacean families Tindariidae and Malletiidae have retained the primitive condition of a single loop on the right side but in comparison with the similar condition in the shallow water species of *Nuculana*, the loop is much enlarged, so much so that anteriorly it abuts the anterior adductor, displacing the mouth posteriorly. In some species of *Tindaria*, part of the body containing the hind gut penetrates the mantle haemocoele to a position close to the inner mantle fold of the mantle margin near the anterior sense organ; in addition the diameter of the lumen is much enlarged and a typhlosole is present.

At no time does a large hind gut chamber form by the coalescence of the tightly packed loops as it does in the one truly abyssal species of the deposit feeding tellinacean lamellibranchs, *Abra profundorum* (Allen & Sanders 1966), nor does the faecal material ever become constricted into pellets; it always remains a continuous and compact rod. There is no evidence of bacterial activity in the gut of the deep sea protobranchs.

Most variation in the form of the hind gut is found in the large and complex family Yoldiellidae. Members of this family are extremely difficult to identify from external shell features, and differences between both genera and species are subtle. In many cases, species of *Yoldiella* can only be identified by differences in the path taken by the hind gut. With one specific exception (*Yoldiella curta*), these differences have been found to be constant. Nevertheless, in some deep-water species of *Yoldiella*, hind-gut configuration can be related to the shape of the
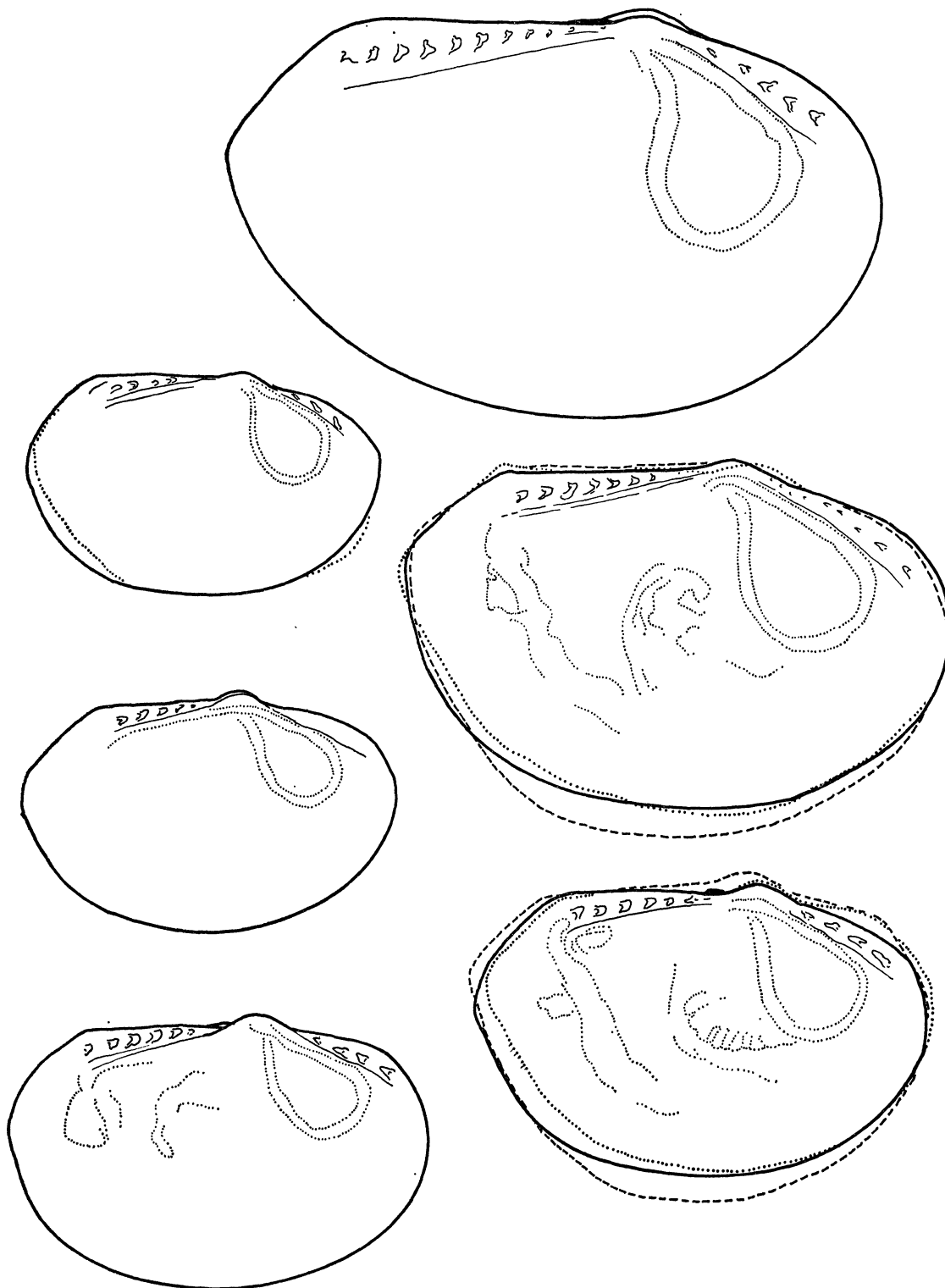
FIGURE 12. Lateral views of the shell outlines of specimens of *Malletia cuneata* from different localities in the Atlantic.

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enclosing mantle/shell. In a species of *Yoldiella* at present designated *Yoldiella* sp. K† which has a deep shell and an elongate foot, advantage is taken of this and the two loops of the hind gut pass deep into the extended neck of the foot, while in a species designated *Yoldiella* sp. L, with an inflated shell, the hind gut forms a complete coil on the right side of the body which displaces other parts of the viscera, notably the stomach and digestive gland, to the left (figure 11).

Radiation of deep-water protobranch species appears to be influenced by at least two major selection pressures. One is what might be regarded as the normal radiation of bivalve body form associated with life in soft sediments and is related to the attitude and habits of the animal within the sediment. It parallels the evolution of the more recent eulamellibranchs of shallow water soft sediments. The second is the special nature of the deep sea environment and especially the influence of the paucity and refractile nature of the food, little of it being in suspension. This not only produces direct modifications to such features as the form of the digestive system but acts generally in favour of deposit feeders and certain physiological and reproductive strategies. The reason that the protobranchs are successful must lie with their physiology and in particular their metabolic physiology. It is known that shallow water protobranchs are slow growing and long lived (20 years at 0.5 mm/a) and that their energy requirements are low (Moore 1931; Allen 1954; Mortimer 1962). Furthermore, because they digest their food extra-cellularly, digestive processes can continue the length of the hind gut. An increase in gut length is essentially a delaying process and enables more time to be spent on the digestion of sclero-proteins.

It might be expected that deep sea protobranchs are even slower growing than those in shallow water and possibly longer lived. Most are small, less than 5 mm in total length. Turekian *et al.* (1975) have shown that at least one species, *Tindaria callistiformis*, can live for more than 100 years and in that time grows to a length of approximately 5 mm. Only specimens of 4 mm and above (over 80 years) exhibit any evidence of developing eggs and sperm.

It would seem that predation pressure must be low. It may be that a small tightly sealed bivalve 'box' can pass unharmed through the gut of a larger animal. Infaunal bivalves in total darkness must be difficult to detect other than by tactile or chemical sense. Deep sea protobranchs are well provided with gland cells, but there is no evidence to determine whether or not the products are repellant.

Small size itself has evolutionary significance in that reproductive habits change. Thus *Microgloma*, one of the smallest bivalves, reaching a maximum length of 1.2 mm, like many interstitial animals produces eggs continuously but only a single egg at a time. It is herma-phrodite and in those specimens with a mature egg (80 μm) there are about 30 mature sperm present. A further point of interest is that miniaturization of all other body cells has occurred (Sander & Allen 1973). Smaller egg numbers in deep sea species of comparable size to closely related shallow water species has been shown by Scheltema (1972). The vastness of the deep ocean, the separation of the individual basins, low densities, small egg numbers, direct develop-ment or at most a short deep-water planktonic phase all point to inbreeding and a low rate of gene flow. It is not difficult to postulate that sibling species might be expected. In fact one of the features of the samples studied here is the subtle differences in form that occur in popu-lations of the same species from different basins. For example, *Malletia cuneata* and *Ledella crassa* are found throughout the Atlantic in deep water; but for the constancy of their internal anatomy

† Descriptions of new species of the genus *Yoldiella* are in preparation.

and that all grades of intermediates are found, the extremes of shell shape apparent in populations from basins far removed from one another would establish different species (figure 12).

Mention must be made of the Order Solemyoidea. Very few species exist and, until recently, were thought to compose a single family. It is now known that species of *Nucinella* belong to this order (Allen & Sanders 1969). Both the Solemyidae and Nucinellidae possess a foot with a divided sole and a gill with filaments that have abfrontal cilia. There the comparison with other protobranchs ends; chevron-teeth are absent, the stomach has no sorting area, there are no palp proboscides. Both *Nucinella* and *Solemya* are highly specialized. *Solemya* builds a deep Y-shaped burrow (Stanley 1970) in which, for long periods, it lies across the top of the stem of the Y at the base of the arms. In contrast, *Nucinella* probably has a roving habit within the surface layers of the sediment, similar to that of *Nucula*. Stempell (1899) and Yonge (1939) believed that the Solemyoidea may be derived from a stock common with the Nuculoidea. Examination of *Nucinella* strengthens that view. Chevron-shaped teeth could well have been preceded by multiple cardinal teeth of the type seen in *Nucinella*. If this is true then it may be from the simple type of palps seen in *Nucinella* and *Solemya* that the complex palps and palp proboscides of nuculoids were derived. Similarly, the complex nuculoid stomach may well have been derived from the simple solemyoid stomach (Allen & Sanders 1969). As Allen & Sanders (1969) have argued, the concept that all bivalves were derived from a *Nucula*-like ancestor is not well supported, but both protobranchs and lamellibranchs could have been derived from a *Nucinella*-like bivalve. *Nucinella* itself may well have actinodont affinities (c.f. *Cyrtodonta*, figure 9 *b*) and if this is true then the point of dichotomy of the two great bivalve subclasses is established.

Before conclusions are drawn, attention must be given to the diversity of the deep sea fauna. Sanders (1968) has shown that the fauna of the abyss (excluding the trenches) is among the most diverse. The Bivalvia are no exception. At any one deep sea sampling station as many as 14 species of protobranchs may be present. Examination of gut contents indicates that they all contain the same type of material, namely mineral sediment and broken remains of the exoskeletons of animals and plants, in particular diatoms and foraminiferans. There is debate as to the origin of this diversity and the degree of competition in the deep sea (Grassle & Sanders 1973; Dayton & Hessler 1972). Sanders (1968) proposed a stability–time hypothesis in which he argued that when physical conditions have been stable over a long period of time, biological speciation and immigration are freed from physical restraint, whereas Dayton & Hessler (1971) argue that diversity is the result of continued biological disturbance in the form of non-selective predator pressure and question the premise that niche diversification, as reflected in feeding behaviour or microhabitat specialization, is the basis for high benthic faunal diversity (Grassle & Sanders 1973). Whether or not one, the other or both theories are correct, it is a fact that 14 species of protobranch feeding on the same abyssal sediment coexist; furthermore, several closely related species of the same genus may be found at the same station. For example, at Station 72 (lat. 38° 16′ N, long. 71° 47′ W, depth 2860 m) in the Bermuda traverse the following species occur: *Pseudotindaria erebus, Neilonella subovata, Malletia cuneata, Malletia estheriopsis, Malletia abyssorum, Yoldiella inflata, Yoldiella inconspicua, Yoldiella* sp. E, *Yoldiella* sp. L, *Yodiella dissimilis, Lametila abyssorum, Pristigloma alba.* All but *Pristigloma* are siphonate nuculanoids. Differences in mantle/shell morphology may be evidence of differences in feeding habits (*Pristigloma, Yoldiella, Malletia, Neilonella*) but it is difficult to conceive that the five *Yoldiella* species, only differing in any degree in their hind gut configuration but not content, do anything but feed

in the same attitude and manner. The species are not present in equal numbers and sampling shows that the abyssal fauna is stratified. Only *Yoldiella inconspicua* and *M. estheriopsis* are in any way dominant at Station 72 and these two species here are close to their maximum density over their depth range. Other less common species (e.g. *Pristigloma alba*) persist in equal low numbers over their depth range – a typical picture of benthic community structure.

Like many controversies the truth probably lies between the two extremes of physical stability which allows species (biological) diversity, and of competition. Because food is scarce and probably because of the low rate of digestion of scleroproteins, growth rate and reproductive rate are extremely low. A low rate of predation of long lived animals would ensure wide separation of individuals, which become progressively more difficult to locate. Population histograms suggest successful year classes occur at very infrequent intervals (more than 30 years for *Tindaria callistiformis*; Sanders & Allen 1977). All the indications are of an attenuated fauna in fine balance.

There are differences of opinion as to the antiquity and the physical stability of the deep oceans (Zenkevitch 1966; Menzies, George & Rowe 1973). It is thought that life originated between 2.0 and 0.8 Ga ago. Protobranch molluscs appeared in the Palaeozoic (0.5 Ga ago), and although not all geologists are in agreement it is probable that the volume and salt content of the Palaeozoic oceans was similar to that of today (Kuenen 1950). While the possibility that Palaeozoic deep sea deposits exist appears to be acceptable to some (Dietz & Holden 1966), no genuine deep-sea benthic fossils have been reported to date. Seismic horizons suggest that the deep oceans may be no older than the Mesozoic (Saito, Burckle & Ewing 1966).

In the instance of the Atlantic, from which most of the examples in this paper have been taken, continental drift has to be taken into account. In this context it is possibly significant that comparison of the bivalve faunas of the deep Atlantic and Pacific shows very few examples of species common to both oceans. Drifting possibly obliterated Palaeozoic evidence. Although sea floor spreading was probably not a steady rate, assuming an average of approximately 1 cm/a this places the time of separation of the Americas at the beginning of the Triassic. Madsen (1961) postulates the origin of the abyssal fauna in the Mesozoic. Menzies *et al.* (1973) point out that temperatures may well not have been maintained at their present 2.5 °C. before the Pliocene but may have ranged up to 15 °C. Despite all this the fact remains that the existing bivalve fauna is dominated by groups with the longest geological records. Many (e.g. *Tindaria*) are only recorded at abyssal depths and qualify for the ranks of the 'living fossils'. Their presence may not just be due to the capability of enduring extreme but stable conditions and of radiation through lack of competition from more recently evolved bivalves. It may also indicate that present conditions in the deep sea are in more subtle ways comparable to conditions in the Ordovician. In fact, all evidence suggests that the composition of the Ordovician bivalve fauna and the overall pattern of life habits dominated by deposit feeding taxa of which the dominant group was the protobranchs, was similar to the present molluscan fauna of the deep sea. It is not assumed that the present day species are that ancient – the absence of *Ctenodonta* and other Ordovician genera would not support that assumption – but that the descendants of ancient groups proved to be the ones that could survive the exacting conditions of the present day abyss.

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